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Studies on panicle characters and yield in relation to panicle numbers in rice cultivars

イネ品種における穂形質と収量およびその穂数との関係に関する研究

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Introduction

Rice is the most important food crop in the world. With the population increase in the world, the requirement for rice yield production increase is more urgent than before. The rice yield should be improved by approximately 1% annually to satisfy the increasing food demand by population growth and economic development (Rosegrant et al., 1995). The achievement of high yield in rice mainly initiate from the efforts in breeding new genotype with adaptive traits to yield production and improvement of management (Peng et al., 2008). However, many morphological and physiological traits would be compensated each other, and it should result in no increase of yield production. So the understandings in morphological and physiological traits interrelationships, compensation among plant parts, and their response to managements such as planting density and fertilization are important for the establishment of targeted traits in breeding (Peng et al., 2008; Marshall et al., 1991).

Rice yield production is determined by 4 yield components, panicle number, spikelet number per panicle, filled grain number per panicle, and single filled grain weight. However, the negative interrelationships among them, such as the relations between the panicle number and spikelet number per panicle, between the large number of spikelet per panicle and the poor grain-filling degree and grain weight, always had restrains on the yield improvement. So the dissection of the negative relationships among the yield components would be helpful for the high yielding achievement in rice.

Among of yield components relations of each other, the relation between the panicle number and spikelet number per panicle has the most magnificent effect. So it is necessary to understand the basis of this relationship in the resolving restrain problem. There was several ways which could be used for the studies.

First way is to understand the relationships from the related morphological traits response. The spikelet number per panicle is composed of the number of primary rachis branches and spikelets on them. And spikelet number per panicle is determined by the difference between the differentiated and degenerated spikelet number per panicle (Matsushima, 1966). Close positive relations between the differentiated and degenerated spikelet number to spikelet number per panicle in rice was reported (Kobayasi et al., 1995). However, Kobayasi et al. (2000) had reported that, with panicle number per unit area increase in the dense planted condition, differentiated primary rachis branches number per panicle decreased, but not the degenerated spikelet per panicle. Mu and Yamagishi et al., (2005) proposed that the shoot apical meristems size enlargement due to the reduction of tiller outgrowth, would benefit for the high branching ability in a panicle.

Breeding efforts had been contributed into 2 main directions. The one is to develop genotypes with high tillering capacity and small spikelet number per panicle (Matsushima, 1973). But most of these cultivars produce a large number of unproductive tillers and have excessive leaf area. These traits may cause the mutual shading and a reduction in canopy photosynthesis and sink size, lodging susceptibility which constrain the yield improvement (Dingkuhn et al., 1991). The other direction is to develop genotypes with limited tillering capacity with large spikelet number per panicle (Wang et al., 1997). According to this direction, NPT (new plant type) at IRRI, and ‘super’ hybrid rice in China were developed. The performance of these rice cultivars were observed in several environmental conditions (Yamagishi et al., 1996; Ladha et al., 1998; Laza et al., 2003; Yuan, 2001; Cheng et al., 2007; Lin et al., 2002; Wang et al., 2002; Zhai et al., 2002; Zong et al., 2000; Kazura et al., 2007; Yao et al., 2000). Concluded from these reports, NPT could not improve the yield effectively since the low production in dry matter due to too less tiller number at the early growth stage, bad grain filling due to the limited source ability, and successive and compact arranged spikelet per panicle. With a comparison, the ‘super’ hybrid genotype in China achieved the yield improvement because of the improvement in morphological traits successfully, such as moderate tillering capacity, plant height of at least 100cm and panicle height of 60cm, and the top three leaves erected.

Several morphological traits have been revealed to be related to the spikelet number per panicle and panicle number in rice. Tiller number, related to panicle number closely, would improve the dry matter production in rice (Wu et al., 1999); and individual tiller dry weight at heading was convinced to contribute to spikelet number per panicle (Shiratsuchi et al., 2007); Tiller number is always negatively related to plant height (Cui, et al., 2004), The proliferation in tillering would elevate the root system growth(Matsuo, et al., 1993) which might be benefit for the nutrients uptake, especially nitrogen uptake, while nitrogen uptake had promotion effects on the spikelet number per panicle (Kobayasi et al., 1995; 2000). Other traits, leaf area, neck internode diameter were also related to the spikelet number per panicle in rice (Yamagishi, et al., 2003). So these traits would build the bridge in understanding of the relations between the panicle number and spikelet number per panicle in rice. Some researches on the restricted root affecting the plant growth were reported in rice. Akita et al. (1989) reported the large rooting zone sizes could increase the percentage of nitrogen content although the genetic difference existed in rice. In the studies of border effects in rice (Sato et al., 1983), the large root space occupied by plant promoted the nitrogen accumulation resulting into the improvement of grain yield. So the dissection of root function would also be helpful in the understanding of interrelationships between the panicle number and spikelet number per panicle.

Quantitative trait locus (QTL) analysis is a useful tool in the understanding the basis of morphological traits interrelationships (Kato, et al., 2009). In rice, the QTLs relating for tillering(Cui et al., 2004; Liu et al., 2009; Yang et al., 2006; Miyamoto et al., 2004), and spikelet number per panicle (Yagi et al., 2001; Xing et al., 2002; Kato et al., 2004; Kobayashi et al., 2004, 2006; Yamgishi et al., 2004; Wei et al., 2006; Zhang et al., 2006 Anto et al., 2008; Xing et al., 2002, 2008; Kato et al., 2009; Zhang et al.,2006, 2009) were widely reported. So the employment of QTLs for the mechanism analysis will be helpful.

In rice, the main stem of a plant produces a large number of tillers until to the maximum tiller number stage. Studies have reported that there is a large variation in spikelet number per panicle in one rice plant. Spikelet number per panicle was larger on early-emerging tillers (Counce et al., 1996), and it decreased from the main stem to primary and secondary stems (Kuroda et al., 1999). Sheehy et al. (2001) reported that differentiated spikelet number per panicle was reduced as tiller number increased in spaced cultivation. Ishii and Kumura et al. (1988) found that differentiated spikelet number per panicle declined and degenerated spikelet number per panicle increased with the reduction in “shoot vigor” (i.e., smaller tillers) in cultivar Nipponbare. When considering the panicle number effects on the spikelet number per panicle, it is not clear that the ‘panicle order’ would change or not with the variation of panicle (tiller number) within hill. Viewed from this point, the studies on the response of panicles on each tiller would provide useful information about the mechanism of the interrelationships between the panicle number and spikelet number per panicle.

Planting density is one of the main management ways in rice cultivation and planting density is an important factor influencing the yield production (Well et al., 1978; Jones et al., 1987; Gravois et al., 1992 and 1996; Ottis et al., 2005; Bond et al., 2008;). Planting density was known to affect tiller production seriously (Matsushima, 1966; Koutroubas et al., 2003), which would affect the spikelet number per panicle. So comprehensive understanding of the relations among the panicle number and spikelet number per panicle with the combination of planting density management will provide the useful information for achievement of high yield in rice.

Therefore, this thesis is trying to make a clear understanding on

1. The response of spikelet number per panicle for each panicle within hill to the variation of panicle number;
2. The response of spikelet number per panicle to panicle number per hill, relating to the possible root function.
3. The effects of spikelet number per panicle on the grain yield and yield components

For these targets, researches were conducted as follows:

Chapter 1, the spikelet number per panicle and its variation within plant in 16 rice cultivars;

Chapter 2, the response of spikelet number per panicle within hill to planting density (Chapter 2-1) and its influence on the yield (Chapter 2-2);

Chapter 3, the response of spikelet number per panicle and yield to planting density with root restriction;

Chapter 4, QTLs analysis for spikelet number per panicle under two nitrogen conditions.

Finally, the response of spikelet number per panicle to panicle number per plant and spikelet number per panicle influencing on yield were discussed based on whole thesis.

Chapter 1. The spikelet number per panicle and its variation within a plant in 16 rice cultivars

1 Introduction

Spikelet production per unit area is closely related to grain production per unit area (Sheehy et al., 2001). Large number in spikelet per panicle (SPP) was considered as the effective way to improve the spikelet production per unit area (Kobayasi et al., 2001). And, there was obvious difference in SPP among the tillers in one plant (Yamagishi et al., 1992, Kuroda et al., 1999, Duy et al., 2004). It was demonstrated that the reduction of SPP from primary, secondary, and tertiary tillers in a plant (Kuroda et al., 1999), and it was also demonstrated that the SPP was reduced with the tillering sequence in rice (Sheehy, et al., 2001). So the variation of SPP in a plant would also be a factor influencing the spikelet production of a plant.

The primary mother tiller, the main stem, is important to the construct of a plant. The leaf appearance on main stem had close relation to tillering (Matsushima 1966; Jaffuel et al., 2005; Tivet et al., 2001), and panicles on tillers get support from the mother tiller at panicle initiation stage (Ishii et al., 1988). So it can be proposed that the SPP on main stem and SPP of all tillers would have some relations, or the SPP on main stem (MSPP) take some effects on the variation of SPP within a hill. On the other side, spikelet number per panicle (SPP) is the difference of differentiated spikelet number per panicle (D-SPP) and aborted spikelet number per panicle (A-SPP) (Matsushima, 1966). Both D-SPP and A-SPP would affect on the variation of SPP. Although it had been reported that there were positive relations of SPP among the main stem, primary and secondary tillers (Kuroda et al., 1999), the positive relations of D-SPP and A-SPP also exist or not is still unclear.

The Coefficient of variation (CV) is a useful parameter in the studying for the variability such as plant-to-plant (Maddonni et al., 2004). It can reflect the variation degrees with comparisons by different units. Furthermore, the SPP showed larger genetic variations (Kuroda et al., 1999; Yamagishi et al., 1992, 2003, 2004). Using CV, the difference in SPP among cultivars can be erased, and variation of SPP within a hill can be compared more accurately.

In this experiment, there are 2 objectives: I: To describe the variation of SPP, D-SPP and A-SPP within hill; II: To analyze the MSPP, D-MSPP, A-MSPP relations to SPP, D-SPP, and A-SPP by using 16 cultivars of rice.

2 Materials and methods

The experiments were conducted in 2005 and 2006 at the University Farm of the University of Tokyo, in Nishitokyo, Japan (35°43'N, 139°32'E). 16 cultivars including 12 *Japonica*, 3 *Indica*, and 2 crossed from *Japonica* and *Indica* (Table 1-1), were used. Seeds were sown in nursery box on 28th, April in green house, and seedlings were transplanted into paddy fields as one seedling per hill on 29th, May in both years. Transplanting density was 22.2 plant m^{-2} (15 cm × 30 cm). In both years, chemical compound fertilizer was applied before transplanting as N : P_2O_5 : K_2O = 60 : 90 : 80 kg ha^{-1}.

Panicles of 5 hills per plot were collected at maturity, and the panicle number (PN) and the panicle traits were measured. Spikelet number per panicle (SPP) was counted. Aborted spikelets per panicle (A-SPP) can be counted as the vestiges that remain on the rachis branches following the method reported previously (Ishii and Kumura, 1988). 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. To compare SPP, D-SPP, A-SPP, and A% of all panicles, the panicles in each plant were arranged in descending order according to the relative size to the panicles on main stems, indicated as ratio of SPP/MSPP (%). Averages of SPP, D-SPP, and A-SPP with all the panicles within the hill were calculated. Panicles on main stems were recorded as MSPP, D-MSPP, and A-MSPP. The coefficients of variation (CV) for SPP, D-SPP and A-SPP in each plant were calculated.

Table 1-1 Cultivars classification in the experiment.

Cultivar	Classification	Cultivar	Classification
Waito C	*Japonica*	Nankin 11	*Indica*
Tanginbouzu	*Japonica*	IR72	*Indica*
Ginbouzu	*Japonica*	Takanari	*Indica*
NPT65 (IR65564 - 44 - 51	*Japonica*		
Nipponbare	*Japonica*	Akenohoshi	*Japonica* × *Indica*
Kochihibiki	*Japonica*	Milyang 23	*Indica* × *Japonica*
Nihonmasari	*Japonica*		
Nakateshinsenbon	*Japonica*		
Dobashi 1	*Japonica*		
IRAT109	*Japonica*		
Akihikari	*Japonica*		

3 Results

3-1 SPP, D-SPP, A-SPP, MSPP, D-MSPP and A-MSPP

The difference in average SPP, D-SPP and A-SPP among cultivars were significant in both years ($P<0.01$) (Table 1-2). SPP on average showed large variation range, from 58 (Waito C) to 385 (NPT65). A-SPP on average also showed great differences among cultivars. The lowest spikelet abortion was 6 for Waito C in 2005, the largest spikelet abortion was 285 for NPT65 in 2006. D-SPP on average was smallest in Waito C, 64 and largest in NPT65, 667.

Similarly, the differences in MSPP, A-MSPP and D-MSPP among cultivars were significant ($P<0.01$). As same as SPP on average, the panicle of NPT65 was largest in MSPP, A-MSPP and D-MSPP in both years. And Waito C was smallest. And for Akihikari, the A-MSPP was also smaller relatively than others. NPT65 had the smallest PN hill^{-1} and Waito C had highest PN hill^{-1} among the cultivars. With comparison of spikelet abortion between the average A-SPP and main stem, A-MSPP, in most cultivars A-MSPP were lower than average A-SPP except Tanginbouzu, Ginbouzu, NPT65 and IR72 in which more spikelets aborted on main stem than on average. With comparison between 2005 and 2006, the panicles were larger in 2006 than 2005 for most cultivars except Takanari, Tanginbozu and NPT65. Excepting NPT65, D-MSPP in all of cultivars showed larger in 2006 than in 2005. The PN hill^{-1} also was higher in 2006 than in 2005.

Table 1-2 Mean SPP, A-SPP, D-SPP within one hill, and MSPP, A-SPP and D-MSPP, panicle number per hill (PN) of 16 cultivars in 2005 and 2006.

Cultivar	Mean				Main stem				PN hill^{-1}
	SPP	A-SPP	D-SPP	aboriton%	SPP	A-SPP	D-SPP	aboriton%	
2005									
Waito C	58	6	64	9.5	76.6	3.8	80.4	4.7	10
Tanginbouzu	91	12	103	12.1	111.2	9.8	121	8.1	8
Ginbouzu	115	26	141	18.5	134.8	32.6	167.4	19.5	8
NPT65	385	283	667	42.4	499.8	314.6	814.4	38.6	3
Nipponbare	91	29	120	24.2	127.2	28	155.2	18.0	11
Kochihibiki	90	16	106	15.1	116.6	12.2	128.8	9.5	11
Nihonmasari	89	20	108	18.1	117	10.6	127.6	8.3	9
Nakateshinsenbon	98	11	109	10.0	125.2	12.4	137.6	9.0	11
Dobashi 1	186	62	248	24.8	244.2	52.4	296.6	17.7	4
Nankin 11	157	46	203	22.6	219.8	34	253.8	13.4	7
IR72	152	72	224	32.3	189.6	72.6	262.2	27.7	11
Takanari	225	46	271	17.1	311.8	46.8	358.6	13.1	6
Akenohoshi	130	36	166	21.4	191.8	29.6	221.4	13.4	9
Milyang 23	180	19	199	9.7	233.2	15.8	249	6.3	8
P for cultivar	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*
LSD $_{0.05}$	*28.53*	*27.07*	*48.32*	*4.29*	*44.78*	*32.15*	*61.78*	*6.44*	*2.02*
LSD $_{0.01}$	*37.95*	*36.00*	*64.26*	*5.70*	*59.55*	*42.76*	*82.17*	*8.56*	*2.69*
2006									
Waito C	62	11	73	15.5	86.8	9.4	96.2	9.8	19
Tanginbouzu	83	20	102	19.3	110.4	24.6	135	18.2	13
Ginbouzu	119	26	145	18.2	159	26.2	185.2	14.1	10
NPT65	288	285	573	49.7	427	326.6	753.6	43.3	4
Nipponbare	102	14	116	12.1	130	11.6	141.6	8.2	11
Kochihibiki	99	11	110	9.9	132.4	10	142.4	7.0	13
Nakateshinsenbon	95	7	102	6.8	119.4	4.8	124.2	3.9	13
IRAT109	141	41	181	22.4	196.4	26.6	223	11.9	6
Akihikari	120	11	131	8.7	145	3.5	148.5	2.4	9
Nankin 11	154	56	210	26.5	246.4	47	293.4	16.0	8
IR72	155	92	247	37.2	183.4	94.8	278.2	34.1	9
Takanari	204	93	297	31.2	304.8	88.4	393.2	22.5	8
Akenohoshi	130	14	144	9.7	166.8	12	178.8	6.7	9
MiLyang 23	184	27	211	13.0	256.2	23	279.2	8.2	8
P for cultivar	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*
LSD $_{0.05}$	*19.31*	*11.61*	*21.80*	*4.34*	*30.48*	*19.81*	*28.40*	*7.38*	*2.61*
LSD $_{0.01}$	*25.69*	*15.44*	*28.99*	*5.78*	*40.53*	*26.35*	*37.77*	*9.81*	*3.47*

3-2 Relationships of MSPP, D-MSPP and A-MSPP to SPP, D-SPP and A-SPP

As shown in Fig.1-1, there was close relationship between MSPP and average SPP (R^2=0.9755), A-MSPP and average A-SPP (R^2=0.9939), D-MSPP and average D-SPP (R^2=0.9927). The cultivars with large number in MSPP, A-MSPP and D-MSPP, had the large average number in SPP, A-SPP, and D-SPP. With the increase of MSPP, A-MSPP, and D-MSPP, the differences between the average of them and MSPP, A-MSPP, and D-MSPP got larger, because they were smaller in tillers than those on main stems..

The negative relation between the PN hill^{-1} and averages of SPP, A-SPP and D-SPP were clear shown in Fig. 1-2. And the negative relation between the PN hill^{-1} and MSPP, A-MSPP and D-MSPP were also obviously observed (Fig. 1-2). Therefore, the cultivars with large number in SPP, A-SPP, and D-SPP, or in MSPP, A-MSPP, and D-MSPP had few panicles hill $^{-1}$.

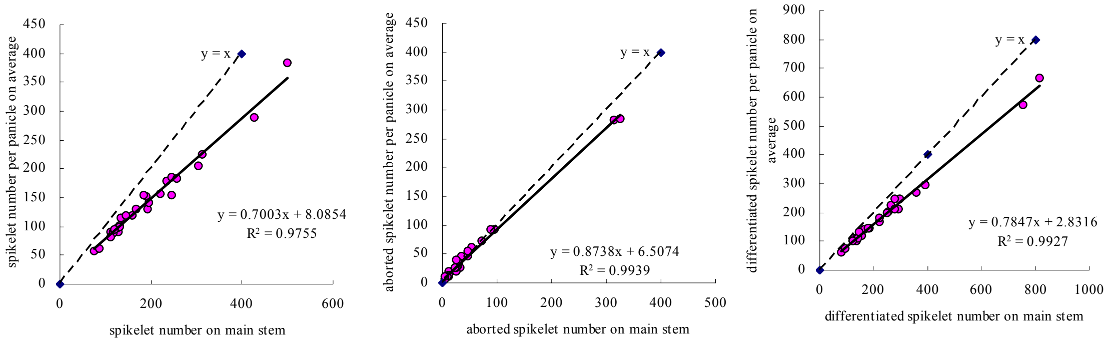


Fig. 1-1 Relationships of SPP, A-SPP and D-SPP between the main stem and tillers on average.

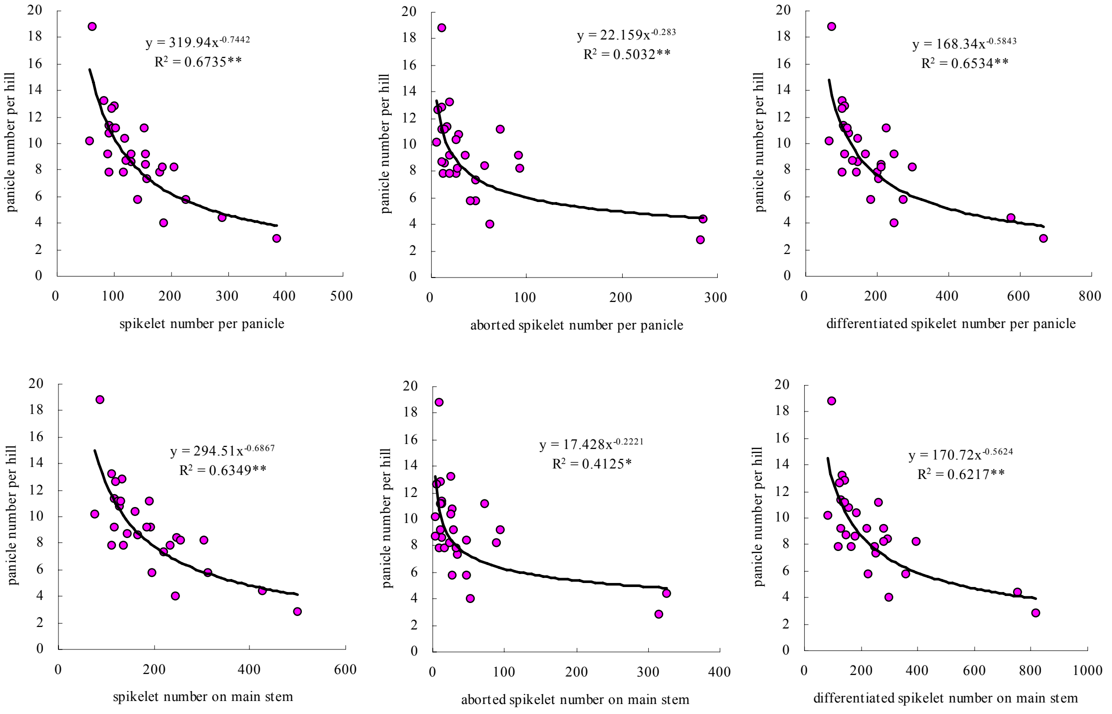


Fig. 1-2. Relationships of SPP, A-SPP and D-SPP on average to PN hill^{-1} (upper); relationships of MSPP, A-MSPP and D-MSPP to PN hill^{-1} (lower). Data was combined of 2005 and 2006.

3-3 Relative SPP, D-SPP and A-SPP of each panicle within a hill to MSPP, D-MSPP and A-MSPP

Relative SPP of each panicle to MSPP ranged from 120% in Akihikari to 19% in Takanari (Fig. 1-3). In most cultivars, relative SPP of each panicle to MSPP ranged within 60% from 100% to 40%. In Waito C, Nipponbare and Kochihibiki, they varied from 100% to 50% of MSPP, narrower variation range to other cultivars. On the contrary, Akihikari, IR72 and Ginbozu varied more than 70% from 120% to 30% of MSPP. For most cultivars, the main stem panicle was the largest panicle within plant, however in Akihikari, IR72, Akenohoshi and Nakateshinsenbon, Ginbozu, and Tanginbozu, there were a few tiller panicles larger than the panicles on the main stems. According to the relative size to MSPP, the tillers could be ordered clearly as continuous decline line and there was no great difference between two years.

Comparatively to SPP, relative D-SPP of each panicle to D-MSPP showed narrower variation ranges for all of the cultivars, the range was from 117% in Akihikari to 36% in Tanginbozu and Ginbozu. Most of cultivars ranged from 100% to 40%. Only Waito C showed narrower range, less 40% from 100% to 60% of D-MSPP, comparing to others. There were only 3 cultivars, Akihikari, Nakatesinsenhone, and Akenohoshi had several tillers having larger panicles than that on the main stem. IR72, Tanginbozu, and Ginbozu showed no difference between the largest tiller panicle and that on the main stem. Similarly to SPP, there was no significant difference between the two years.

Spikelet abortion percentage (A%) showed increasing tendency along the tiller order according to SPP (Fig. 1-4). Nankin11, IR72, Akenohoshi, Nakateshinsenbon, Dobashi 1 and IRAT109 showed clearer increase of spikelet abortion percentage with the panicle order increase than other cultivars. And there was increase rate difference among cultivars. In Akenohoshi, Nakateshinsenbon, IR72, the panicle order lines of spikelet abortion percentage increased slowly on the higher order panicles than on the lower order panicles, while in Nankin11, Dobashi 1 and IRAT109, there was no obvious variation with the panicle order decrease. Relatively, Waito C, Tanginbozu, Ginbozu, NPT65, Takanari, Kochihibiki, Milyang23, Nihonmasari and Akihikari showed disarray about the spikelet abortion percentage along the SPP order within hill. There was noticeable difference between 2005 and 2006, especially in Milyang23, Takanari, Nipponbare, Akenohoshi, Kochihibiki, and Nakateshinsenbon. The cultivars, Nipponbare, Akenohoshi, Kochihibiki, and Nakateshinsenbon had higher spikelet abortion in 2005 than in 2006; while in Takanari and Milyang23 had lower spikelet abortion percentage in 2005 than in 2006.

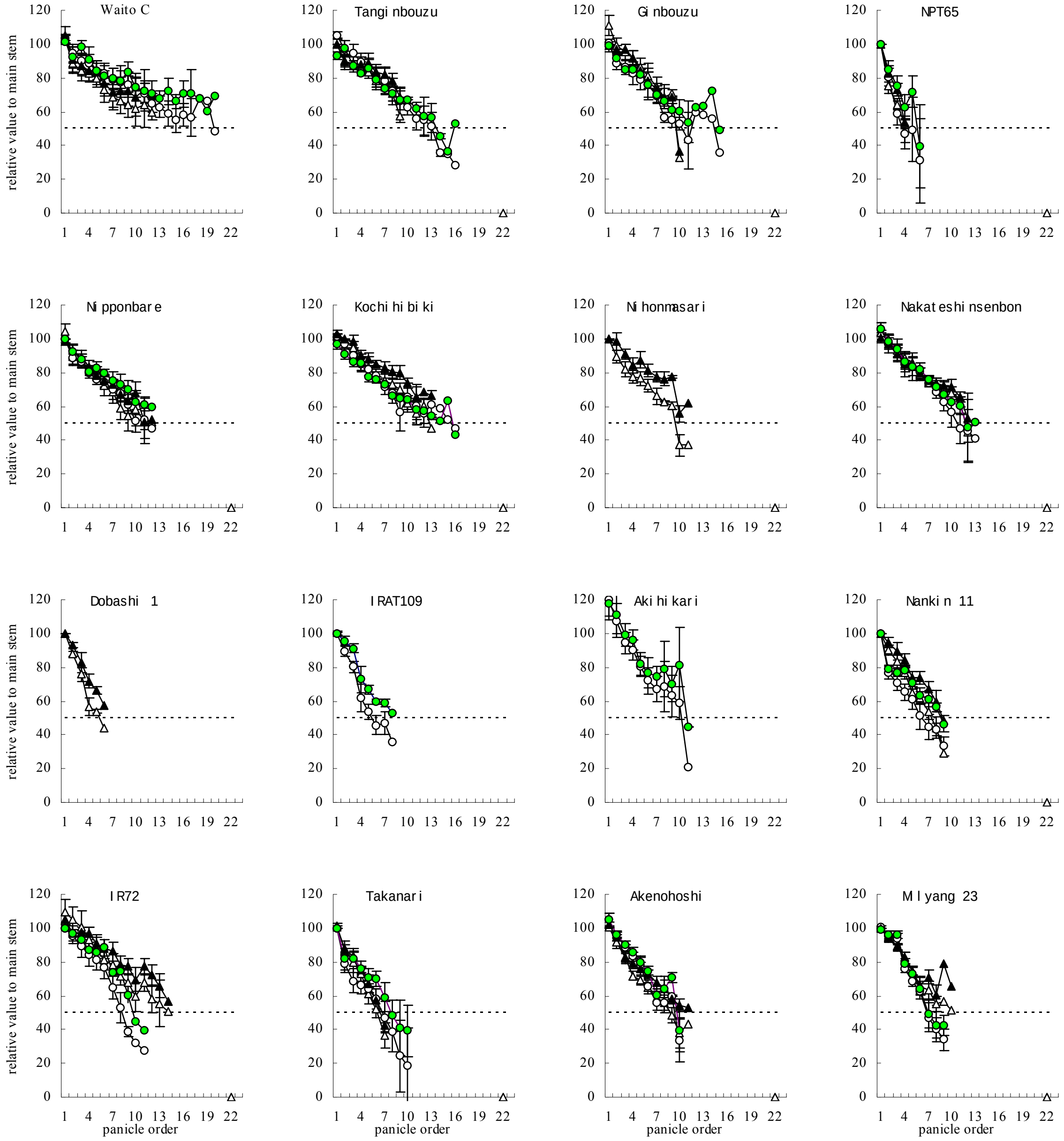


Fig. 1-3. Relative SPP (△:2005; ○:2006), D-SPP (▲: 2005; ●: 2006) to MSPP and D-MSPP respectively within hill for 16 cultivars . Dotted line means the 50%.

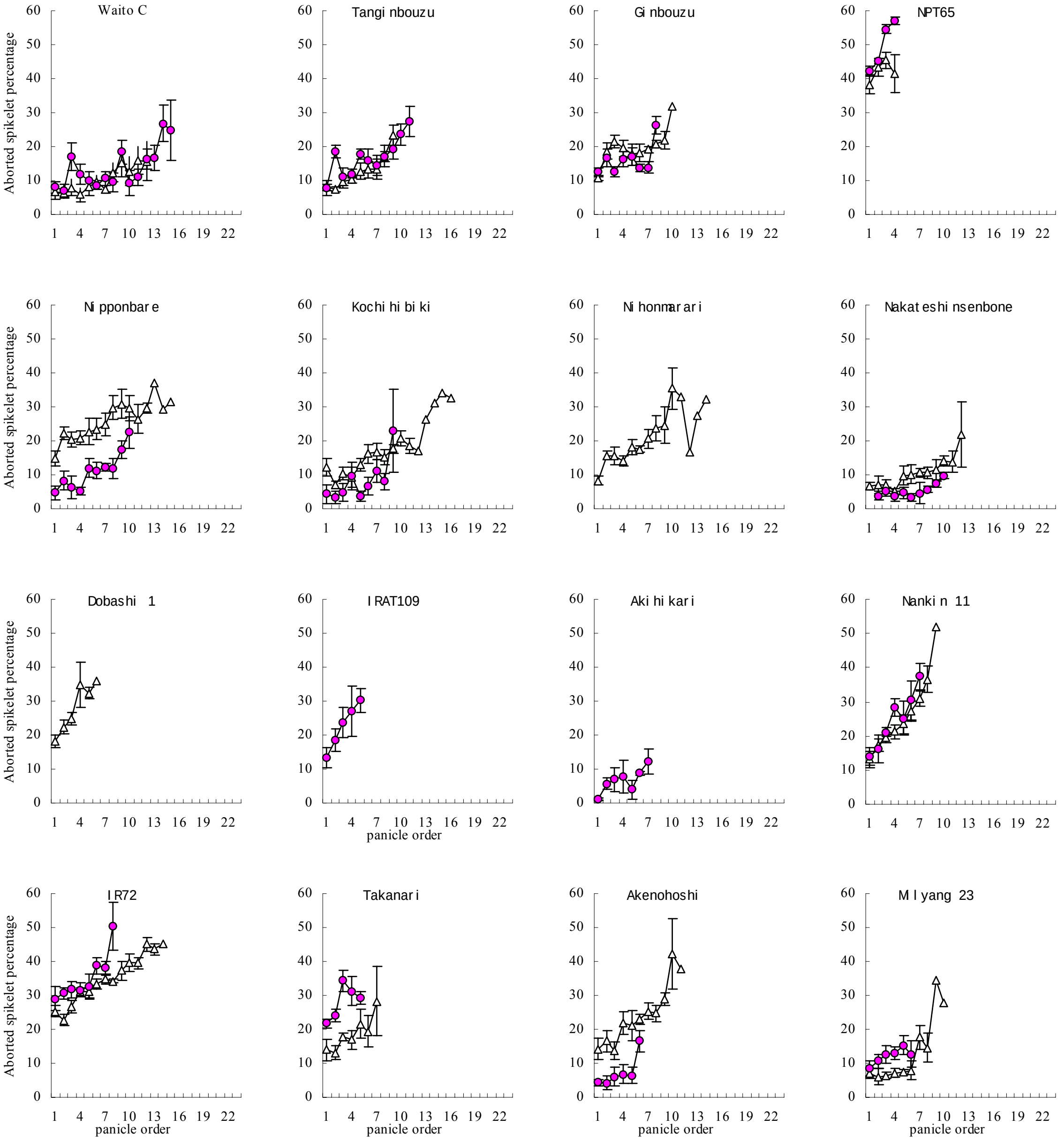


Fig.1-4 .Aborted spikelet percentage variation within hill for 16 cultivars in 2005 (△) and 2006(●)

3-4 Coefficients of variation (CV) for SPP, D-SPP, and A-SPP within a hill

CV of SPP, A-SPP and D-SPP had obvious cultivar difference for both years ($P<0.01$) (Table 1-3). Nankin11, Takanari, NPT65, Milyang23 and Akenohoshi had the higher CV in SPP, A-SPP and D-SPP as compared to other cultivars as a combination of the two years. CV of A-SPP was highest, followed by SPP, and CV of D-SPP was lowest. Comparison between the two years results, the CV was relatively higher in 2006 than in 2005.

SPP and MSPP were positively related to the CV in 2006, although the relationship was not clear in 2005 (Fig. 1-5). A-SPP and A-MSPP reduced with the increase of CV, and the reducing rate got slower as CV was over 0.4. No relationship were observed between the D-SPP, D-MSPP to their CVs. In 2006, panicle number per hill reduced with the increase of CVs of SPP and D-SPP.

Table 1-3 The coefficients of variation (CV) of SPP, A-SPP and D-SPP within hill of 16 cultivars in 2005 and 2006.

Cultivar	2005			2006		
	SPP	A-SPP	D-SPP	SPP	A-SPP	D-SPP
Waito C	0.20	0.48	0.17	0.21	0.53	0.16
Tanginbouzu	0.14	0.39	0.11	0.27	0.38	0.20
Ginbouzu	0.19	0.32	0.17	0.23	0.29	0.18
NPT65	0.21	0.17	0.17	0.33	0.16	0.22
Nipponbare	0.23	0.23	0.17	0.22	0.47	0.17
Kochihibiki	0.18	0.37	0.13	0.27	0.90	0.20
Nihonmasari	0.19	0.31	0.12			
Nakateshinsenbo	0.20	0.51	0.16	0.31	0.23	0.20
Dobashi 1	0.25	0.23	0.16			
IRAT109				0.24	0.77	0.19
Akihikari				0.25	0.97	0.20
Nankin 11	0.26	0.21	0.18	0.33	0.28	0.23
IR72	0.24	0.15	0.16	0.28	0.19	0.17
Takanari	0.28	0.29	0.24	0.29	0.20	0.22
Akenohoshi	0.28	0.34	0.21	0.24	0.53	0.20
Milyang 23	0.21	0.63	0.18	0.30	0.37	0.27
P for cultivar	*0.01*	*0.00*	*0.00*	*0.05*	*0.00*	*0.30*
$LSD_{0.05}$	*0.07*	*0.14*	*0.06*	*0.08*	*0.24*	*0.07*
$LSD_{0.01}$	*0.09*	*0.18*	*0.07*	*0.11*	*0.32*	*0.09*

4 Discussion

4-1 The relationships of MSPP, D-MSPP and A-MSPP to SPP, D-SPP and A-SPP

The SPP, D-SPP and A-SPP on average of plant positively related with MSPP, D-MSPP, and D-MSPP (Fig.1-1). Kuroda et al. (1999) reported there was positive relationship between spikelet per panicle on mains stem and on tillers. In this experiment, it was shown that there were also positive relationships of the differentiated and aborted spikelets per panicle between panicles on main stem and on tillers. It had been reported by Kobayasi et al. (1995), that the SPP was mainly determined by the D-SPP, so the enlargement of D-SPP on main stem will promote the D-SPP of tillers, and spikelets per hill will be improved. On the other side, the high spikelet abortion on main stem could be accompanied by the high spikelet abortion on tillers (Fig.1-1). So it can be estimated that the reduction of spikelet abortion on main stem will be accompanied by the reduction of the spikelet abortion in whole plant.

The supply of assimilates from main stem to tillers would be the main reason for the close relations of the SPP, D-SPP and A-SPP between main stem and tillers. It was evidenced that the competition for assimilates between the tillers to main stem at the early growth stage in barely (Kirby et al., 1977). It was also proposed by Ishii et al. (1988) that, at the panicle initiation stage, the strong tillers would supply assimilates to tillers resulting into the large number of spikelets were differentiated. So when the D-SPP on main stem can increase, the D-SPP on tillers can also be increased simultaneously. During the spikelet growth, the assimilates required by panicle will be increased. If the source ability will not be improved equivalently, the abortion of spikelet will happen both on main stem and tillers. So not only the D-SPP, but also A-SPP might show positive relations between main stem and tillers.

4-2 The variation of SPP, D-SPP and A-SPP within a hill

SPP, D-SPP reduced gradually as the panicle order decreased respectively. This just indicated that the difference between the primary and secondary tillers was similar to the difference within the primary tillers or secondary tillers. Kuroda et al. (1999) reported the difference of spikelet number per panicle among the tillers of different type, just not considering the difference within the same tiller type. In this experiment, not only the difference of tiller type, but also the difference within the same tiller type varied similarly.

SPP showed greater variation than D-SPP. CV was higher in SPP than D-SPP (Table 1-3). That is because of the larger variation of spikelet abortion between tillers. There was some variation of panicle development among the tillers (Matsushima, 1966). And the growth of spikelet was easily influenced by the environmental factor, especially the air temperature and sun light intensity (Ellis et al., 1993). So changes in environmental conditions, and supply of assimilate can influence the spikelet abortion.

The larger value in MSPP, SPP, and smaller value in panicle number hill^{-1} had large CV of total panicles within a hill (Fig.1-5), indicating the differences among the panicle sizes on tillers would be enlarged in the cultivars which had larger panicle in MSPP and SPP with few panicle number per hill. These results were the same as the report of Kuroda et al. (1999) that SPP differences among the tillers were smaller in the cultivars which had larger panicle number per hill. In the present experiments, A-SPP and A-MSPP also showed negative relations with the CV of A-SPP. Cultivars with more spikelet aborted on average and main stem, had small difference on A-SPP within hill. The A-MSPP had negative relations with the CV of A-SPP. This indicated that the tillers could not get support from mother stem, when the 'assimilate supply ability' of mother stem was limited since there was larger number of aborted spikelet on the main stem Panicle number per hill had no clear relations with the CV of A-SPP just indicating the independences of tillers in the supporting for spikelet survival. However, D-SPP showed no clear relations on the CV of D-SPP, neither of D-MSPP (Fig.1-5). Panicle number per hill had negative relations with the CV of D-SPP. This just indicated the differences of D-SPP among the tillers were not related with the D-SPP on average or on main stem. The cultivars with more tillers, have small differences of D-SPP among tillers.

So it could be concluded that cultivars with smaller differentiated spikelet number per panicle on main stem have smaller differences of D-SPP among tillers, this is not same as SPP, and that the differences of D-SPP was larger in cultivars with fewer tiller number per hill, this is same as SPP.

Since the panicles on tillers tend to be smaller than panicles on main stems, the improvement in MSPP could not necessarily result the increase in SPP of each panicle or spikelet number per hill. And, it was also proposed that, although cultivars have large differences of MSPP, the differences of SPP among them were small (Kuroda et al., 1999). Therefore, reducing the differences of SPP among each panicle within a plant was a way to improve the spikelet production per plant. While this was not suitable for D-SPP, since the improvement in D-MSPP was not accompanied by the increase in D-SPP of tillers, when A-SPP was not decreased.

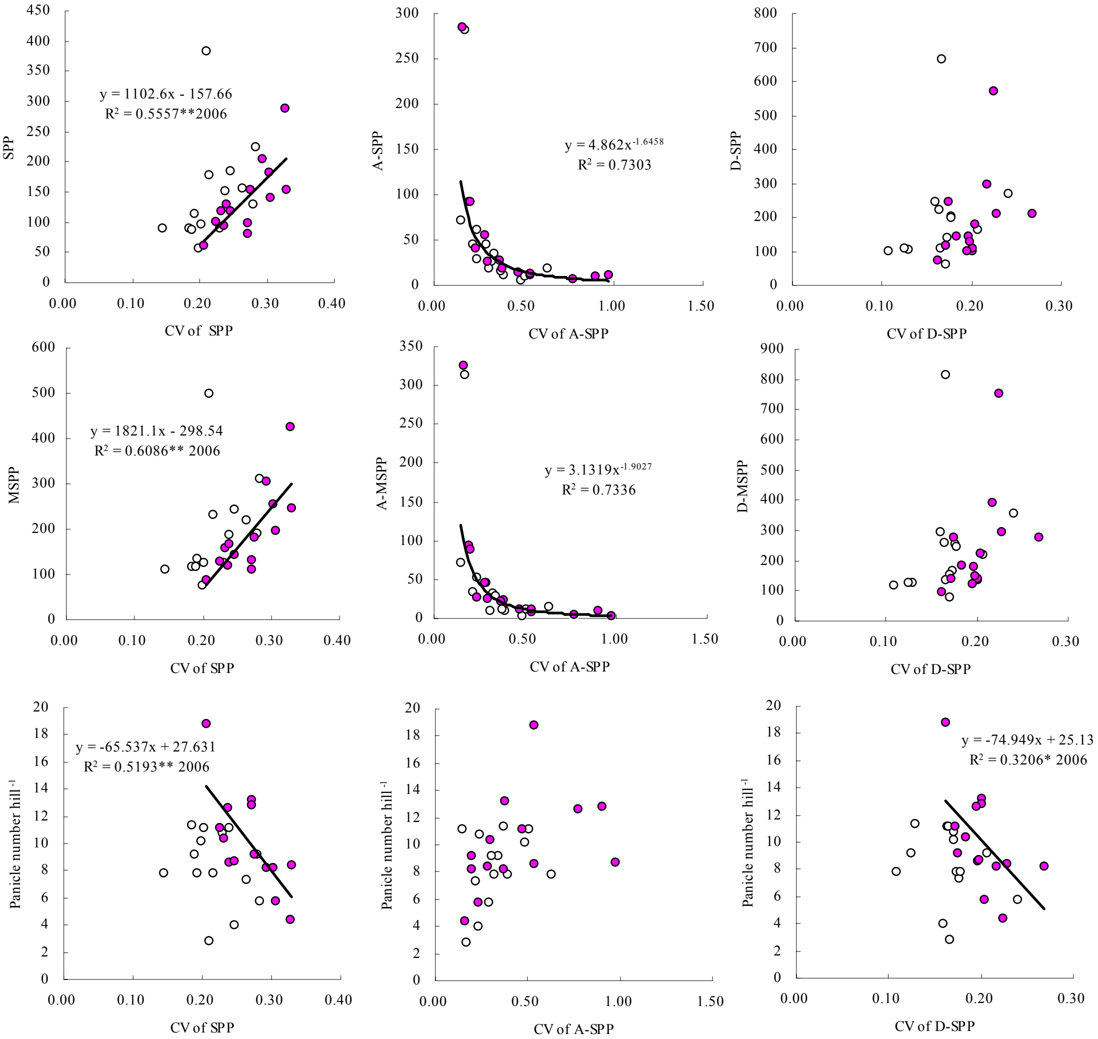


Fig. 1-5. Relationships between SPP, A-SPP and D-SPP to their CV respectively (upper); Relationships between the MSPP, A-MSPP and D-MSPP to their CV respectively (middle); Relationships between the panicle number hill^{-1} to CV of SPP, A-SPP and D-SPP (lower). ○:2005; ●:2006.

Chapter 2 The response of spikelet number per panicle to transplanting density and its influence on yield in rice

1 Introduction

In the previous chapter, it was clarified that (1) Cultivars with the large number in SPP, D-SPP and A-SPP tend to have small panicle number hill $^{-1}$; (2) the cultivars with large panicle number hill^{-1} would reduce the variation of SPP and D-SPP in a plant, but not variation of A-SPP; (3) average of SPP, D-SPP and A-SPP in a plant were positively related to MSPP, D-MSPP and A-MSPP closely. It indicated that the panicle number hill^{-1} affected not only SPP, D-SPP and A-SPP, but the within hill variation of them. These results were based on the cultivar differences. It is well known that the panicle weight type have less panicle number per hill and that panicle number type have relatively small panicle size (Matsuo et al., 1993). So, it is necessary to know how the culture conditions affect SPP, D-SPP and A-SPP and how the variation of tiller number per hill influence them. It is well evidenced that the variation of transplanting distance is an effective way to change the tiller number per hill. So, in this chapter, the response of SPP, D-SPP and A-SPP and their variation in a plant to transplanting distance, and the effects of transplanting density on the yield production were investigated.

2 The response of spikelet number per panicle to planting density

2-1 Introduction

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 reported 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 with 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 have large effects on 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 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. 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 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) under different planting densities. Tiller size, leaf area per tiller, neck internode diameter and tiller height, were examined to compare panicle characters among cultivars.

2-2 Materials and Methods

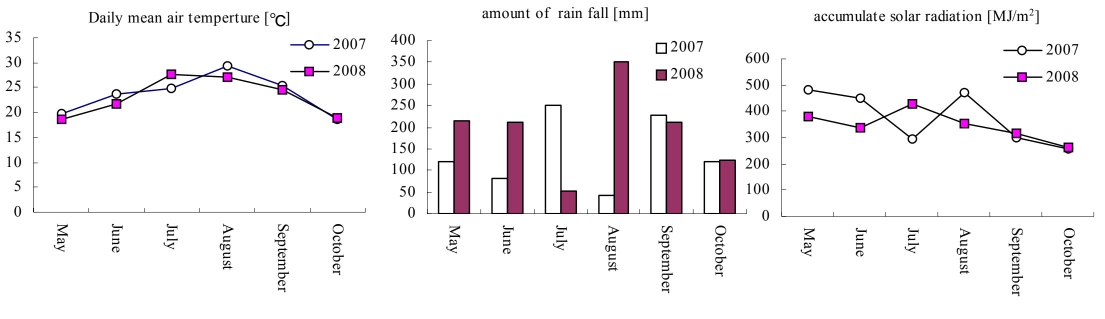
The experiments were conducted at the Field Production Science Center of the Graduate School of Agricultural and Life Sciences, University of Tokyo, Nishitokyo, Tokyo, Japan (35°43'N, 139°32' E, 53-m elevation) in 2007 and 2008. Meteorological conditions of growing duration in 2007 and 2008 were shown in Fig.3-1. Average air temperature was lower in 2008 than 2007 in June and August with more rain fall and less solar radiation. In July, 2007, average air temperature was lower with more rain fall and less solar radiation than in 2008. Five cultivars, Akihikari, IRAT109, Nipponbare, Akenohoshi, and IR65564-44-51 (NPT65), were planted during the 2 years. Four cultivars except 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 density, medium density, and low density respectively. The fields were designated as split-plots with three replications. The cultivar was designated as the main plot (19.8 m^2), and density was designated as the subplot in both years (high density, 3.51m^2; medium density, 8.19m^2; low density, 8.1m^2).

The seeds were sown on 28 April, and seedlings were transplanted to the paddy field on 28 May in both years. A single seedling per hill was transplanted. In both years, before transplanting, chemical compound fertilizer was applied as N: P_2O_5 : K_2O at a rate of 60:90:80 kg ha^{-1}. Ammonium sulfate was applied at 2 kg ha^{-1} 5 weeks 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 following the method reported previously; 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. To compare 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 higher 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 compared.

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

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



Daily mean air temperture [℃]

amount of rain fall [mm]

accumulate solar radiation [MJ/m^2]

Fig 2-1-1. Climate conditions for the two growing seasons.

2-3 Results

2-3-1 Panicle characteristics and panicle number

Average D-SPP, SPP, A-SPP, and A% of the panicles in a plant are shown in Table 2-1-1. On average, these four characters were not significantly different 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. D-SPP and SPP did not differ significantly among the other four cultivars, but the values in IRAT109 and Akenohoshi tended to be higher than those in Akihikari and Nipponbare. Among planting density treatments, the four panicle characters were higher at low and medium densities than at the high planting density. The interactions between year and cultivar, year and planting density, and cultivar and planting density were significant for D-SPP, SPP, A-SPP, and A%, except the interaction between year and planting density for A-SPP. Significant interaction among year, cultivar and planting density was also observed. For each cultivar, D-SPP and SPP were not significantly different among planting densities, except SPP in IRAT109 and D-SPP and SPP in NPT65 in 2008 (Table 2-1-1), although D-SPP and SPP tended to be higher at low planting density than at higher densities. A-SPP was also not significantly different among planting densities except in NPT65 in 2008, although A% was higher at low planting density than at high density in Nipponbare and Akenohoshi in 2007.

On average, panicle number per plant and per unit area showed significant differences between years, among cultivars, and among planting densities (Table 2-1-1). 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 numbers per plant were significantly higher at low planting density than at higher densities; however, on a per unit area basis, panicle numbers at low planting density were significantly lower than at high and medium densities. The panicle number per unit area for each cultivar was also significantly higher at the high planting density than at lower density, except in NPT65 in both years and Nipponbare in 2008, which showed no difference among planting densities.

Table 2-1-1. Panicle characters, panicle number and heading date of 5 rice cultivars under three transplanting densities in 2007 and 2008.

Cultivar	Density	D-SPP ($panicle^{-1}$)	SPP ($panicle^{-1}$)	A-SPP ($panicle^{-1}$)	A%	PN($hill^{-1}$)	PN(m^{-2})	Heading date(mo/d)
2007								
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
2008								
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	
$LSD_{0.05}$								
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.

2-3-2 Spikelet number and abortion in each panicle

The panicles were arranged by descending order of SPP. The panicle orders for D-SPP and A% are shown in Fig. 2-1-2 and 2-1-3, respectively. Generally, the D-SPP values were higher at low planting densities than at higher densities when comparing the same panicle order in the same cultivar and year, and they declined as the panicle order increased in all cultivars and years (Fig. 2-1-2). In contrast, A% increased with increasing panicle order at all planting densities and in all cultivars and years. Therefore, the higher order panicles had fewer SPP because of less spikelet differentiation and a higher percentage of spikelet abortion.

The D-SPP ranges in plants (i.e., the difference between maximum and minimum D-SPP) were larger at low planting density than at high and medium densities for all cultivars (Fig. 2-1-2). This is because the maximum D-SPP values of the lowest order panicles were the greatest at low planting density, followed by medium density, although the minimum D-SPP values of the highest 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 low planting density in 2007. The narrowest range of D-SPP values, from 96 to 127, was observed in Nipponbare at high planting density in 2008.

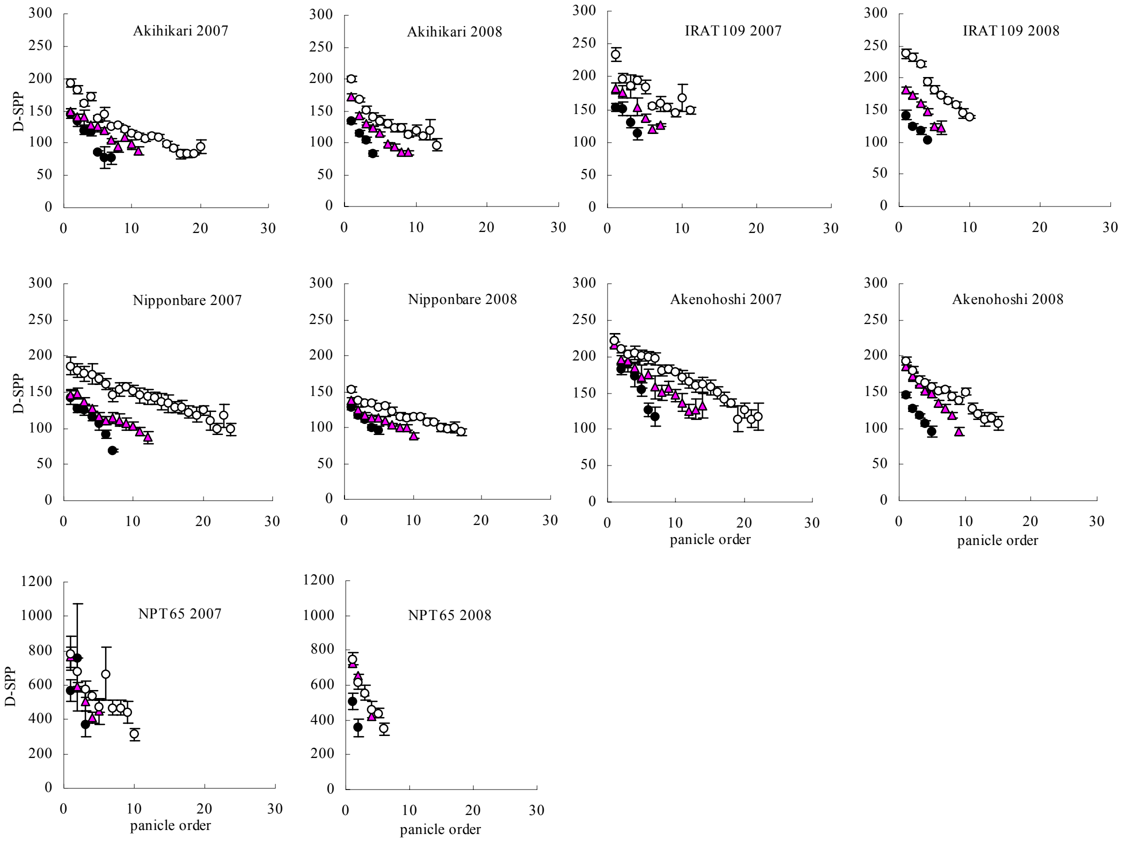


Fig.2-1-2. Differentiated spikelet number per panicle (D-SPP) as a function of panicle order at three transplanting densities (●: high density; ▲: medium density; ○: low density) in 2007 and 2008. The standard error was shown.

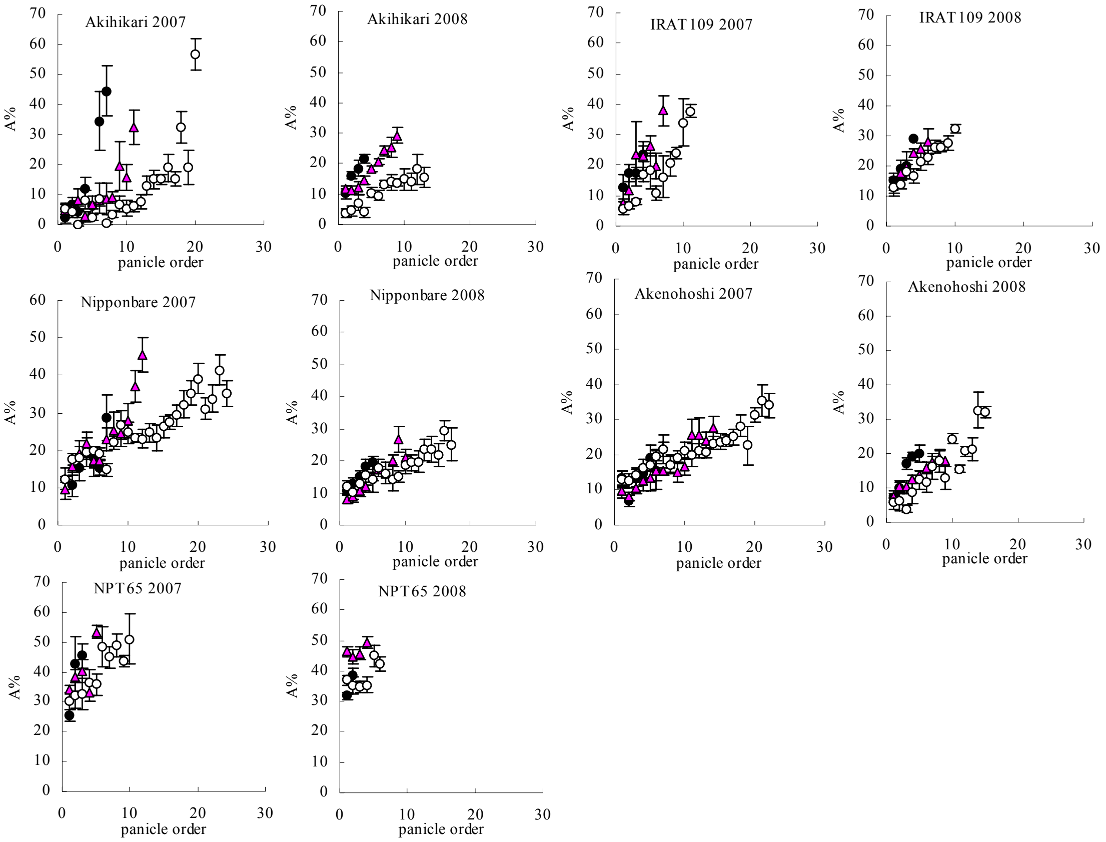


Fig.2-1-3. Ratio of aborted spikelet number per panicle to differentiated spikelet number per panicle (A%) as a function of panicle order at three transplanting densities (●: high density; ▲: medium density; ○: low density) in 2007 and 2008. The standard error was shown.

2-3-3 Relationships of leaf area, tiller height, and neck internode diameter to SPP, D-SPP, and A%

The average leaf area per tiller, tiller height, and neck internode diameter of tillers are shown in Table 2-1-2. Statistically significant differences among cultivars existed 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 highest in NPT65, followed by Akenohoshi, and lowest in Akihikari. Leaf area per tiller showed significant interaction effects between cultivar and planting density, and in IRAT109, Akenohoshi, and NPT65 leaf area per tiller was higher at low planting density than at high density, although in Akihikari and Nipponbare it did not differ among planting densities. 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 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. 2-1-4). 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.

Spikelet production efficiency for SPP or for D-SPP (SPP or D-SPP per leaf area) in each tiller are shown in Fig. 2-1-5. 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. 2-1-4. With the panicle order increase, 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 spikelet production efficiency between D-SPP and SPP (i.e., spikelet abortion efficiency for A-SPP) was larger with the higher order panicle than with the lower order panicle 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, though the number of panicles was much less than the other cultivars.

Table 2-1-2. Averages and ranges of leaf area per tiller, tiller height, and neck internode diameter at heading in five cultivars under three transplanting densities in 2008.

Cultivar	Density	Leaf area (cm^2 tiller $^{-1}$)		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.

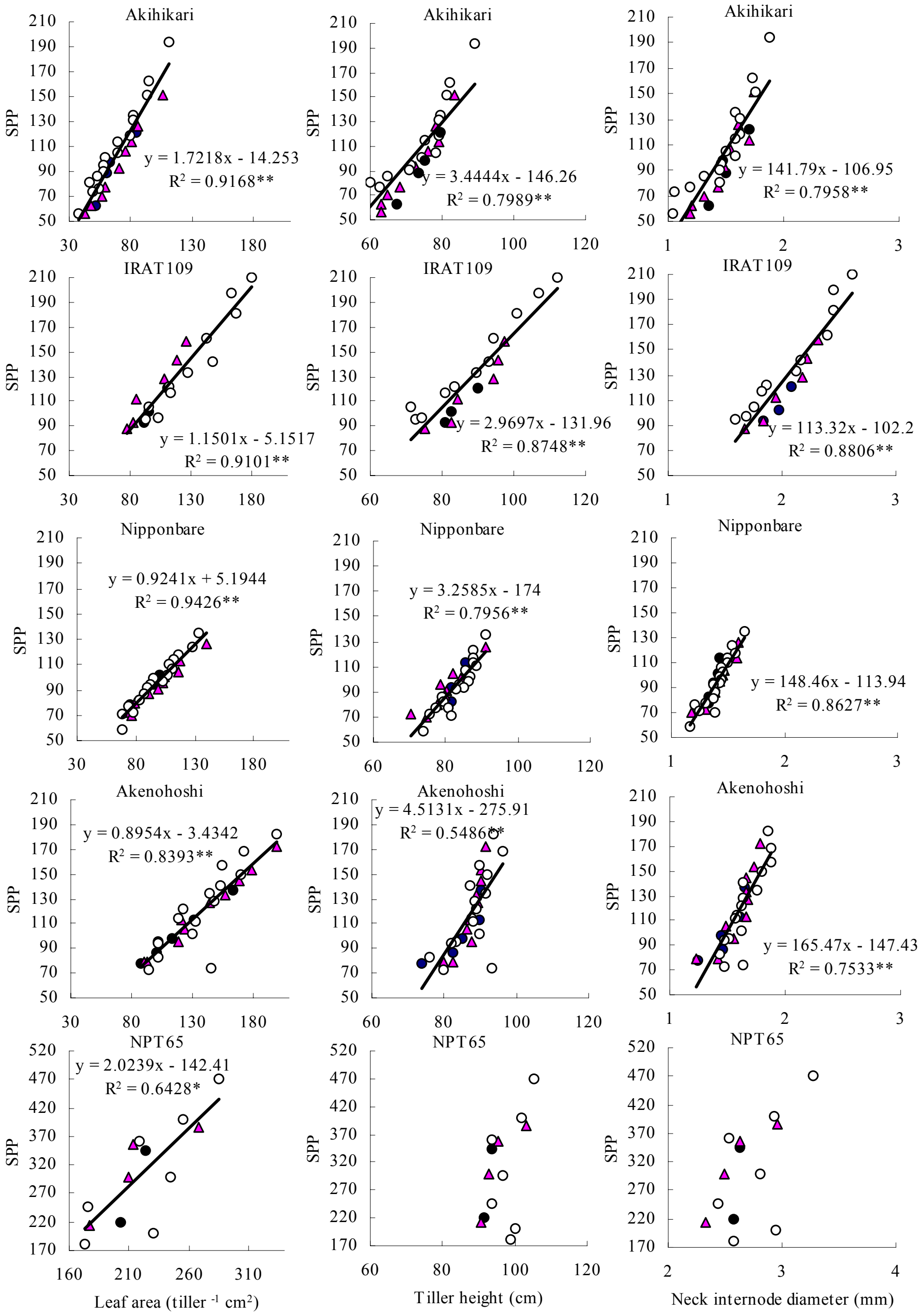


Fig.2-1-4. Relationships between tiller size (leaf area per tiller, tiller height, and neck internode diameter) and spikelet number per panicle (SPP) in five cultivars at three transplanting densities (●: high density; ▲: medium density; ○: low density). *,** showed the coefficient of determinations were significant at the 5%, 1% level

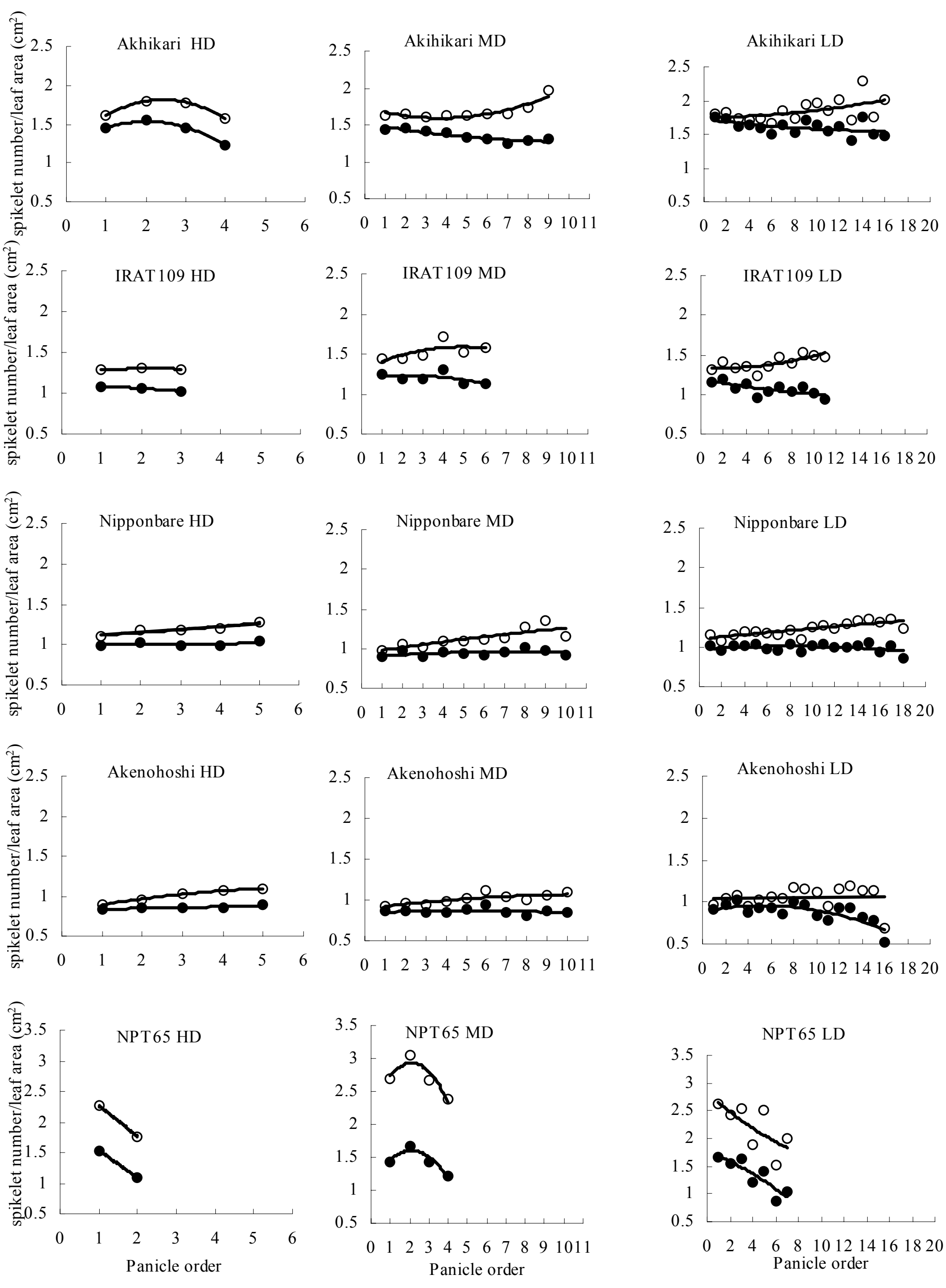


Fig. 2-1-5. Spikelet production efficiency of each panicle in five cultivars in 2008. ○: Spikelet production efficiency for D-SPP (cm^2); ●: Spikelet production efficiency for SPP (cm^2).

2-4 Discussion

2-4-1 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 2-1-1). 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. For each cultivar, although the differences in D-SPP and SPP values among planting densities were not statistically significant, D-SPP or SPP tended to be larger at low planting density than at high planting density, and, in contrast, panicle number per unit area were smaller at low planting density than at high and medium 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 et al. (1995) reported a strong positive relationship between D-SPP and A-SPP, though the relationships between D-SPP and A-SPP were not always consistent.

2-4-2 Effects of planting density on SPP, D-SPP, and A-SPP in each panicle

Plants showed a broader range of D-SPP values at 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 there were smaller differences in D-SPP on higher order panicles among planting densities. Pham et al. (2004b) reported that, in a system with low planting density with nitrogen topdressing, compared with in conventional planting density, the spikelet number per panicle on secondary tillers, which were relatively smaller panicles, were significantly larger, but those on main stem and primary tillers, which were relatively larger panicles, were not. This result would show that the effect of low planting density on spikelet number per panicle is 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 lower order panicles, which had relatively larger panicles, was much larger at low planting density than at high planting density, though D-SPP in higher order panicles was almost the same between at low planting density and at high planting density. This inconsistency might be caused by the difference of 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). And, 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 or 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 large tiller dry weight, which causes high SPP.

However, SPP represents the difference between D-SPP and A-SPP. With increasing panicle order, D-SPP decreased and spikelet abortion (A%) increased (Fig. 2-1-2), resulting in reduced SPP in all cultivars and planting densities. In four cultivars except NPT65, spikelet production efficiency for D-SPP increased with increasing panicle order, especially at low planting density, whereas spikelet production efficiency for SPP were constant or decreased with increasing panicle order (Fig. 2-1-5). This finding indicates that, irrespective of planting density in the field condition, the higher order panicles produce more spikelets than they can afford physiologically, but they were regulated downward to a nearly constant value in four cultivars except 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; higher order tillers obtained assimilates from lower order tillers at the spikelet differentiation stage, but this transfer did not last until heading. In addition, the photosynthetic ability in 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 increase of panicle order (data not shown). Thus, we may infer that the difference in the photosynthetic ability in leaves of the tillers was related to the high A% and low SPP recorded in higher order panicles. Kobayasi and Shintani et al. (2003) reported that SPP was closely related to nitrogen content in the shoot at heading. The nitrogen content of a leaf can influence the leaf's photosynthetic ability; that is, increasing 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 panicle order increase. It may indicate that in NPT65 each tiller is independent of the photosynthetic assimilate, and that the photosynthetic ability in leaves might decline with the increase 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.

3 Influence of panicle characters and spikelet number per panicle on yield and yield components

3-1 Introduction

The large number of spikelet per panicle was supposed to contribute the yield production in rice (Iskandar et al., 2003; Peng et al., 2008; Laza et al., 2004). Simultaneously, the distribution of spikelet on panicle was related to the grain growth. Spikelet located on the higher braches of panicle had the development priority than those located on the lower rachis branches, and the spikelet on the primary rachis branches also grow better than that on the secondary rachis branches (Nagato et al., 1942; Chaudhry et al., 1970; Yamagishi et al., 2003; Terai et al., 2008). This is attributed to the more difficulties in the transport of assimilates to secondary rachis branches than to primary rachis branches because of the vascular bundles difference between them (Muhammad et al., 1975; Terai et al., 2008). Both of spikelet number per panicle and distribution of spikelet within panicle were related to the yield production closely.

Recently the breeding efforts were paid on developing cultivars with large panicle size (Peng et al., 2008). The enlargement in spikelet per panicle was attributed to both of the increase of primary rachis number per panicle and spikelet number per primary rachis branch (Chapter 2-1). However, the increase of spikelet number per primary rachis was mainly due to the increase of the spikelet on secondary rachis branches than on the primary rachis branch (Kobayasi et al., 2001). The spikelet located on the primary rachis branches got more priority in grain size and filling degree than the spikelet located on the secondary rachis branches. This results in the reduction of grain weight while the spikelet production is improved. As the sum for all of spikelet within panicle, the large panicle size was not supposed to contribute to the yield directly (Yamagishi et al., 2003). As indicated of previous results in this chapter, the panicle size was enlarged in LD than in HD, so its effects on the yield, and its components, especially the grain weight, and filled grain percentage should be studied.

In this part, the relationship of panicle characters and panicle size on yield and yield components were measured. These results would be used to estimate the effects of the enlargement in spikelet per panicle due to reduction in transplanting density on yield and its components.

3-2 Materials and methods

Location and cultivars were the same as described in chapter 2-1

Samples were harvested at heading and maturity. At each time, the shoot dry matter was weighted after stove drying at 80℃. The leaf area per plant was calculated by the sum of leaf area tiller^{-1} measured in Chapter 2-1.

At the maturity stage, panicles were collected and threshed by hand. The grains were divided into filled grain and unfilled grain by soaking in water. After the stove drying at 80 ℃, filled and unfilled grain numbers and filled grain weights were recorded and yield and yield components were calculated.

ANOVA analysis was conducted according to the procedure of Statistical Procedures for Agricultural Research on the basis of sub split-plot design. (Gomez and Gomez, 1984)

3-3 Results

3-3-1 Leaf area and shoot dry matter

Leaf area (cm^{2} tiller^{-1}), leaf weight (mg cm^{-2}) and tiller weight (g tiller^{-1}), plant height (cm), were obviously larger in LD than in HD at heading (Table 2-2-1). They were larger in 2007 than in 2008 although there was no difference in shoot dry matter tiller^{-1} between the two years. NPT65 had significantly higher values in leaf area per tiller, specific leaf weight, and tiller weight per tiller than other cultivars. IRAT109 had higher specific leaf weight than Akihikari, Nipponbare, Akenohoshi, while Akenohoshi had the larger leaf area per tillers than Akihikari, IART109, and Nipponbare. Akihikari and Nipponbare showed no difference in the tiller size traits.

Tiller number m^{-2} was clearly lower in LD than HD, although statistically it was not different in 2008. To Akihikari and Nipponbare, the tiller number m^{-2} in LD was much lower than that in HD, but in NPT65, the difference between LD and HD was not observed..

LAI at heading and shoot dry matter m^{-2} were lower in LD than in HD, because of less panicle number m^{-2} (Table 2-2-1). In general, LAI was largest in MD, and smallest in LD. Akenohoshi had the largest leaf area and NPT65 showed the smallest leaf area among the 5 cultivars. The shoot dry matter m^{-2} was lower in LD than other two densities in general. Akenohoshi had the highest shoot dry matter with the large tiller number m^{-2} and leaf area. Akihikari had the lowest shoot dry matter with the smallest shoot dry matter tiller $^{-1}$ although the tiller m^{-2} was larger than others. At maturity, shoot dry matter showed the same tendency with that at heading. The leaf area and shoot dry matter was lower in 2008 than 2007.

Table 2-2-1 Tiller size at heading and shoot dry matter production at heading and maturity for 5 cultivars under 3 transplanting densities in 2007 and 2008.

Genotype	Density	Heading							Maturity
		Shoot dry matter (g m^{-2})	Tiller number (m^{-2})	LAI(m^2 m^{-2})	Leaf area(cm^2 tiller^{-1})	Average tiller weight (g tiller^{-1})	Specific leaf weight (mg cm^{-2})	Plant height (cm)	Shoot dry matter (g m^{-2})
2007									
Akihikari	HD	681.1 a	379.2 a	3.5 a	92.5 a	1.8 a	4.9 b	82.5 a	955.3 ab
	MD	523.3 ab	285.2 b	2.9 ab	100.2 a	1.8 a	5.1 ab	86.4 a	946.7 b
	LD	430.8 b	220.3 c	2.3 b	106.8 a	2.0 a	5.5 a	90.0 a	1017.9 a
IRAT109	HD	686.1 a	203.4 a	2.6 ab	127.7 b	3.4 ab	6.6 b	90.8 c	936.5 a
	MD	679.8 a	207.4 a	2.9 a	140.9 ab	3.3 b	6.6 b	97.1 b	830.0 b
	LD	555.2 a	142.6 b	2.2 b	156.0 a	3.9 a	7.3 a	103.9 a	918.5 ab
Nipponbare	HD	887.0 a	360.0 a	5.2 b	113.2 b	2.5 a	5.6 b	102.6 a	1213.3 a
	MD	838.0 ab	331.4 a	6.2 a	138.2 a	2.5 a	5.4 b	101.8 a	1182.0 a
	LD	708.1 b	271.3 b	4.4 c	134.7 a	2.6 a	6.1 a	97.4 b	1222.7 a
Akenohoshi	HD	1009.6 a	276.5 a	6.4 a	188.7 b	3.7 a	5.9 b	98.6 b	1597.0 a
	MD	1043.9 a	284.2 a	6.7 a	205.7 ab	3.7 a	5.4 c	100.7 ab	1483.6 b
	LD	820.4 b	238.9 b	5.1 b	214.4 a	3.4 a	6.1 a	104.5 a	1413.3 b
NPT65	HD	778.8 a	147.5 a	1.7 a	230.4 ab	5.3 a	6.3 b	94.6 ab	1096.4 a
	MD	737.8 a	139.8 a	1.9 a	236.3 a	5.3 a	6.6 b	96.0 a	1107.9 a
	LD	626.8 a	115.7 a	1.6 a	214.5 b	5.4 a	7.4 a	91.1 b	937.5 b
2008									
Akihikari	HD	394.6 a	177.8 ab	1.1 b	65.3 a	2.2 a	3.5 b	73.9 a	955.3 a
	MD	403.0 a	192.6 a	1.3 a	71.5 a	2.1 a	3.0 b	72.9 a	946.7 a
	LD	304.2 a	148.1 b	1.0 b	69.3 a	2.1 a	4.7 a	73.3 a	1017.9 a
IRAT109	HD	454.7 a	140.7 a	1.3 a	96.6 b	3.2 b	5.4 b	84.9 b	936.5 a
	MD	452.7 a	113.0 a	1.1 b	103.9 b	4.0 a	6.9 a	90.5 a	830.0 b
	LD	453.3 a	113.0 a	1.4 a	133.3 a	4.0 a	6.4 a	90.2 a	918.5 ab
Nipponbare	HD	577.8 a	200.0 a	1.9 ab	95.5 a	2.9 a	3.5 a	83.4 a	1213.3 a
	MD	573.6 a	201.8 a	2.1 a	102.0 a	2.8 a	3.3 a	81.4 a	1182.0 a
	LD	540.2 a	190.7 a	1.8 b	96.7 a	2.8 a	3.7 a	83.3 a	1222.7 a
Akenohoshi	HD	670.6 a	192.6 a	2.4 b	126.9 b	3.5 b	3.6 b	87.0 a	1597.0 a
	MD	746.8 a	198.1 a	2.9 a	145.9 a	3.8 b	3.4 b	88.2 a	1483.6 b
	LD	748.7 a	162.9 a	2.3 b	142.8 a	4.6 a	5.5 a	88.1 a	1413.3 b
NPT65	HD	557.9 a	85.2 a	1.8 ab	204.3 b	6.5 b	8.7 b	92.9 b	1096.4 a
	MD	560.2 a	85.2 a	1.8 a	215.8 ab	6.6 b	8.6 b	93.2 b	1107.9 a
	LD	491.9 a	68.5 a	1.6 b	230.2 a	7.2 a	11.2 a	98.4 a	937.5 b
Main factor means									
Year	2007	733.8 a	240.2 a	3.7 a	160.0 a	3.4 a	6.0 a	95.9 a	1123.9 a
	2008	528.7 a	151.3 b	1.7 b	126.7 b	3.9 a	5.4 b	85.4 b	1123.9 a
Genotype	Akihikari	456.2 c	233.9 ab	2.0 b	84.2 c	2.0 b	4.5 c	79.8 b	973.3 bc
	IRAT109	547.0 bc	153.3 bc	1.9 b	126.4 bc	3.6 b	6.5 b	92.9 a	895.0 c
	Nipponbare	687.5 ab	259.2 a	3.6 a	113.4 bc	2.7 b	4.6 c	91.6 a	1206.0 b
	Akenohosh	840.0 a	225.5 ab	4.3 a	170.7 ab	3.8 b	5.0 c	94.5 a	1498.0 a
	NPT	625.5 abc	107.0 c	1.7 b	221.9 a	6.0 a	8.1 a	94.4 a	1047.3 bc
Density	HD	669.8 a	216.3 a	2.8 b	134.1 b	3.5 b	5.4 b	89.1 b	1159.7 a
	MD	655.9 a	203.9 b	3.0 a	146.0 a	3.6 ab	5.4 b	90.8 a	1110.0 b
	LD	568.0 b	167.2 c	2.4 c	149.9 a	3.8 a	6.4 a	92.0 a	1102.0 b
LSD$_{0.05}$									
Year		393.6	31.8	0.5	13.8	1.0	0.6	5.1	151
Genotype		218.1	98.0	1.3	82.0	2.1	1.2	10.7	288
density		52.1	12.1	0.1	4.9	0.3	0.2	1.4	29
Y×G		308.4	138.6	1.9	116.0	3.0	1.7	15.1	407
Y×D		73.6	17.2	0.2	7.0	0.4	0.3	2.0	41
G×D		116.4	27.1	0.3	11.0	0.6	0.4	3.2	65
Y×G×D		164.6	38.4	0.4	15.6	0.9	0.6	4.6	92

Note: the same letter attached to the value means no difference at 0.05 level.

3-3-2 Yield and yield components

Generally, yield was lower in the low density than in the high density, in 2007 than in 2006 and 2008. Yield was highest in Akenohoshi (Table 2-2-2). Yield was lowest in 2008 with NPT65 220 g m^{-2} in LD and highest in 2007 with Akenohoshi 723 g m^{-2} in HD (Table 2-2-2).

PN m^{-2} was more in HD than in LD, in 2007 than in other two years, and in Nipponbare than other cultivars. The highest PN m^{-2} was 292 in Nipponbare in HD in 2007, and lowest was 63 of NPT65 in LD of 2008. SPP was higher in LD than in HD. NPT65 had the largest SPP than other cultivars. Consequently, the spikelet number per m^2 was constant among 3 transplanting densities on average. FG% was constant among densities and years. As a result, grain number per m^2 was also invariable on varying transplanting densities. For the cultivar difference, NPT had the lowest FG% than other cultivars. The lowest FG% was in NPT65 of MD in 2007, 32.25%, comparing to the highest, 87.53%, in Akihikari in low density of 2008. 1000-GW was heavier in HD than LD, in the 2008 than in other two years, and in IRAT109 than other cultivars. The lowest 1000-GW was in NPT69 in 2006 of LD, 21.33g, and highest in IRAT109 in 2008 of MD 35.48g.

Table 2-2-2 Grain yield and its components in 6 cultivars under 3 transplanting densities in 2006, 2007, and 2008.

Genotype	Density	yield (g m^{-2})	PN (m^{-2})	SN(m^{-2})	GN(m^{-2})	FG%	1000-GW	SPP
2006								
Akihikari	HD	412 a	222 a	25543 a	18122 a	70.95 a	22.60 a	115 a
	MD	367 a	194 a	23292 a	16839 a	72.29 a	21.84 ab	120 a
	LD	411 a	194 a	23941 a	19050 a	79.57 a	21.55 b	123 a
IRAT109	HD	325 a	148 a	16002 a	10674 a	66.70 a	30.20 ab	108 b
	MD	307 a	130 a	18450 a	10355 a	56.13 b	29.60 b	142 a
	LD	352 a	124 a	19627 a	11354 a	57.85 ab	30.99 a	158 a
Nipponbare	HD	478 a	267 a	26172 ab	19792 ab	75.62 a	24.35 a	98 a
	MD	419 a	226 b	21794 b	17874 b	82.01 a	23.32 b	96 a
	LD	479 a	269 a	29185 a	20883 a	71.55 a	22.89 b	109 a
Akenohoshi	HD	523 a	252 a	27550 a	21726 a	78.86 a	23.96 a	109 b
	MD	533 a	233 ab	29533 a	21941 a	74.29 a	24.33 a	127 b
	LD	498 a	202 b	32631 a	20585 a	63.08 b	24.26 a	162 a
NPT69	HD	572 a	148 a	43273 a	25289 a	58.44 a	22.64 a	292 c
	MD	413 b	96 ab	32901 b	18922 b	57.51 a	22.07 ab	342 b
	LD	392 b	76 b	29341 b	18246 b	62.19 a	21.33 b	386 a
2007								
Akihikari	HD	445 a	264 a	25746 a	15704 a	61.00 ab	23.03 ab	98 a
	MD	318 b	247 a	25605 a	14118 a	55.14 b	22.51 b	104 a
	LD	399 ab	211 b	23322 a	16924 a	72.57 a	23.58 a	110 a
IRAT109	HD	359 a	177 a	20335 a	11225 a	55.20 a	31.65 ab	115 a
	MD	315 a	160 a	19225 a	10102 a	52.54 a	31.00 b	120 a
	LD	363 a	134 b	18283 a	11384 a	62.26 a	31.86 a	136 a
Nipponbare	HD	469 a	292 a	28025 a	18924 a	67.53 a	24.74 a	96 a
	MD	453 a	284 a	26101 a	18570 a	71.15 a	24.35 ab	92 a
	LD	493 a	262 b	28336 a	20719 a	73.12 a	23.81 b	108 a
Akenohoshi	HD	723 a	277 a	40609 a	27847 a	68.57 a	25.11 a	147 a
	MD	613 b	274 a	38167 ab	25064 ab	65.67 a	24.50 a	140 a
	LD	539 b	243 b	31901 b	21875 b	68.57 a	24.56 a	131 a
NPT65	HD	341 a	121 a	31011 a	14636 a	47.20 a	23.36 a	256 b
	MD	275 a	110 a	38628 a	12458 a	32.25 b	21.99 a	350 a
	LD	290 a	110 a	34847 a	12708 a	36.47 ab	22.84 a	315 a

To be continued to table 2-2-2

2008								
Akihikari	HD	337 a	190 a	17593 a	14769 a	83.95 a	22.87 a	93 b
	MD	328 a	174 a	17124 a	14290 a	83.45 a	22.96 a	98 ab
	LD	363 a	155 b	17921 a	15686 a	87.53 a	23.26 a	116 a
IRAT109	HD	379 a	143 a	15238 a	10722 a	70.36 a	35.28 a	106 b
	MD	363 a	119 b	15032 a	10183 a	67.74 a	35.48 a	127 ab
	LD	356 a	96 c	14027 a	10063 a	71.74 a	35.31 a	146 a
Nipponbare	HD	382 a	217 a	20850 a	15171 a	72.76 b	25.09 a	96 a
	MD	393 a	212 a	20373 a	15897 a	78.03 ab	24.83 a	96 a
	LD	395 a	193 b	18589 a	15857 a	85.30 a	24.87 a	96 a
Akenohoshi	HD	403 b	193 a	20575 b	15258 b	74.16 a	26.47 a	107 a
	MD	493 a	189 a	23673 a	18458 a	77.97 a	26.73 a	125 a
	LD	423 b	163 b	20437 b	16220 ab	79.37 a	26.09 a	125 a
NPT65	HD	233 a	86 a	24390 ab	9409 a	38.58 a	24.79 b	282 b
	MD	257 a	78 ab	25903 a	10025 a	38.70 a	25.77 a	333 a
	LD	220 a	63 b	21121 b	8765 a	41.50 a	25.12 ab	335 a
Main factor means								
Year	2006	432 a	185 a	26616 a	18110 a	68.47 a	24.39 a	166 a
	2007	426 a	211 a	28676 a	16817 a	59.28 a	25.26 a	154 a
	2008	355 a	151 a	19523 a	13385 a	70.08 a	27.00 a	152 a
Genotype	Akihikari	376 bc	206 a	22232 bc	16167 b	74.05 a	22.69 b	108 b
	IRAT109	347 c	137 b	17358 c	10673 c	62.28 a	32.37 a	129 b
	Nipponbare	440 ab	247 a	24381 b	18188 ab	75.23 a	24.25 b	99 b
	Akenohoshi	528 a	225 a	29453 ab	20997 a	72.28 a	25.11 b	130 b
	NPT	333 c	99 b	31268 a	14495 bc	45.87 b	23.32 b	321 a
Density	HD	426 a	200 a	25527 a	16618 a	65.99 a	25.74 a	141 c
	MD	390 b	182 b	25053 a	15673 a	64.33 a	25.42 b	161 b
	LD	398 b	166 c	24234 a	16021 a	67.51 a	25.49 b	171 a
LSD0.05								
Year		132.63	94	15317	8964	18.52	4.16	22
Genotype		92.28	56	5490	4002	13.66	3.67	82
density		22.98	8	2006	1427	4.11	0.25	8
Y×G		159.84	97	9509	6931	23.66	6.35	143
Y×D		39.80	14	3475	2471	7.12	0.42	14
G×D		51.39	17	4486	3190	9.19	0.55	18
Y×G×D		89.00	30	7770.14	5525.03	15.92	0.95	30.51

Single value for each genotype, at each density for each year, followed by same letters means no significant difference between densities at 5% level;

Means of years, genotypes and densities for all of the data, followed by same letter means no significant difference at 5% level.

3-3-3 Grain yield with differently located grains in panicle in 2008

As shown in Table2-2-3, transplanting density had clearer effects total grain weight on secondary rachis branches than on primary rachis branches, grain yield, FG%, 1000-GW, and SPP. Grain yield and its components on primary rachis branches kept constant among the 3 transplanting densities, while, grain yield, FG%, 1000-GW, and SPP on secondary rachis branches had higher values in LD than in HD. Comparing with the yield and components between on the primary and on the secondary rachis branches, they showed obviously larger values on primary than on secondary rachis branches. Although the spikelet production m^{-2} showed higher in secondary rachis than on the primary ones, the grains m^{-2} showed no difference between them because of the lower FG% on the secondary rachis branches.

The differences among cultivars were apparent. NPT65 had more grain yield on secondary than primary rachis branch, other 4 cultivars had greater grain yield on the primary rachis branches. NPT65 had same FG% on primary and on secondary rachis branches, while other 4 cultivars had higher FG% on primary than secondary rachis branches. The spikelet number m^{-2}, grain number m^{-2} and SPP were higher on the secondary rachis than on the primary ones in NPT65 and Akenohoshi. The other 3 cultivars, Akihikari, IRAT109 and Nipponbare, had the larger number in spikelet m^{-2}, grain m^{-2} and SPP on primary than on secondary rachis branches. All of the cultivars showed constantly larger 1000-GW on primary than secondary rachis branches.

Table 2-2-3. Grain yield and its components of grains located on primary rachis and secondary rachis in 2008.

Cultivar	**Density**	**Grain yield ($g\ m^{-2}$)**	**SN (m^{-2})**	**GN (m^{-2})**	**FG (%)**	**1000-GW (g)**	**SPP**
		Priamry rachis branch					
Akihikari	**HD**	197.8 a	9405.4 a	7680.7 a	81.7 a	25.8 b	48.8 a
	MD	177.2 b	8906.6 a	6828.9 b	76.7 a	25.9 b	48.8 a
	LD	193.0 a	8484.6 a	7241.9 ab	85.4 a	26.6 a	51.3 a
IRAT109	**HD**	256.9 a	9309.7 a	7073.4 a	76.0 a	36.3 b	65.2 b
	MD	212.4 b	8858.4 ab	5810.5 b	65.6 b	36.4 b	73.1 ab
	LD	234.5 a	7594.3 b	6208.6 b	81.8 a	37.7 a	76.0 a
Nipponbare	**HD**	242.9 a	11160.0 a	9184.3 a	82.3 a	26.3 b	55.9 a
	MD	256.7 a	11703.7 a	9376.8 a	80.1 a	27.5 a	51.1 a
	LD	243.3 a	11449.7 a	9554.6 a	83.4 a	25.4 c	54.4 a
Akenohoshi	**HD**	218.1 c	9832.5 a	7895.5 c	80.3 b	27.8 b	51.4 a
	MD	290.9 a	11285.1 a	10121.2 a	89.7 a	28.8 a	49.7 a
	LD	247.0 b	10167.5 a	8813.9 b	86.7 ab	28.0 b	55.4 a
NPT65	**HD**	51.7 a	4212.5 a	1999.8 a	47.5 a	26.1 a	55.4 a
	MD	38.8 ab	3749.2 a	1548.0 ab	41.3 a	25.2 b	52.9 a
	LD	32.3 b	3187.2 a	1353.6 b	42.5 a	23.7 c	47.6 a
		Seconday rachis branch					
Akihikari	**HD**	121.8 c	8310.0 b	5384.6 b	64.8 b	22.4 b	43.7 b
	MD	136.1 b	8624.1 ab	5380.9 b	62.4 b	23.7 a	49.5 b
	LD	189.8 a	9972.8 b	8197.3 a	82.2 a	23.1 a	64.4 a
IRAT109	**HD**	100.6 b	5899.4 a	3207.1 b	54.4 b	31.3 b	41.2 c
	MD	105.2 b	6363.4 a	3362.6 b	52.8 b	30.8 b	53.7 b
	LD	143.6 a	6711.1 a	4349.6 a	64.8 a	32.8 a	69.7 a
Nipponbare	**HD**	134.2 b	8694.9 a	5732.8 b	65.9 c	23.2 a	40.0 a
	MD	173.1 a	9518.0 a	7258.5 a	76.3 b	23.8 a	44.8 a
	LD	164.7 a	8071.0 a	7077.1 a	87.7 a	23.0 b	41.8 a
Akenohoshi	**HD**	176.0 b	10680.5 b	7280.8 b	68.2 b	24.3 b	55.5 b
	MD	280.9 a	14284.7 a	11106.3 a	77.7 a	25.4 a	75.6 a
	LD	179.0 b	11404.1 b	7319.6 b	64.2 b	24.4 b	70.0 a
NPT65	**HD**	135.5 b	16740.2 b	6443.8 a	42.5 a	22.3 b	193.7 c
	MD	152.9 a	18355.0 a	6477.1 a	36.7 a	23.4 a	236.0 a
	LD	156.7 a	14311.1 c	6766.0 a	45.4 a	23.0 a	227.3 b
		Therminal rachis branch					
NPT65	**HD**	28.2	2858.3	1214.7	46.8	23.9	33.1
	MD	28.3	3433.7	1259.1	39.6	22.5	44.2
	LD	37.9	3811.0	1731.3	41.9	21.7	60.5

To be continued to Table 2-2-3

		Primary rachis branch					
Means of density	**HD**	193.5 a	8784.0 a	6766.7 a	73.5 a	28.5 a	55.4 a
	MD	195.2 a	8900.6 a	6737.1 a	70.7 a	28.7 a	55.1 a
	LD	190.0 a	8176.7 a	6634.5 a	75.9 a	28.3 a	57.0 a
		Scondary rachis branch					
Means of density	**HD**	133.6 b	10065.0 a	5609.8 b	59.2 b	24.7 b	74.8 b
	MD	169.6 a	11429.1 a	6717.1 a	61.2 ab	25.4 a	91.9 a
	LD	166.8 a	10094.0 a	6741.9 a	68.9 a	25.2 ab	94.6 a
	Primary	192.9 a	8620.4 b	6712.8 a	73.4 a	28.5 a	55.8 b
	Secondary	156.7 b	10529.4 a	6356.3 a	63.1 b	25.1 b	87.1 a
P value by ANOVA	**C**	0.00	0.01	0.00	0.00	0.00	0.00
	D	0.07	0.39	0.14	0.14	0.19	0.00
	Location	0.00	0.00	0.01	0.00	0.00	0.00
	C× D	0.01	0.31	0.02	0.84	0.47	0.02
	C× Location	0.00	0.00	0.00	0.00	0.08	0.00
	D× Location	0.00	0.01	0.00	0.96	0.43	0.01
	C× D× Location	0.07	0.55	0.04	0.04	0.66	0.26

Note: Same letter means no difference at 5% level.

3-4 Discussion

3-4-1 Yield and yield components under different transplanting density

Grain number m^{-2} is one of the main factors in the determination of yield production in crops (Fischer et al., 2008; Ugarte et al., 2007; Kobayasi et al., 2001; Arcreche et al., 2006; Slafer et al., 2004). Grain number per m^2 is positively related to spikelet number per m^2. Spikelet per m^2 can be dissected into spikelet per panicle and panicle number per m^2. With the reduction of panicle number m^2, the spikelet per panicle would be increased in rice (Table 2-2-2, Fig.2-2-1). Consequently, the production of spikelet per m2 showed constant among the 3 transplanting densities. With the constant filled spikelet or filled grain degree, grain per m^2 was also shown stability on varying transplanting densities. So the compensation between the spikelet per panicle and panicle number per m^2 is the main reason for the stable production of grain per m^2 in this experiment. This just indicated the enough mediation capacity of spikelet per panicle and panicle number per m^2 to grain production per m^2 under different transplanting density.

However, the yield was lower in LD as compared to HD (Table2-2-2) because of the slight reduction of 1000-grain weight in LD with comparison to HD. It had been reported the negative relations between the grain number and grain weight in rice (Matsushima, 1966). The competition for assimilate among grains was attributed to be main reason for the negative relation between them (Gambín et al., 2007, Duy et al., 2004). In this experiment, without the obvious variation of grain number per m^2, and the yield production was reduced by 1000-GW.

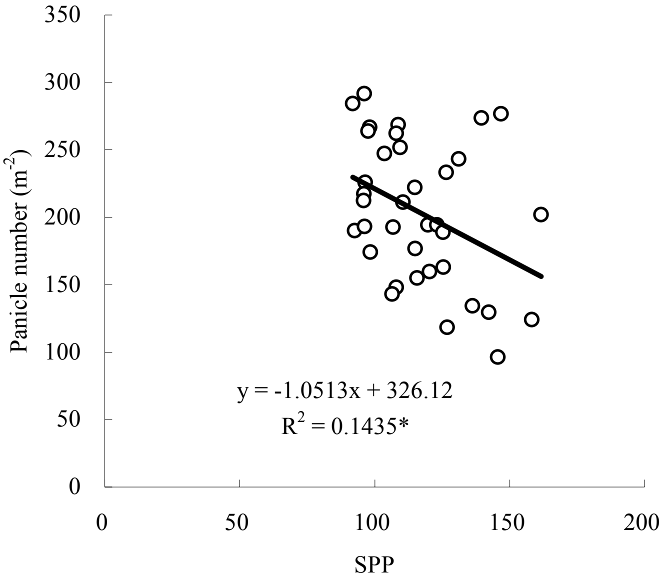


Fig.2-2-1 The relations between the SPP and panicle number per m^2.

3-4-2 Grain yield and yield components of differently located grains in panicle

With the comparison of grain yield and yield components on different location on panicle, the grain located on primary rachis branches had clearly higher grain yield, FG% and 1000-GW than those on the secondary rachis branches (Table 2-2-3). It was evidenced that with the location difference in panicle, the grain filling was different because of the difficulty in transporting assimilates to the grains on secondary rachis than on primary rachis in rice. (Nagato et al., 1941;

Terai et al., 2008; Kobato et al., 2006; Jeng et al., 2006, Acreche et al., 2006). The SPP was clearly larger in LD than HD (Table 2-2-2) accompanied with the larger tiller size in leaf area tiller $^{-1}$, leaf weight tiller $^{-1}$, and shoot dry matter tiller^{-1} in LD(Table 2-2-1, Fig.2-2-2, Shiratsuchi et al., 2007). The increase of SPP was mainly because of the enlargement of spikelet on secondary rachis branches (Table 2-2-3, Kobayasi et al., 2001). So the variation of panicle branching or spikelet location among 3 transplanting densities resulted in the lower 1000-GW in LD than in HD.

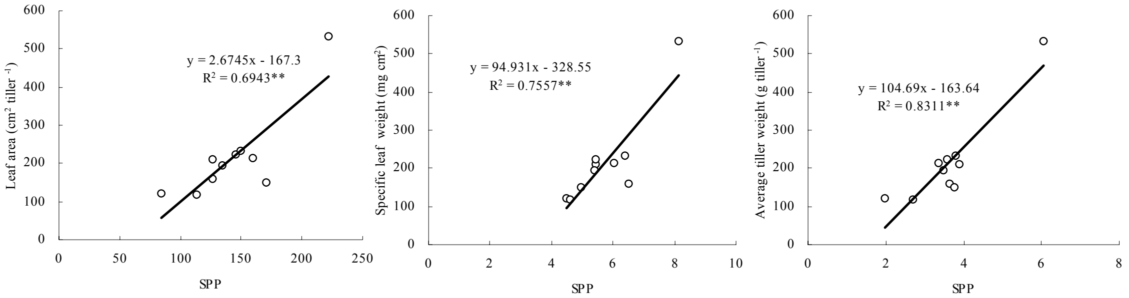


Fig. 2-2-2. Relationships between the leaf area (cm^2 tiller^{-1}), specific leaf weight (mg cm^{-2}), and average tiller weight (g tiller^{-1}) to SPP at heading in 2007 and 2008.

Chapter 3 The response of spikelet number per panicle and yield to transplanting density with root restriction in rice

1 Introduction

As indicated in Chapter 2, the smaller tiller size in terms of tiller height, leaf area per tiller and dry matter per tiller due to the dense planting density resulted into the smaller panicle size in high planting density than in low planting density, so the possible reasons for the smaller tiller size in the high planting density should be clarified.

There is obvious difference in the competition among tillers with aerial part and with below ground part in high planting density and low planting density, both of them could affect the shoot growth resulting into the difference in the shoot size and panicle size. On aerial parts, with the variation of crop community, the light quality changed (García del Moral et al., 1995), and tiller mortality was enhanced due to the low red/far-red ratio in low canopy. Shimizu et al. (1962) also reported that tiller number decreased by the weak light intensity in rice. The difference in nutrients availability from soils for single plant might be caused by the different root volume between the high planting density and low planting density, the difference in nutrients availability caused by the transplanting density may play the important role in the competition. However, relatively, few reports were concerned about the effects of below ground parts in the response to planting density. In the limited reports, it was convinced that root system development was affected by planting density (Morita et al., 1987b, San-no et al., 2006). The percentage of nodal roots reaching deep soil layers decreased in higher planting density in rice (Morita et al., 1987a, 1987b). The close relationships between the shoot and root growth in rice were verified (Li et al., 1970), the close relationships were found between the root morphological and physiological traits to yield traits in rice (Matsuo and Hoshikawa, 1996). The difference in root volume would result into the nitrogen uptake traits in rice reported by Akita (1989). With dense planted rice, the root growth might be limited compared to the spare planted plant. So it will be proposed that planting density will affect the root rhizosphere sizes per plant, and it will influence on the shoot growth, grain yield, and yield components. The estimation of the response of yield and yield traits to the root restriction possibly help elucidating the effects of planting density through the below ground in rice.

Some researches on the restricted root effects on the plant growth reported in rice (Akita et al., 1989), in Maize (Xu et al., 2009), in winter wheat (Peterson et al., 1984), in bean (Carmi et al., 1983), in cucumber (Robbinset et al., 1988; Kharkina et al.,1999), in tomato (Shi et al., 2007), and in chrysanthemum (Goto et al., 2001). Reduced root growth due to the restricted soil volume was associated with the reduced shoot growth in terms of leaf area, stem, and shoot dry weight in beans, cucumber, and winter wheat. Not only the morphological growth traits, but also the physiological traits, such as the leaf starch, hormones, water and nutrients accumulation, were affected by the root restriction treatment. In rice, Akita et al. (1989) reported that the large rooting zone sizes could increase the percentage of nitrogen content in plant, although the genetic difference existed. In the studies of border effects in rice (Sato et al., 1983), the large root space occupied by plant promoted the nitrogen accumulation resulting into the improvement of grain yield. So the limitation of nutrients accumulation from soil by root, especially the nitrogen uptake, is the possible factor to limit shoot morphology, yield and yield traits in rice.

The objectives of this study were to identify the effects of planting density on rice yield and yield related characters, with emphasis on rooting zone size. Therefore, we examined the effects of two different planting density with root restriction treatment on yield, yield related characteristics and nitrogen accumulation using two *Japonica* cultivars, Akihikari and IRAT109 in 2007 and 2008.

2 Materials and methods

The experiments were conducted in 2007 and 2008 at the University Farm of the University of Tokyo, in Nishitokyo, Tokyo, Japan (35°43'N, 139°32'E).

In both years, Japonica cultivars, Akihikari and IRAT109 were used. Relatively, Akihikari was panicle number type and IRAT109 was panicle weight type. Seeds were sown in nursery box on 28th, April in green house, and seedlings were transplanted into paddy fields as one seedling per hill on 29th, May in both year. The paddy fields used for experiments were different between in 2007 and in 2008. Two transplanting distances, 15 cm×15 cm and 30 cm×30 cm were designed as two high planting density (HD) and low planting density (LD) respectively.

Root restriction treatment was conducted by using clapboards, enclosing each hill at 225 cm^2 of soil surface area, and they were the same area of the average area for one hill in LD. The clapboards were inserted into the soil 20cm depth, and the bottoms of them were open. The treatments were same for both planting densities. In both years, chemical compound fertilizer was applied before transplanting as N : P_2O_5 : K_2O = 60 : 90 : 80 kg ha^{-1}. In 2008, nitrogen topdressing treatments were added. Ammonium sulfate was applied for two times, 30 kg N ha^{-1} and 20N kg ha^{-1} on eighth, June and third, July respectively. As comparison, only basal fertilizer was applied in control plots.

The plots were designed as split-plot and split-split-plot designs for 3 replications in 2007 and 2008 respectively. Cultivars as main plot and density as sub plot. In 2008, the nitrogen topdressing as the main plots, and cultivars as the sub-plot, and density as sub-sub-plot.

During the two growing seasons, Tiller number was counted. Samples were harvested at heading stage (50% heading) and maturity stage. At each time, two plants from one plot and 3 replications for each treatment were harvested. The samples were dried at 80 ℃ for several days until the weights were constant and measured. After the milling of sample, total nitrogen content was measured with SUMIGRSPHNC-90A (Sumika Chemical Analysis Service, Ltd. Japan). At the maturity stage, panicles were collected and threshed by hand. The grains were divided into filled grain and unfilled grain by soaking in water. After the stove drying at 80 ℃, filled and unfilled grain numbers and filled grain weights were recorded and yield and yield components were calculated.

Spikelet number per panicle was measured using the samples at the heading stage. Primary rachis branch number (PB) and total spikelets number per panicle (SPP) were counted. The spikelet number per primary rachis branch was calculated as ratio of SPP to PB (S/P). The aborted spikelets per panicle were counted and differentiated spikelets per panicle (D-SPP) were calculated by sum of SPP and aborted spikelet number per panicle. Spikelet abortion percentage (abortion%) was the ratio of aborted spikelet number to D-SPP. All of the panicles within the hill were examined and the average was calculated for SPP, D-SPP and aborted spikelet number. The abbreviations were shown in Table 3-1.

Table 3-1 Abbreviations

abbreviations	explains	abbreviations	explains
PN	panicle number	PB	primarty rachis branch number
GPP	grain number per panicle	S/P	spikelet number per primary rachis branch
FG%	filled grain percentage	NT+	nitrogen topdressing in2008
1000-GW	1000 grains weight	NT-	no nitrogen topdressing in 2008
HI	harvest index	HD	high planting density
SPP	spikelet number per panicle	LD	low planting density
D-SPP	differentiated spikelets number per panicle	RRT	root restriction treatment

3 Results

3-1 Phenology

As shown in Table 3-2, 50% heading stage in Akihikari was about one week earlier than in IRAT109. 1 to 3 days delay was observed in LD comparing to HD in both cultivars. No difference between the RRT and control was observed in both cultivars and years. In 2008, the nitrogen topdressing delayed heading for 1 or 2 days.

Table 3-2 Heading date of Akihikari and IRAT109 on varying planting density with root restriction treatment in 2007 and 2008.

Denstiy	Treatment	2007		2008 NT-		2008 NT+	
		Akihikari	IRAT109	Akihikari	IRAT109	Akihikari	IRAT109
HD	RRT	6 Aug	12 Aug	4 Aug	10 Aug	5 Aug	11 Aug
	Cont.	6 Aug	12 Aug	4 Aug	10 Aug	5 Aug	11 Aug
LD	RRT	7 Aug	14 Aug	6 Aug	13 Aug	7 Aug	14 Aug
	Cont.	7 Aug	14 Aug	6 Aug	13 Aug	8 Aug	15 Aug

3-2 Growth traits

Growth traits in 2008 were shown in Table 3-3. Compared between HD and LD without root restrictions at heading, the plants had the larger values in leaf area for single leaf and per plant, SPAD reading of leaf, neck internode diameter, crown root number per plant, tiller number per hill and tiller height in LD than in HD in both cultivars. And the lower tiller abortion percentage was observed in LD than HD. Compared between nitrogen topdressing and no nitrogen topdressing, the nitrogen topdressing improved the single leaf area, leaf area per plant, crown root number, tiller number per hill, tiller abortion percentage and tiller height, but not the SPAD reading in leaf and neck internode diameters for both cultivars. Compared between root restriction treatment and control, the high interactions effects between the density and root restrictions were observed. In HD, the plant growth traits was not affected by the root restrictions, while in LD, the growth of plants was limited by the root restrictions significantly. And also, the obvious interaction effects between the nitrogen topdressing and root restrictions were observed. With nitrogen topdressing, all of growth traits measured in experiment, showed larger difference between the root restriction and control than without the nitrogen application. Compared between the Akihikari and IRAT109, Akihikari had the lower values in single leaf area, SPAD reading in leaf, neck internode diameter, and tiller height than IRAT109, while larger values in crown root number per plant and tiller number per hill. The nitrogen topdressing improved the leaf area per plant, crown root number and tiller number per hill more significantly in Akihikari than IRAT109 as same as indicated by the interactions between the cultivars and nitrogen effects, while the tiller abortions was increased more in IRAT109 than in Akihikari by the nitrogen application.

Table 3-3 Growth traits under two planting densities with root restriction at heading in 2008.

Cultivar	Nitrogen	Density	RRT	Leaf area of single leaf (cm^2)			Leaf area per plant	Leaf SPAD	Neck Internode diameter(mm)	Crown root number	Tiller number (hill^{-1})	Tiller abortion%	Tiller height (cm)
				LA1	LA2	LA3							
								Akihikari					
Akihikari	NT-	HD	RRT	13.8	17.5	14.9	235.1	32.6	1.493	181.3	4.0	18.3 *	72.3
			Cont.	12.6	16.6	15.7	244.6	33.3	1.454	194.5	4.0	32.7	71.5
		LD	RRT	15.0 *	15.8 **	13.0 **	363.8 **	35.6 **	1.481	253.2 **	6.7 **	21.3	71.7
			Cont.	17.3	21.1	18.4	1005.2	38.7	1.547	406.7	14.3	13.1	74.3
	NT+	HD	RRT	14.2	19.6	22.0	473.5	33.9	1.349 **	229.5	6.2	30.6	74.7 **
			Cont.	17.8	24.0	22.7	527.9	34.8	1.469	232.8	6.0	32.3	82.0
		LD	RRT	14.6 **	17.3 **	17.6 *	609.4 **	34.3 *	1.352 **	326.3 **	9.0 **	27.3 **	72.7 **
			Cont.	23.0	28.3	24.0	2243.1	39.2	1.580	522.8	23.7	7.5	84.8
								IRAT109					
IRAT109	NT-	HD	RRT	24.5 *	26.1	24.8	350.3	39.2	1.993 *	115.5	3.3	4.2	87.0
			Cont.	21.4	25.9	24.0	294.8	37.8	1.915	109.0	3.2	8.3	84.9
		LD	RRT	32.7 **	34.1 *	27.5 **	746.1	47.0	2.357 **	188.7 *	6.3	4.5	93.9
			Cont.	27.6	37.2	36.1	1172.9	39.7	2.151	274.0	10.2	11.4	90.2
	NT+	HD	RRT	25.3	30.7	34.2	442.7	36.6	1.863	136.3	4.0	36.8	90.7
			Cont.	27.7	33.9	37.2	503.1	39.0	1.873	125.8	4.0	41.8	94.1
		LD	RRT	25.1 **	32.1 **	30.2 **	786.5 **	43.5	1.988 **	186.2 **	6.5 **	32.1 **	89.3 **
			Cont.	35.5	51.7	47.0	2133.3	42.4	2.266	324.0	13.0	20.7	100.6
Probability		N		0.02	0.00	0.00	0.00	0.98	0.80	0.00	0.01	0.00	0.00
		C		0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.07	0.00
		D		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.04
		T		0.02	0.00	0.00	0.00	0.64	0.12	0.00	0.00	0.72	0.00
		N×C		0.42	0.03	0.05	0.01	0.38	0.23	0.01	0.00	0.00	0.30
		N×D		0.24	0.91	0.02	0.00	0.56	0.73	0.02	0.00	0.11	0.33
		C×D		0.09	0.00	0.00	0.11	0.22	0.00	0.00	0.00	0.35	0.12
		N×T		0.00	0.00	0.01	0.00	0.02	0.00	0.01	0.00	0.05	0.00
		C×T		0.24	0.30	0.01	0.02	0.00	0.13	0.00	0.00	0.41	0.17
		D×T		0.06	0.00	0.00	0.00	0.55	0.15	0.00	0.00	0.01	0.11
		N×C×D		0.27	0.94	0.31	0.38	0.43	0.42	0.05	0.01	0.46	0.49
		N×D×T		0.12	0.04	0.26	0.00	0.43	0.10	0.00	0.00	0.37	0.22
		C×D×T		0.71	0.28	0.01	0.05	0.00	0.76	0.00	0.00	0.14	0.84
		N×C×T		0.17	0.15	0.03	0.99	0.13	0.29	0.60	0.00	0.73	0.73
		N×C×D×T		0.23	0.04	0.47	0.51	0.88	0.11	0.90	0.00	0.32	0.36

Note: LA1, LA2 and LA3 indicate the flag leaf, the next to flag leaf and the third leaf from top.

Values shown with ** and * is significant at 0.01 and 0.05 level respectively; ANOVA analysis is base on split-split-split plot design. N: nitrogen topdressing; C: Cultivar; D: Density; T: Root restriction treatment.

3-3 Shoot dry matter and nitrogen content

In 2007, between the cultivars, the shoot dry matter per unit area was significantly higher in IRAT109 than in Akihikari at heading and maturity (Table 3-4). In 2008, without topdressing, shoot dry matter per unit area was higher in IRAT109 than Akihikari at heading, and similar at maturity, though, with top dressing, shoot dry matter was equal between two cultivars at both heading and maturity (Table 3-4). Comparing with HD and LD without RRT, shoot dry matter per unit area at maturity are almost the same except in IRAT109, 2007 and in Akihikari, NT-, 2008. With root restrictions in LD, the shoot dry weights of both cultivars were severely limited. However, in HD, the effects of root restrictions on shoot dry weight per unit area showed much less comparing to that in LD. Irrespective of cultivars, topdressing and growth stage, root restriction in LD reduced the shoot dry matter, on average, by 40% and 42% at heading, and 42% and 50% at maturity in Akihikari and IRAT109 respectively as compared to control in 2007.

Nitrogen contents in shoot per unit area were higher in IRAT109 than in Akihikari, with top dressing than without topdressing, and at maturity than at heading in 2008 (Table 3-4). In both cultivars, with root restriction in LD, the nitrogen content was reduced severely, irrespective of with or without topdressing and growth stage. Without topdressing, about 56% and 37% of nitrogen content, and, with topdressing, about 65% and 60% of nitrogen content were reduced in Akihikari and IRAT109 respectively, as compared to control. With root restriction in HD, the nitrogen content reduction was much smaller than in LD.

The relationships of shoot dry matter production and nitrogen content were compared at heading and at maturity per hill (plant) (Fig 3-1). The shoot dry matters were significantly correlated to the nitrogen content per hill. It showed that the amount of absorbed nitrogen was closely related to biomass production per hill.

Table 3-4 Shoot dry matter and nitrogen content under two transplanting densities with root restriction in 2007 and 2008.

Density		Heading						Maturity					
		Shoot dry matter (g m^{-2})			Nitrogen content (g m^{-2})			Shoot dry matter (g m^{-2})			Nitrogen content (g m^{-2})		
		Cont.	RRT		Cont.	RRT		Cont.	RRT		Cont.	RRT	
2007 Akihikari													
	HD	760.4	711.6	ns	--	--		1068.1	1325.1	**	--	--	
	LD	559.6	334.7	*	--	--		1019.2	592.3	**	--	--	
	LSD$_{0.05}$	142.2						238.4					
2007 IRAT109													
	HD	993.8	775.5	ns	--	--		1484.9	1119.4	*	--	--	
	LD	672.3	391.5	**	--	--		1054.0	529.0	**	--	--	
	LSD$_{0.05}$	379.7						239.0					
Main factor means													
Density	HD	810.3		a	--			1249.4		a	--		
	LD	489.5		b	--			798.6		b	--		
Cultivars	AK	591.6		b	--			1001.2		b	--		
	IR	708.3		a	--			1046.8		a	--		
Treatment	Cont.	746.5		a	--			1156.6		a	--		
	RRT	553.3		b	--			891.4		b	--		
2008 Akihikari													
NT-	HD	385.0	348.2	*	3.4	3.0	*	758.4	637.4	*	6.3	5.7	ns
	LD	345.6	136.9	**	4.1	1.3	**	803.6	290.9	**	7.0	2.6	**
	LSD$_{0.05}$	27.6			0.4			60.8			0.7		
NT+	HD	641.5	647.5	ns	6.4	5.9		1315.9	1100.9	**	9.1	7.7	*
	LD	569.7	209.4	**	7.2	2.1	**	994.3	430.2	**	8.6	3.0	**
	LSD$_{0.05}$	97.2			1.8			141.5			1.2		
Main factor means													
Nitrogen	NT-	303.9		b	2.9		b	622.6		b	5.4		a
	NT+	517.0		a	5.4		a	960.3		a	7.1		a
Density	HD	505.5		a	4.7		b	953.1		a	7.2		a
	LD	315.4		b	3.7		a	629.8		b	5.3		b
Treatment	Cont.	485.5		a	5.3		a	968.0		a	7.7		a
	RRT	335.5		b	3.1		b	614.9		b	4.8		b
2008 IRAT109													
NT-	HD	407.4	459.4	ns	3.5	4.2		731.2	632.9	ns	6.2	6.3	
	LD	451.8	238.9	*	4.1	3.0	**	758.5	361.0	**	6.9	3.8	**
	LSD$_{0.05}$	211.2			2.4			267.5			1.9		
NT+	HD	658.8	619.9	ns	5.4	5.1		1147.7	960.2	ns	9.6	9.1	
	LD	667.7	252.0	**	6.6	2.6	**	1103.4	416.2	**	10.4	4.4	**
	LSD$_{0.05}$	199.9			1.5			409.0			4.4		
Main factor means													
Nitrogen	NT-	389.4		b	3.7		b	620.9		b	5.8		b
	NT+	549.6		a	4.9		a	906.9		a	8.4		a
Density	HD	536.4		a	4.6		a	868.0		b	7.8		b
	LD	402.6		b	4.1		a	659.8		a	6.4		a
Treatment	Cont.	546.4		a	4.9		a	935.2		a	8.3		a
	RRT	392.6		b	3.7		b	592.6		b	5.9		b

NT(+,-), and RRT mean the topdressing(have, no)and root rhizosphere restriction respectively.

D: Density; T: root restrains treatment; C: cultivar; N: nitrogen application.

* and ** indicate the difference between RRT and Cont. within sub plot at 5% and 1% significant level respectively using LSD.

$LSD_{0.05}$ is the comparison of CON. or RRT between HD and LD.

With 2007, means of density, cultivars, and treatment, and within cultivars means of nitrogen, density, and treatment in 2008 followed by the different letter are significantly different at 5% level using LSD.

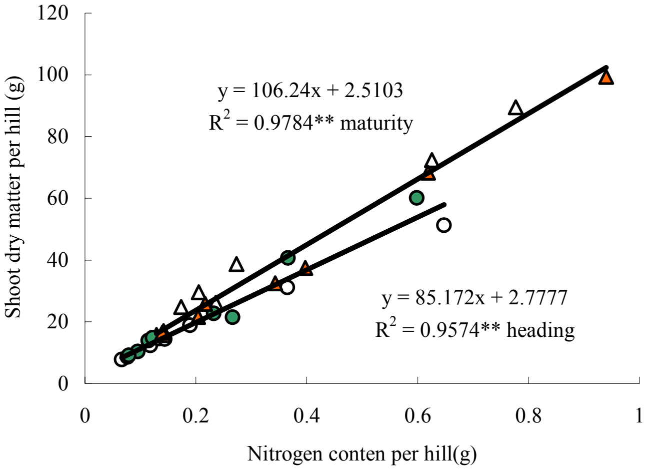


Fig.3-1 Relationship between shoot dry matter and nitrogen content per hill in Akihikari (○, heading; △, maturity) and IRAT109(●, heading; ▲, maturity) in 2008.

3-4 Grain yield and yield components

Grain yields per unit area and per hill were showen in Table 3-5. Grain yield per unit area showed no significant difference between cultivars and between planting densities without root restriction in both years. In 2008, with nitrogen topdressing, both cultivars had higher grain yield than that without nitrogen topdressing. Root restriction severely limited grain yields per unit area and per hill in both cultivars in LD, but not in HD. In 2007, with root restriction in LD, 40% and 53% of grain yields were reduced in Akihikari and IRAT109 respectively. In 2008, without topdressing, 63% and 56% of grain yields were reduced with root restriction in LD in Akihikari and IRAT109 respectively, and with topdressing, the reductions were 51% and 70% of grain yield in Akihikari and IRAT109 respectively.

PN (panicle number m^{-2}) in Akihikari was higher than in IRAT109 in every plot. In 2008, panicle numbers per unit area in Akihikari were same in HD (178 panicles m^{-2}), LD (180 panicles m^{-2}) without root restriction and in HD with root restriction (178 panicles m^{-2}). In IRAT109, panicle number per unit area in LD without root restriction (111 panicles m^{-2}) was similar to in HD with root restriction (148 panicles m^{-2}) and without root restriction (133 panicles m^{-2}). The root restrictions limited PN in both cultivars in LD, but not in HD. In 2007, with root restriction in LD, 44% of PN were reduced in Akihikari and 34% in IRAT109 respectively. In 2008, without topdressing, 61% and 49% of PN were reduced in Akihikari and IRAT109 respectively, and the reduction was 52% and 47% of PN with topdressing in Akihikari and IRAT109 respectively.

Grain number per panicle was higher in IRAT109 than in Akihikari in average of all plots. In 2007 and 2008, Akihikari showed almost no variation in grain number per panicle between HD (100.8 grain $panicle^{-1}$) and LD (107.8 grain $panicle^{-1}$) with and without root restriction. However, IRAT109 had larger number in spikelets number per panicle in LD (164.5 grains $panicle^{-1}$) than in HD (112.9 grains $panicle^{-1}$) without root restriction. In 2007, root restriction reduced grain number per panicle in IRAT109 in LD, but not in HD. In 2008, root restriction reduced grain number per panicle with top dressing in IRAT109. Grain number per panicle was closely related with panicle number per hill in both cultivars (Fig 3-2), the range of grain number per panicle was much larger in IRAT109 than that in Akihikari.

Filled grain percentage, and 1000 grains weight were not affected by density, or RRT, while FG% was reduced due to the root restriction in LD of IRAT109 without topdressing, and it was increased due the RRT in LD of Akihikari with topdressing application in 2008. HI was not affected by density, nitrogen topdressing, or root restriction at all.

Table 3-5 Grain yield per unit area and plant on transplanting density with root restrains in 2007 and 2008.

	Density	Treatmen	Yield (g m^{-2})	Yield (g $hill^{-1}$)	PN(m^{-2})	FG%	GPP	1000-GW	HI	TN($hill^{-1}$)at heading
2007	Akihikari									
	HD	RRT	467.06	10.51	267 *	0.72	100.28	23.89	0.37	6
		Cont.	373.59	8.41	237	0.65	99.08	23.05	0.38	7
	LD	RRT	289.45 **	26.05 **	163 **	0.74	93.43	24.49	0.51	13 **
		Cont.	479.77	43.18	289	0.74	91.34	24.14	0.50	26
2007	IRAT109									
	HD	RRT	428.55	9.64	222	0.64	101.53	30.41	0.42	4
		Cont.	513.28	11.55	237	0.63	112.90	30.49	0.39	5
	LD	RRT	201.24 **	18.11 **	93 **	0.52	116.19 **	32.09	0.41	9 **
		Cont.	430.44	38.74	141	0.56	164.50	33.17	0.45	13
Probability										
C			0.89	0.53	0.21	0.15	0.29	0.00	0.69	0.21
D			0.06	0.00	0.00	0.46	0.09	0.18	0.04	0.00
T			0.01	0.00	0.00	0.83	0.08	0.99	0.95	0.00
C×D			0.16	0.18	0.00	0.14	0.00	0.17	0.09	0.01
C×T			0.12	0.20	0.39	0.58	0.07	0.36	0.86	0.00
D×T			0.01	0.00	0.00	0.53	0.41	0.56	0.49	0.00
C×D×T			0.29	0.93	0.01	0.94	0.41	0.84	0.33	0.00
2008	Akihikari									
N-	HD	RRT	290.56	6.54	178	76.20 *	87.33	23.78	0.41	4
		Cont.	316.93	7.13	178	83.98	90.83	23.88	0.42	4
	LD	RRT	140.25 **	12.62 **	74 **	79.27	99.50	24.73	0.48	7 **
		Cont.	381.68	34.36	159	77.89	111.51	24.30	0.47	14
N+	HD	RRT	501.14 *	11.28	274	72.56	96.37	24.14	0.46	6
		Cont.	565.65	12.73	267	68.69	106.12	24.39	0.43	6
	LD	RRT	209.20 **	18.83 **	100 **	73.92 *	96.09 **	24.64	0.49	9 **
		Cont.	426.27	38.37	263	61.31	118.44	24.32	0.43	24
2008	IRAT109									
N-	HD	RRT	326.41	7.35	148	61.66	97.10	34.63	0.47	3
		Cont.	339.67	7.64	141	64.95	109.38	34.41	0.46	3
	LD	RRT	162.08 **	14.59 **	70 **	56.01 **	148.21	34.73	0.45	6 **
		Cont.	367.32	33.06	113	66.36	144.85	34.40	0.48	10
N+	HD	RRT	430.62	9.69	178	59.00	101.98 **	33.54	0.45	4
		Cont.	481.88	10.84	178	60.06	122.55	33.98	0.42	4
	LD	RRT	141.86 **	12.77 **	72 **	44.76	117.95 **	33.33 *	0.45	7 **
		Cont.	468.21	42.14	144	54.20	160.67	35.05	0.42	13
Probability										
C			0.56	0.95	0.00	0.01	0.00	0.00	0.95	0.00
D			0.00	0.00	0.00	0.17	0.00	0.26	0.35	0.00
T			0.00	0.00	0.00	0.41	0.00	0.67	0.34	0.00
C×D			0.74	0.66	0.29	0.51	0.00	0.70	0.34	0.00
C×T			0.64	0.78	0.00	0.05	0.56	0.49	0.70	0.00
D×T			0.00	0.00	0.00	0.88	0.01	0.98	0.87	0.00
C×D×T			0.33	0.65	0.00	0.06	0.89	0.43	0.44	0.00
N			0.00	0.00	0.00	0.00	0.30	0.59	0.97	0.01
N×C			0.25	0.62	0.00	0.74	0.23	0.40	0.56	0.00
N×D			0.06	0.59	0.11	0.42	0.11	0.94	0.60	0.00
N×T			0.10	0.34	0.00	0.13	0.00	0.31	0.20	0.00
N×C×D			0.45	0.57	0.66	0.58	0.53	0.46	0.55	0.01
N×C×T			0.16	0.18	0.19	0.25	0.03	0.40	0.89	0.00
N×D×T			0.84	0.67	0.00	0.92	0.24	0.64	0.65	0.00
N×C×D×T			0.16	0.18	0.02	0.96	0.17	0.62	0.86	0.00

NT(+,-), and RRT mean the topdressing(have, no)and root rhizosphere restriction respectively.

D: Density; T: root restrains treatment; C: cultivar; N: nitrogen application.

* and ** indicate the difference between RRT and Cont. within sub plot at 5% and 1% significant level respectively using LSD.

$LSD_{0.05}$ is the comparison of CON. or RRT between HD and LD.

With 2007, means of density, cultivars, and treatment, and within cultivars means of nitrogen, density, and treatment in 2008 followed by the different letter are significantly different at 5% level using LSD.

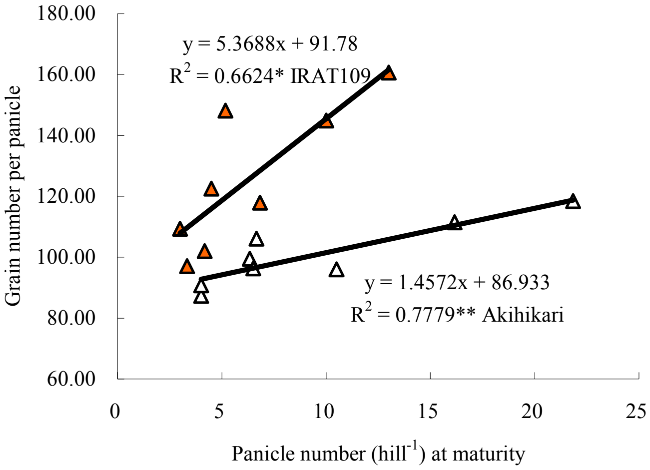


Fig. 3-2 Relationships of GPP to panicle number per hill at maturity in 2008. (△: Akihikari, ▲: IRAT109)

To compare the yield to yield components, simple regression analyses were conducted (Table 3-6 and 3-7). The yields per unit area are closely related to panicle numbers per unit area positively, and the yields per hill are closely related to the panicle number per hill followed by grain numbers per panicle.

Therefore, panicle number per hill was the most important factor related to the variation of yield in different planting density and rhizosphere size, followed by grain number per panicle, Akihikari showed higher variation in panicle number per hill, and IRAT109 showed higher variation in panicle size.

Table 3-6 Simple linear correlation coefficients of the yield (g m^{-2}) and yield components at different cultivars, densities, nitrogen topdressing, and root restriction treatment in 2008.

	PN(m^{-2})	FG%	1000-GW	HI	GPP
Akihikari	0.98 **	-0.54	-0.29	-0.44	0.40
IRAT109	0.89 **	0.49	0.18	-0.38	0.02
HD	0.85 **	-0.31	-0.12	-0.03	0.53
LD	0.80 *	0.01	0.01	-0.43	0.44
NT-	0.76 *	0.11	0.06	0.04	-0.10
NT+	0.85 **	0.35	-0.13	-0.67	0.13
Cont.	0.69	-0.49	-0.03	-0.44	0.23
RRT	0.95 **	0.17	-0.11	-0.26	-0.45

* and ** indicate the significant level at 5% and 1% respectively.

Table 3-7 Simple linear correlation coefficients of the yield (g hill^{-1}) and yield components at different cultivars, densities, nitrogen topdressing, and root restriction treatment in 2008.

	PN (hill^{-1})	FG%	1000-GW	HI	GPP
Akihikari	0.99 **	-0.54	0.33	0.26	0.89 **
IRAT109	0.98 **	-0.03	0.49	-0.12	0.84 **
HD	0.85 **	-0.31	-0.12	-0.03	0.53
LD	0.80 *	0.01	0.01	-0.43	0.44
NT-	0.93 **	0.01	0.03	0.58	0.58
NT+	0.87 **	-0.19	0.01	-0.32	0.71 *
Cont.	0.87 **	-0.38	0.05	0.24	0.70
RRT	0.89 **	-0.02	-0.13	0.62	0.38

* and ** indicate the significant level at 5% and 1% respectively.

The relationships of grain yield per hill and panicle number per hill with nitrogen content at heading and at maturity were shown in Fig 3-3. The yield per hill positively related to nitrogen content per hill, and panicle number per hill also closely related to the nitrogen content per hill at heading and at maturity. The shoot dry matter per hill showed positive relationships to the nitrogen content per hill at heading and at maturity (Fig.3-1). Panicle number per hill and grain number per panicle also showed positive relationships with the nitrogen content per hill at heading. These relations existed in both cultivars.

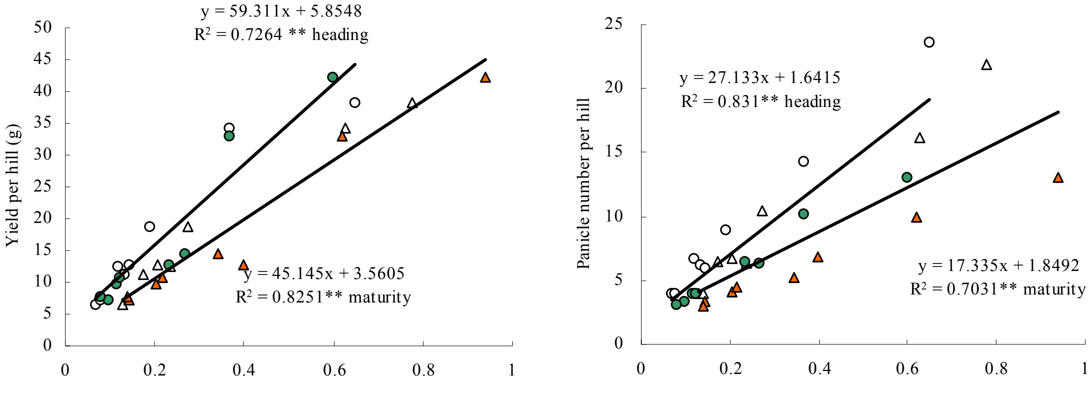


Fig.3-3 Relation of nitrogen content to grain yield per hill $^{-1}$ and panicle number hill $^{-1}$ in Akihikari (○, heading; △, maturity) and IRAT109(●, heading; ▲, maturity) in 2008.

3-5 Spikelet number per panicle

Under different planting density and root restriction treatment, panicle size, grain number per panicle, was shown as important factor as yield component, following to panicle number, especially in IRAT109. The results of detailed panicle traits analysis including the spikelet number per panicle, differentiated spikelet per panicle and spikelet abortion before flowering were shown in Table 3-8.In 2007, in Akihikari, there was no obvious difference among the treatments about the spikelet number per panicle (SPP), differentiated spikelet number per panicle (D-SPP), and the percentage of spikelet abortion, without root restriction. In contrast, in IRAT109, D-SPP was higher in LD than in HD, and spikelet abortion percentage was lower in LD than in HD, consequently, SPP was higher in LD than in HD. In IRAT109, the spikelet number per primary rachis branch was promoted in LD than in HD. In 2008, D-SPP was larger in LD than in HD in both cultivars, and greater promotion in D-SPP was observed in IRAT109 than in Akihikari. The improvements in D-SPP were 53 spikelets and 18 spikelets per panicle in IRAT109 and Akihikari respectively. In both cultivars, there was no difference in percentage of spikelet abortion between in HD and in LD. As a result, SPP was higher in LD than in HD in both cultivars without root restriction.

The root restriction in LD greatly reduced D-SPP and SPP in IRAT109, but not in Akihikari in 2007. In 2008, D-SPP in both cultivars was reduced greatly by root restriction in LD, especially in IRAT109. The percentage of spikelet abortion was reduced by root restriction in IRAT109, but not Akihikari. Root restriction in HD showed no effects on D-SPP and SPP in both cultivars.

With nitrogen topdressing, the D-SPP was increased in both cultivars in 2008, while the SPP were not increased at all because of the simultaneous increase of spikelet abortion percentage, although the increase in Akihikari was not significant statistically.

Therefore, in IRAT109, the increase in the number of differentiated spikelet per panicle was the main determinant of the increase of spikelet number per panicle in LD comparing to in HD. And with root restriction, not only the abortion rate increase but also the reductions of the number of differentiated spikelet per panicle reduced the spikelet number per panicle.

The relationships between spikelet number per panicle to nitrogen content at heading was shown in Fig 3-4. The spikelet number per panicle and differentiated spikelet number per panicle closely related to the nitrogen content per hill at heading, while there was no relation between the spikelet abortion to nitrogen content in both cultivars. It showed that the amount of nitrogen seriously related to the spikelet number per panicle through the spikelet differentiation.

Table 3-8 Spikelet, differentiated spikelet number per panicle, and aborted spikelet percentage on planting density treatment with root restriction of Akihikari and IRAT109 in 2008.

	Density	panicle potential size						panicle size						abortion %	
		P		D-SPP		S/P		P		SPP		S/P			
2007	Akihikari	Cont.	RRT	Cont.	RRT	Cont.	RRT	Cont.	RRT	Cont.	RRT	Cont.	RRT	Cont.	RRT
	HD	10.1	9.7	113.6	112.4	11.3	11.6	9.8	9.3	101.2	97.2	10.3	10.4	11.0	13.5
	LD	8.6	9.3	103.2	101.6	12.0	10.9	8.6	9.2	94.4	95.2	11.0	10.3	8.6	6.3
2007	IRAT109														
	HD	13.0	10.9	147.8	126.0	11.4	11.6	12.1	10.2	113.9	99.7	9.4	9.8	23.0	20.9
	LD	12.1	11.4	187.3	141.8	15.5	12.5	12.0	11.3	165.1	121.4	13.8	10.7	11.9	14.4
Main factor means															
Density	HD	10.9		124.9		11.5		10.3		103.0		10.0		17.1	
	LD	10.4		133.5		12.7		10.3		119.0		11.5		10.3	
Cultivars	AK	9.4		107.7		11.4		9.2		97.0		10.5		9.8	
	IR	11.8		150.7		12.7		11.4		125.0		10.9		17.5	
Treatment	Cont.	10.9		138.0		12.5		10.6		118.6		11.1		13.6	
	RRT	10.3		120.4		11.6		10.0		103.4		10.3		13.8	
LSD$_{0.05}$															
Density		ns		5.12		0.87		ns		14.42		1.21		ns	
Cultivar		0.30		7.65		0.81		0.33		5.97		ns		2.51	
Treatment		0.61		14.16		0.78		ns		15.17		ns		ns	
D*C		0.43		9.06		1.16		0.47		8.45		1.38		ns	
D*T		0.86		14.88		ns		ns		ns		ns		ns	
C*T		0.68		ns		1.12		ns		ns		1.68		ns	
D*C*T		ns		ns		ns		ns		ns		ns		ns	
2008	Akihikari														
NT-	HD	9.6	9.2	107.5	107.0	11.2	11.7	9.5	9.1	92.5	89.2	9.7	9.8	14.5	17.6
	LD	10.0	9.6	129.4	106.3	12.9	11.0	9.7	9.3	115.7	95.7	11.9	10.3	11.9	11.0
NT+	HD	9.4	9.2	124.9	116.2	13.3	12.7	9.3	9.1	101.5	91.6	10.9	10.1	19.2	23.3
	LD	9.9	9.8	138.1	109.9	14.0	11.2	9.8	9.7	118.6	94.6	12.1	9.8	15.7	14.9
Main factor means															
Nitrogen	NT-	9.6		112.6		11.7		9.4		98.3		10.4		13.7	
	NT+	9.6		122.3		12.8		9.5		101.6		10.7		18.3	
Density	HD	9.3		113.9		12.2		9.3		93.7		10.1		18.7	
	LD	9.8		120.9		12.3		9.6		106.1		11.0		13.4	
Treatment	Cont.	9.7		125.0		12.8		9.6		107.1		11.2		15.3	
	RRT	9.4		109.9		11.6		9.3		92.7		10.0		16.7	
LSD$_{0.0}$															
Nitrogen		ns		9.34		0.85		ns		ns		ns		ns	
Density		0.46		5.32		ns		ns		ns		0.42		3.52	
Treatment		ns		5.64		0.54		ns		5.33		0.63		ns	
N*D		ns		ns		ns		ns		ns		1.64		ns	
N*T		ns		ns		ns		ns		ns		ns		ns	
D*T		ns		7.98		0.77		ns		8.86		0.75		ns	
N*D*T		ns		ns		ns		ns		ns		ns		ns	
2008	IRAT109														
NT-	HD	11.1	11.1	128.1	132.8	11.6	11.9	10.9	11.1	106.4	112.8	9.7	10.2	17.1	15.6
	LD	12.5	12.1	184.7	165.6	14.7	13.6	11.9	11.6	145.7	150.8	12.2	13.0	22.1	9.3
NT+	HD	13.5	12.4	160.8	148.9	11.9	12.0	13.1	12.3	117.7	106.7	9.0	8.7	27.3	29.0
	LD	14.4	12.6	211.4	154.5	14.7	12.3	13.8	11.9	162.5	118.7	11.7	10.0	24.5	23.7
Main factor means															
Nitrogen	NT-	11.7		152.8		13.0		11.4		128.9		11.3		16.0	
	NT+	13.2		168.9		12.7		12.8		126.4		9.9		26.1	
Density	HD	12.0		142.6		11.9		11.8		110.9		9.4		22.3	
	LD	12.9		179.1		13.9		12.3		144.4		11.8		19.9	
Treatment	Cont.	12.9		171.3		13.2		12.4		133.1		10.7		22.8	
	RRT	12.1		150.5		12.5		11.7		122.3		10.5		19.4	
LSD$_{0.05}$															
Nitrogen		1.34		12.94		ns		0.83		ns		1.23		7.69	
Density		0.28		8.90		0.62		0.27		9.23		0.68		ns	
Treatment		0.52		9.86		0.53		0.45		ns		ns		2.66	
N*D		1.37		ns		ns		0.86		ns		ns		ns	
N*T		ns		15.51		0.78		ns		16.81		1.44		ns	
D*T		0.59		13.22		0.82		0.90		ns		ns		ns	
N*D*T		ns		ns		ns		ns		ns		ns		ns	

NT(+,-), and RRT mean the topdressing(have, no)and root rhizosphere restriction respectively.

D: Density; T: root restrains treatment; C: cultivar; N: nitrogen application

* and ** indicate the difference between RRT and Cont. within sub plot at 5% and 1% significant level respectively by using LSD.

$LSD_{0.05}$ is the comparison of CON. or RRT between HD and LD

With 2007, means of density, cultivars, and treatment, and within cultivars means of nitrogen, density, and treatment in 2008 followed by the different letter are significantly different at 5% level using LSD.

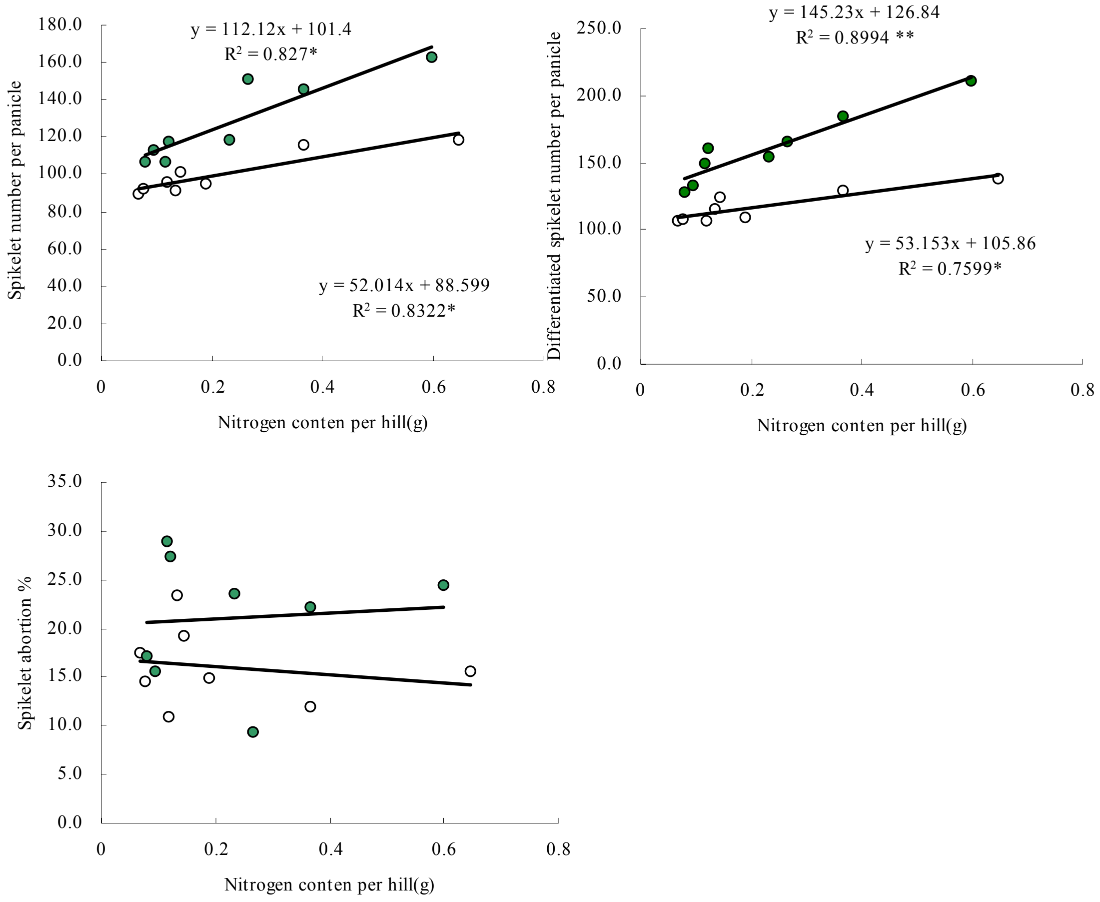


Fig.3-4 Relation of nitrogen content at heading to spikelet per panicle, differentiated spikelet number per panicle and spikelet abortion percentage of Akihikari (○) and IRAT109 (●) in 2008. * and ** indicate the significant level at 5% and 1% respectively.

4 Discussion

4-1 Yield and its components under the treatments

Panicle number showed closely positive relationships to yield production irrespective of cultivars, treatments, densities, or topdressing (Table 3-6 and Table 3-7, Wu et al., 1998; Jones et al., 1978). Similar panicle number m^{-2} in HD and LD in Akihikari, and the little difference of SPP between the planting densities, resulted into the similar grain yield between the two planting densities in Akihikari. While in IRAT109, with the reduction of panicle number m^{-2} in LD as comparing to HD, GPP and SPP was more increased in LD compared to HD (Table 3-8), resulting into the same grain yield in both cultivars between the HD and LD. As compensation, when the panicle number per unit ground area was less, the grain number per panicle was higher (Jones et al., 1978), IRAT109 in the present experiments.

The root restriction in LD reduced panicle number per hill evidently in both cultivars. Panicle number per hill was reduced by 52.1% in Akihikari and 59.6% in IRAT109 in LD respectively. Panicles were relatively smaller comparing to control. Grain number per panicle was reduced by 10% (97.9 versus 107.8) in Akihikari and by 17% (118.8 versus 142.8) in IRAT109. Grain yield reduced nearly 50% (212.95 g m^{-2} versus. 429.26 g m^{-2}) in Akihikari and 53% (190.84g m^{-2} versus 408.01g m^{-2}) in IRAT109 as compared to control plots. So both of the panicle number per hill and panicle size, as two main mediators for grain yield, were reduced significantly by the root restriction in LD, while, they were similar in HD with and without root restriction. Consequently, the yield per unit area in plots with root restriction in LD was lowest as compared to other plots.

From the comparison between the two planting densities without restriction of root, the panicle number per plant was limited due to high planting density. Panicle number per plant was reduced 74.5% in Akihikari and 64% in IRAT109. Panicles were also relatively smaller in HD than in LD. Grain number per panicle in high density compared to that in LD, reduced 6.5% (100.75 versus 107.82) in Akihikari and 27.8% (114.93 versus 159.20) in IRAT109. So the panicle number per hill and spikelet number per panicle were reduced by high planting density. The result, that, the root restriction reduced the panicle number per hill and panicle size in LD but not in HD, can be explained partly by the reduction of rooting zone size in HD than in LD. With comparison between panicle number per plant in LD with the root restriction and in HD without root restriction, it was less in HD without root restriction than in LD with root restriction irrespective of the cultivars, topdressing and planting density. SPP and D-SPP showed similar between them. In 2008, in plots without topdressing of IRAT109, SPP and D-SPP were larger in LD with root restriction than in HD without root restriction. While without root restriction, panicle size was larger in LD than in HD companying with the increase of panicle number per hill. With root restriction, the panicle size enlargement was inhibited. These results indicated that rooting zone size of plants could influence the panicle size as same as panicle number, and the effect was companied by the nitrogen condition or nitrogen uptake by plants. It was reported that the cultivars with thicker crown root diameter and deeper elongation into soil, always had larger panicle size (Li et al., 1970; Morita et al., 1987a, 1987b). And in high planting density, root diameter was thinner and distributed more in shallow soil layer (Xie et al., 2006). So it is possible that root restriction will reduce the root diameter or distribution in the deep soil resulting into the small panicle size. The root number per plant was positively related to the stem number per plant in rice (Matsuo and Hoshikawa, 1993). However, root diameter or distribution is not related to panicle number per hill because rice plants having many stems always had large number of adventitious roots with small diameters (Morita et al., 1987a). So the compensation among the root characters, root number, root diameter, or distribution in the soil, may play some roles in the mediation for compensation relationship between the panicle number and panicle size. The root characters and distribution under planting density effects relating to panicle characters should be studied.

In 2008, the more nitrogen was applied to the plants with root restriction in LD, there was no obvious improvement in yield in IRAT109. However for Akihikari, PN hill $^{-1}$ was increased without the SPP reduction, resulting in the improvement in grain yield (Table 3-5). So, the amount of nutrients uptake by root under different planting densities, was responsible for shoot growth and genotype difference exists in this response.

4-2 Dry weight accumulation, panicle number hill $^{-1}$, panicle size and nitrogen uptake

Dry weight was reported to be related to the tillering ability closely in rice (Wu et al., 1998). The greater tillering ability caused more dry matter accumulation. Panicle number was closely related to tiller number (Wu et al., 1998). Dry matter m^{-2} in this experiment, was worst with root restriction in low density because the poorest panicle number m$^{-2,}$ resulted by small panicle number hill $^{-1}$. At heading, the total shoot dry matter was positively related to the panicle number hill $^{-1}$ in both cultivars (linear regression, R^2= 0.9714, $P < 0.01$, in Akihikari; R^2= 0.9821, $P < 0.05$ in IRAT109, data not shown). While, at maturity, the shoot dry matter m^{-2} was significantly related to panicle number m^{-2} in both cultivars. It was showed more clearly in Akihikari than IRAT109. It was probably that the greater difference among the tillers within hill in IRAT109 than Akihikari, the dry weight accumulation was more depended on the tiller size than tiller number in IRAT109. So, tiller size, should be paid attention in functioning to dry weight accumulation.

The nitrogen content per hill was positively related to shoot dry matter per hill closely at heading (R^2 = 0.9574, $P < 0.01$) and at maturity (R^2 = 0.9784, $P < 0.01$) (Fig.3-1). Lemaire et al. (2007) reported that the nitrogen uptake was co-regulated by both soil N supply and biomass accumulation, and the relation between the nitrogen uptake and dry weight accumulation reflects the feed-back regulation of nitrogen absorption capacity of roots by shoot growth (Lemaire, et al., 2007). In the experiment, the nitrogen uptake and dry weight accumulation were limited by the root restriction in low density, just indicating that the changes on rooting zone size effected on the shoot growth and dry weight accumulation through changing the nitrogen uptake by roots. This just evidenced that the competition on rooting zone play roles in the regulation of nitrogen accumulation by shoot effecting on the dry weight accumulation and yield production.

Panicle number per hill and spikelet number per panicle were closely related to the nitrogen accumulation per hill at heading (Fig.3-3 and Fig.3-4). The spikelet production efficiency was improved by high nitrogen content through shoot dry matter increase (Kobayashi et al., 2003). So the high nitrogen content may improve both tillering ability and spikelet production. Both the increase in differentiated spikelet number per panicle and reduction in aborted spikelet number per panicle improved the spikelet number per panicle, However, the increase in spikelet number per panicle was mainly depended on the increase of differentiated spikelet number per panicle (Table 3-8).

4-3 The possible role of root restriction in the tiller production and spikelet number per panicle determination

The root restriction limited both of the spikelet number per panicle and tiller number per hill, especially in the LD (Table 3-8, Table 3-3), There was evident increase of tiller abortion percentage by root restrictions in LD with nitrogen topdressing application, but not in the condition of without nitrogen topdressing (Table 3-3). The tillering was limited by root restriction although the nitrogen supply from soil was improved. As induced in the discussion 2, the spikelet number per panicle had closely positive relations to the tiller number per hill at heading, mainly through influencing on the nitrogen accumulation. This indicated the stress of soil volume had the limitation for tiller survival, irrespective of the amount of nitrogen supply from the soil.

In the experiment, the nitrogen concentration in shoot was higher and similar with RRT in LD than RRT in HD in IRAT109 and Akihikari respectively (Data not shown). Although the high nitrogen concentration in shoot in IRAT109, the tiller number per hill was still small. The nitrogen uptake efficiency could be affected by root volume size (Akita et al., 1993), and shoot nitrogen concentration had positive effects on the tillering (Zhong et al., 2003). It was reported that, the tiller should produce more than 3 roots to guarantee the survival (Matsuo and Hoshikawa, 1996). So it might be that, the restriction on root volume, could not supply enough space for root growth and result into the higher abortion of young tiller than that in controls. So the nitrogen use efficiency (reciprocal of nitrogen concentration) was lower in the RRT than in the Cont. It should be that, the root restriction on soil volume per plant, through effecting on the nitrogen use efficiency for tillering and dry matter production. Because of the lower nitrogen use efficiency due to the root restriction, the plants with small root volume size had the smaller plant size in leaf area, tiller height, tiller number and so on (Table 3-3). Without the root restriction, the crown root number per tiller was clearly higher in HD than in LD in both cultivars. So viewed from the competition, the small root volume size in the high density as comparison with low density, produced more crown root number per tiller to improve the uptake efficiency of nitrogen in soil and nitrogen use efficiency was also improved. And also, the cultivars difference response to the root restrains treatment should be due to the genetic difference in nitrogen use efficiency. It was cited that the root traits in morphology, root vigor, and root metabolism should be related to the plant nitrogen use efficiency (Garnett et al., 2003), so the root trait variation due the root volume limitation should be investigated.

Chapter 4 QTL analysis of panicle size under two nitrogen conditions

1 Introduction

As the previous results in Chapter 3, the panicle size, especially the differentiated spikelet number per panicle, was enlarged by nitrogen application, and the improvement in differentiated spikelet number per panicle could contribute to the yield production. In addition, the plants grown in rich nitrogen soil, the competition with neighbors would be less than plants in the soil with poor nitrogen. The released competition would have some effects on the morphological variation of plants which had been certified to be related to the spikelet number per panicle and differentiated spikelet number per panicle (Chapter 2). However, the varietal differences were also observed. Differentiated spikelet number per panicle in IRAT109, as compared to Akihikari, showed more obvious increase due to the nitrogen application (Chapter 3). The genetic variation of plant nitrogen use has existed widely (Senthilvel et al., 2008; Kobayashi et al., 2008; Namai et al., 2009), while genetic basis of the panicle size of rice response to nitrogen topdressing is not clear. Although the genetic basis had been researched under different location, years, planting density, and water irrigation, the genetic basis of panicle size formation under different nitrogen condition has not been clarified.

Recently, many quantitative trait loci (QTLs) relating to panicle size were reported (Yagi et al., 2001; Xing et al., 2002; Kato et al., 2004; Kobayashi et al., 2004, 2006; Yamgishi et al., 2004; Wei et al., 2006; Zhang et al., 2006 Anto et al., 2008; Xing et al., 2002, 2008; Kato et al., 2009; Zhang et al., 2006, 2009). Partitioning of panicle size into the underlying morphogenetic components would be helpful in understanding the complicated genetic control of panicle size (Yamagishi et al., 2004). QTLs for the panicle size components including primary rachis branch and spikelet number on it, were also detected (Yamagishi et al., 2004, Ando et al., 2008, Kato et al.,

2009) Though QTLs of the preflowering spikelet abortion percentage were also detected in Yamagishi et al. (2004) and Kato et al. (2009), it was inferred that the stability of these QTLs for %FA should be estimated under different environmental conditions (Yamagishi et al., 2004).

The phenotypic expression of complicated traits is generally affected by both environmental effects and pleiotropic effects of genes (Xing et al., 2002; Piepho et al., 2005; Anto et al., 2008). It was also cited that single QTL was sensitive to environment. So the genotype × environment interaction and pleiotropism are both important factor to influence the QTLs expression (Zhuang et al., 1999). Panicle size has complicated characteristics such as it is affected by both branching system and spikelet development on it (Yamagishi et al., 2003)

So in this study, by using a 105BILs derived from the cross of temperate japonica and tropical japonica, genetic basis of the panicle size and its components under two levels nitrogen application was investigated.

2 Materials and methods

2-1 Mapping population and field design

The 105BILs set used in the experiment derived from the cross between ‘Akihikari’ and ‘IRAT109’. In 1998, ‘Akihikari’ (as the maternal parent) was crossed with ‘IRAT109’, and in 1999, a resultant F_1 plant (as the maternal parent) was backcrossed with ‘Akihikari’. From the resultant BC_1F_1 (Akhikari/IRAT109/Akihikari) population, the BILs were developed by the single-seed descent method. After surveying about 650 simple sequence repeat (SSR) markers, the resultant 105 lines were genotyped with a selected set of 112 polymorphic marker, with an average distance between markers of 14.6 cM (Yamagishi et al., 2004).The BC_1F_8 and BC_1F_9 of the 105BILs set were used in 2006 and 2007 respectively. The field experiments were conducted at farm of the University of Tokyo, Nishitokyo, Japan. The fields were divided into 6 blocks, using plastic board inserted into soil 20cm. The 6 blocks were ranged randomly and separated into 2 groups, 3 blocks for high nitrogen level as 3 replications, and 3 blocks for low nitrogen level for each large plot as 3 replications. For each block, seeds of 105BILs and their parents were sown on 18th in April in green house, and seedlings were transplanted in 18th in May in both years with transplanting distance 15cm×30cm. Before the transplanting, chemical compounds fertilizer 50 kg ha $^{-1}$ (N : P_2O_5 : K_2O = 60:90:80 kg ha $^{-1}$)) was applied in all of plots. 30days after transplanting, Ammonium sulfate (N= 20 kg ha $^{-1}$) was applied for 5 times as interval of 2 weeks in high level nitrogen plots during the growth period, N= 160 kg ha $^{-1}$ was used totally. No topdressing in low level nitrogen plots.

2-2 Panicle characters measurement

The panicle size could be counted as the sum of survived and aborted differentiated spikelet number per panicle. A aborted spikelet number could be easily recognized at the mature panicle according to the vestiges remained (Matsushima, 1966; Ishii, et al., 1988). So the panicle size, differentiated spikelet number per panicle (D-SPP) is easily counted using the mature panicle.

At the maturity, two plants of each line and their parents in each plot were harvested and the panicles on main stem were used to check the panicle characters including the panicle size characters as differentiated spikelet number per panicle (D-SPP) including the survived and aborted spikelet before flowering, and branch number of primary rachis per panicle (BPP), spikelet number per primary rachis branch (SPB) was calculated as the D-SPP/BPP, and spikelet abortion percentage before anthesis (A%) was calculated as ratio the aborted spikelet to SPP. The means of 6 panicles (2 panicles × 3 replications) were used for QTL analysis. Two factors variance analysis (ANOVA) was conducted. Broad-sense heritability was calculated as $h^2 = (MS_G - MS_e) / MS_G$ based on the ANOVA analysis. MS_G is the mean square of lines, and MS_e is the means square of error.

2-3 Map construction and QTL analysis

Linkage analyses were performed with MAPL, using the "BC_1F_1-derived RI mode" (Ukai et al., 1995). QTLs were detected by composite interval mapping using

Windows QTL Cartographer, version 2.0 (Wang et al., 2003). The significant threshold was estimated by performing 1000 permutations (Chruchill and Doerge 1994) of each character ($P<0.05$) as implemented by QTL cartographer.

3 Results

3-1 Traits variations

All of the traits were distributed as continuously in 105BILs and transgressive segregation was observed for all characters (Fig.4-1.). The ANOVA results showed the significant difference in genetic variation in 105BILs (Table 4-1). Nitrogen topdressing had significant effects on D-SPP and showed no effects on A% in both years, while the nitrogen effects on SPB was observed only in 2006, and on BPP in 2007. The interactions effects of genetic variation and nitrogen topdressing effecting were only observed on A% and BPP in 2007. All of traits showed high h_B^2 in two years (Table 4-1).

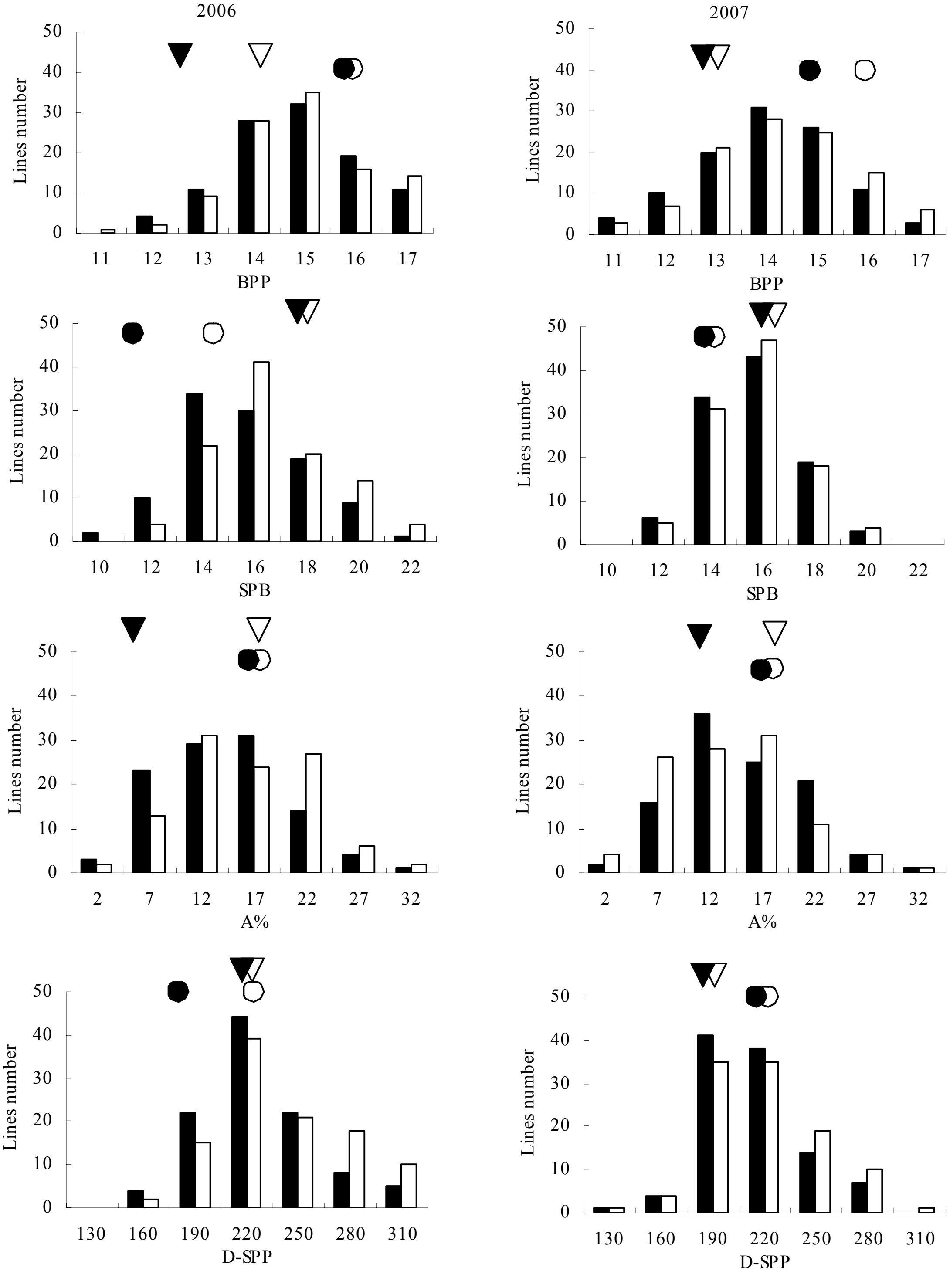


Fig.4-1. Panicle characters distribution in 105BILs under two nitrogen levels (Black bar: LN; Blank bar: HN) in 2006 and 2007. (▼, Akihikari LN; ▽: Akihikari HN; ●: IRAT109 LN; ○: IRAT109 HN)

Table 4-1. Panicle characters of parents (Akihikari(A) and IRAT109(I)), and 105 back cross lines (BILs) under two nitrogen levels(LN and HN) in 2006 and 2007. Broad-sense heritabilities (h^2) and effects of genotype (G), nitrogen (N) and interactions between genotype and nitrogen (G×N) were shown.

	LN					**HN**					**Significant effects**		
	A	**I**	**BILs**	**Range**	h^2	**A**	**I**	**BILs**	**Range**	h^2	N	G	G×N
2006													
BPP	12.7	15.3	14.4	11.0 — 19.5	0.90	13.5	15.2	14.5	10.0 — 19.0	0.91	n.	**	n.
SPB	15.9	12.2	14.8	9.0 — 23.5	0.93	16.3	13.5	15.6	9.6 — 24.3	0.92	**	**	n.
A%	4.1	12.5	11.8	0.0 — 41.7	0.84	13.0	12.3	13.4	0.0 — 35.1	0.82	n.	**	n.
D-SPP	200	188	213	134 — 355	0.93	220	205	225	139 — 356	0.92	**	**	n.
2007													
BPP	12.3	15.3	13.6	8.0 — 17.5	0.87	12.3	14.9	13.9	8.0 — 18.0	0.89	**	**	*
SPB	14.3	13.1	14.6	9.5 — 23.9	0.87	14.6	13.9	14.8	9.7 — 21.2	0.86	n.	**	n.
A%	5.3	10.2	12.6	0.0 — 38.2	0.80	7.8	8.6	11.2	0.0 — 31.7	0.82	n.	**	**
D-SPP	176	200	198	121 — 299	0.88	180	208	204	113 — 303	0.91	*	**	n.

n, *, and ** means not significant, 0.05 level, and 0.01 level significant respectively

3-2 QTLs for panicle characters

Totally, 11 QTLs and 12 QTLs were detected in LN and HN in two years respectively (Table 4-2 and Fig.4-2.). Among of them, the two QTLs for D-SPP were harbored at the same genomic regions on chromosome 5 (RM334-RM7271) and on chromosome 6 (RM454-RM1370) in both years and both nitrogen conditions. Both of them larger responsibility for the phenotypic variations, QTL on chromosome 5 could explain the phenotypic variation for 22.0%(LN, 2006), 23.2% (HN, 2006), 23.7%(LN, 2007) and 24.3(HN, 2007) and QTL on chromosome 6 could explain the phenotypic variation for 11.1%(LN,2006), 15.5(HN,2006), 21.9%(LN,2007), and 27.0(HN,2007). One QTL for D-SPP was only posited on chromosome 1 (RM7383-243) in 2006 under two nitrogen levels. Although it was not observed in 2007, it could explain the 12.5% and 20.7% phenotypic variation in LN and HN respectively. The allelic contribution on chromosome 5 was from 'Akihikari', while allelic contribution on chromosome 6 and 1 was from 'IRAT109'.

One QTL for BPP was detected repeatedly on chromosome 5 (RM3790-RM334) under LN in two years and it was also detected under HN only in 2007. While several other QTLs for BPP were located at some genomic regions such as QTLs on chromosome 1, 6, and 10 in LN and chromosome 1 in HN. There were two QTLs, with different position on chromosome 6 for SPB detected only under HM in both years consistently while they were not detected in LN. QTLs for A%, located at the chromosome 1 (RM1297-RM297) and chromosome 3 (RM231-RM3864), were detected in both LN and HN in 2006 and in LN in 2007. QTL on chromosome 4 and 11 were also found for A% under LN in 2006 and 2007 respectively, while QTLs on chromosome 1 and 7 were found only under HN in 2007.

Table 4-2. Location, peak LOD, additive effects, and percent of the phenotypic variation explained (R^2) for QTLs detected for rice panicle characters in backcross inbred lines from the cross 'Akihikari' × 'IRAT109' across two N treatments for 2 years.

	Chr.	Marker	Marker interval	Position[a]	Peak LOD	R^2 (%)	Add. effect[b]
2006							
Low-N treatment							
D-SPP	1	2	RM7383-RM243	3.5	4.00	12.5	-13.6
D-SPP	5	9	RM334-RM7271	0.0	8.11	22.0	19.7
D-SPP	6	6	RM454-RM1370	18.0	3.23	11.1	-13.3
BPP	1	8	RM297-RM3447	6.0	3.47	12.3	-0.51
BPP	5	8	RM3790-RM334	4.5	3.15	11.0	0.52
BPP	10	6	RM258-RM171	0.0	3.45	10.1	0.49
A%	1	7	RM1297-RM297	6.0	3.75	13.4	-2.5
A%	3	2	RM231-RM3864	0.0	3.56	11.3	2.1
A%	4	2	RM335-RM5953	0.0	3.12	9.0	-2.0
High-N treatment							
D-SPP	1	2	RM7383-RM243	6.0	6.48	20.7	-18.3
D-SPP	5	9	RM334-RM7271	0.0	8.37	23.2	21.3
D-SPP	6	6	RM454-RM1370	14.0	4.06	15.5	-16.3
BPP	1	4	RM23-RM9	25.5	4.82	19.1	0.68
BPP	5	1	RM7029-RM267	0.0	4.47	13.6	0.65
SPB	6	2	RM225-RM276	11.0	3.90	12.3	1.02
SPB	6	6	RM454-RM1370	13.0	4.19	23.4	-1.27
A%	1	7	RM1297-RM297	6.0	3.18	10.3	-2.3
A%	3	2	RM231-RM3864	0.0	5.83	18.3	2.8
2007							
Low-N treatment							
D-SPP	5	9	RM334-RM7271	0.0	8.47	23.7	16.4
D-SPP	6	6	RM454-RM1370	9.0	5.64	21.9	-14.6
BPP	1	4	RM23-RM9	22.5	3.73	19.6	0.72
BPP	5	8	RM3790-RM334	1.5	3.30	10.1	0.54
BPP	6	2	RM225-RM276	12.0	5.13	16.0	-0.67
A%	1	7	RM1297-RM297	6.5	9.14	29.0	-3.9
A%	3	2	RM231-RM3864	0.0	5.10	14.3	2.4
A%	11	2	RM332-RM5599	3.5	3.32	11.2	-2.3
High-N treatment							
D-SPP	5	8	RM3790-RM334	6.5	9.12	24.3	18.3
D-SPP	6	6	RM454-RM1370	12.0	6.01	27.0	-18.1
BPP	5	8	RM3790-RM334	3.5	5.31	19.0	0.73
SPB	6	2	RM225-RM276	6.0	3.43	12.0	0.73
SPB	6	6	RM454-RM1370	15.0	4.91	21.9	-0.93
A%	1	8	RM297-RM3447	7.0	3.17	10.5	-2.2
A%	7	8	RM8249-RM5720	0.0	3.43	11.3	2.4

a; Distance from the left franking marker in cM

b; Positive value show that allelic contribution is from 'Akihikari' and negative values from 'IRAT109'

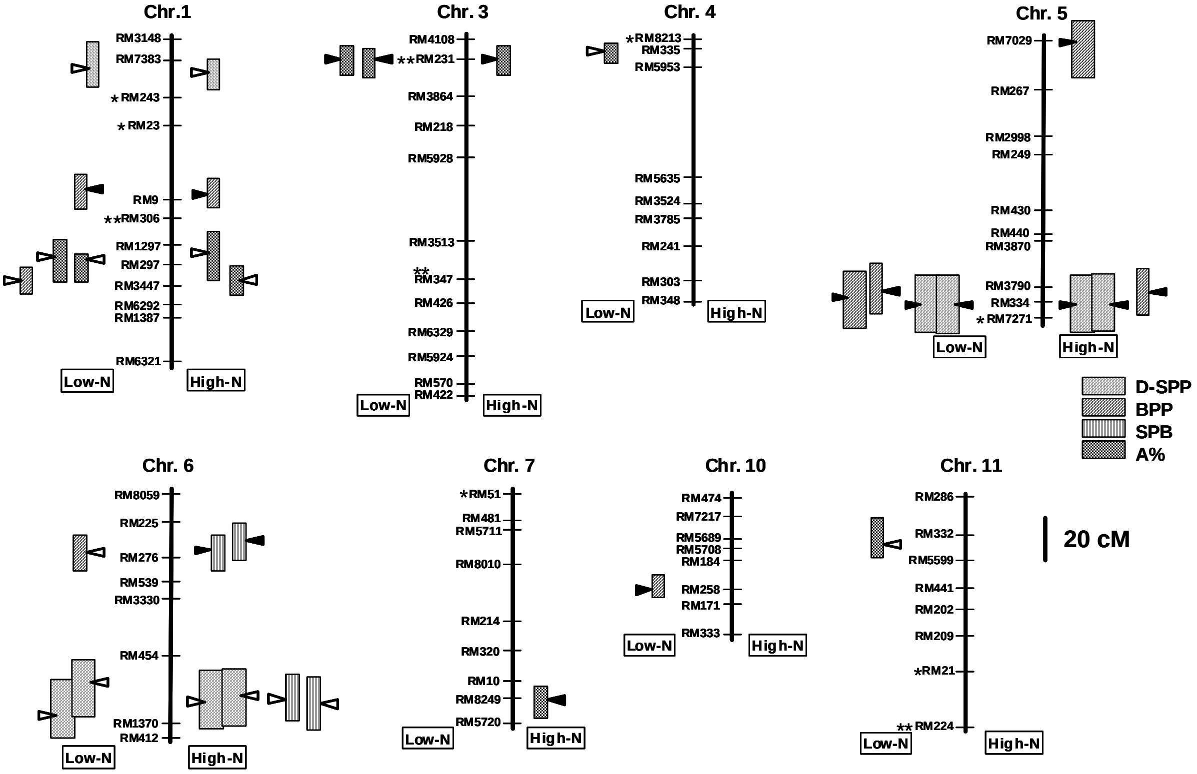


Fig.4-2. Chromosomal locations of QTLs for panicle traits. Bars to the left and right of the chromosomes indicate 1-LOD likelihood genomic regions in Low-N (left) and High-N (right) treatments. The arrowheads to the left and right of the bars indicate the position of the peak LOD in the genomic region in 2006 (left) and 2007 (right). Black arrowheads indicate allelic contribution from ‘Akihikari’; white arrowheads, ‘IRAT109’. Segregation distortion from the expected ratios is based on the chi-squared test at *P* = 0.05 (*) and *P* = 0.01 (**).

4 Discussion

Stable QTLs responsible for panicle characters (2 QTLs for FPP, 1 QTL for BPP and 2 QTLs for A%) were constantly detected in present experiment, such as QTLs on chromosome 5 and chromosome 6 for D-SPP, QTL on chromosome 5 for BPP, and

QTLs on chromosome 1 and 3 for A% irrespectively the years or nitrogen conditions. Especially the QTLs for D-SPP, on chromosome 5 and 6, they were also detected by using same 105BILs under different irrigation conditions by Kato et al. (2009), these QTLs detected irrespective of the environmental variation, just illustrated strong genetic effects of these QTLs on the D-SPP in rice. In contrast to that, few stable QTLs specific to one environmental condition were detected. The same QTLs for SPB, were detected under the HN in both 2006 and 2007, but not in LN.

QTLs for D-SPP and for SPB were co-located on chromosome 6(RM454-RM1370), therefore this genomic region was not only contribute to D-SPP, but also SPB under HN condition in this study. This just signed the close relationship should be existed between the D-SPP and SPB. Because the more stable in floret on primary rachis directly, the floret on the secondary rachis is contributed importantly to the SPB, and also it had been certified that the close relations between the spikelet number on secondary rachis and D-SPP by Kobayasi et al. (1997).

Co-location QTLs for different characters will help us to understand the relationship between the morphological traits. By using the same BILs in the same experiment in 2006 (Ogasawara, 2007), QTLs for D-SPP on chromosome 5 (RM334-RM7271) and 6 (RM454-RM1370) detected were also found to responsible for panicle number and grain weight which are important traits for yield production, and QTL for D-SPP on chromosome 1 (RM7383-RM243) was also found to be related to filled grain percentage at the maturity; these results just inferred the relations between the panicle size and panicle number, panicle size and grain filling degree during the filling stage. Simultaneously, the QTLs for A % on chromosome 3 were also responsible for the filled grain percentage. With the comparison between the QTLs for SPAD value for the flag leaf at heading in same BILs, A % should be related to the leaf photosynthetic capacity traits at heading and the growth days before heading. This just indicated genetic reasons that the source ability before heading was important grantee for the spikelet survive.

General discussion

In the thesis, the main study was focused on the spikelet number per panicle based on the different transplanting densities. T The relations between the spikelet number per panicle and panicle number in plant are discussed with two points follow.

1. The spikelet number per panicle within one plant

Spikelet number per panicle of each panicle within one plant was ranged as decline with the panicle order ascending. The panicle order of spikelet number per panicle in the plant was determined by the panicle orders of differentiated spikelet number per panicle and panicle order of aborted spikelet number per panicle. This conclusion was drawn from the studies for 16 cultivars (Chapter 1) and 5 gave cultivars with 3 transplanting densities (Chapter 2-1). The panicle order of spikelet number per panicle was attributed by the tillering sequence and closely related to the leaf area per tiller (Sheehy, 2001). The flowering priority of tiller was depending on the order, rank and emergence time (Sylvie and Dauzat, 2005). The relationships among the tiller especially the leaf growth relationships should be most possible response to spikelet number per panicle relations within one plant in rice (Tivet, F., et al., 2001; Sylvie and Dauzat, 2005). In Chapter 1, the close relations were observed between the spikelet numbers per panicle on main stem and on tillers (Fig. 1-1). Average spikelet number per panicle was positively related to the spikelet number on the main stem. In Chapter 2, there were close positive relations between the leaf area and spikelet number per panicle were observed (Fig. 2-1-4). The markedly different leaf growth pattern existed between the tillers and main stem in rice (Tivet, et al., 2001). And the leaves on tillers developed synchronously to the leaves on the main stem, and tiller growth was related to the main stem development stage (Matsushima, 1966; Sylvie, and Dauzat, 2005). In this study, it was evidenced that the lower order tillers could provide ‘help’ to the higher order tillers during the panicle initiation stage and panicles of higher orders could produce more spikelet than they could afford afterwards. So the relations among the tillers during the panicle development process should not only between the main stem and tillers, but also among the tillers. Though this reason could explain the results in Chapter 2 (Fig. 2-1-3 and Fig.2-1-5), the expansion of leaves on the tillers, especially the leaves on the top 3 on the tillers with high orders, should also response for the spikelet abortion before anthesis. It was because that the 3 top leaves expanded during the panicle development duration (Tivet, et al., 2001; Sylvie, and Dauzat, 2005, Xin, and Kropff, 1998), and competed the assimilates with the panicle initiation or spikelet growth which would influence the spikelet number at anthesis. In this study, the leaf area of top 3 leaves at heading showed positive relations to the aborted spikelet number per panicle before anthesis (Fig. A). Differentiated spikelet number per panicle (D-SPP) and aborted spikelet number per panicle (A-SPP) were more closely related to leaf area of the third leaf from top than other 2 leaves. Beside this, the duration of panicle development was also pointed to be related to the spikelet number per panicle at heading, because it would influence the dry matter production (Gonzalez, et al, 2005) and the tiller dry matter at heading was reported to closely related to the spikelet number per panicle positively (Shiratsuchi, et al., 2007).So the difference of the panicle development duration among the tillers should be investigated.

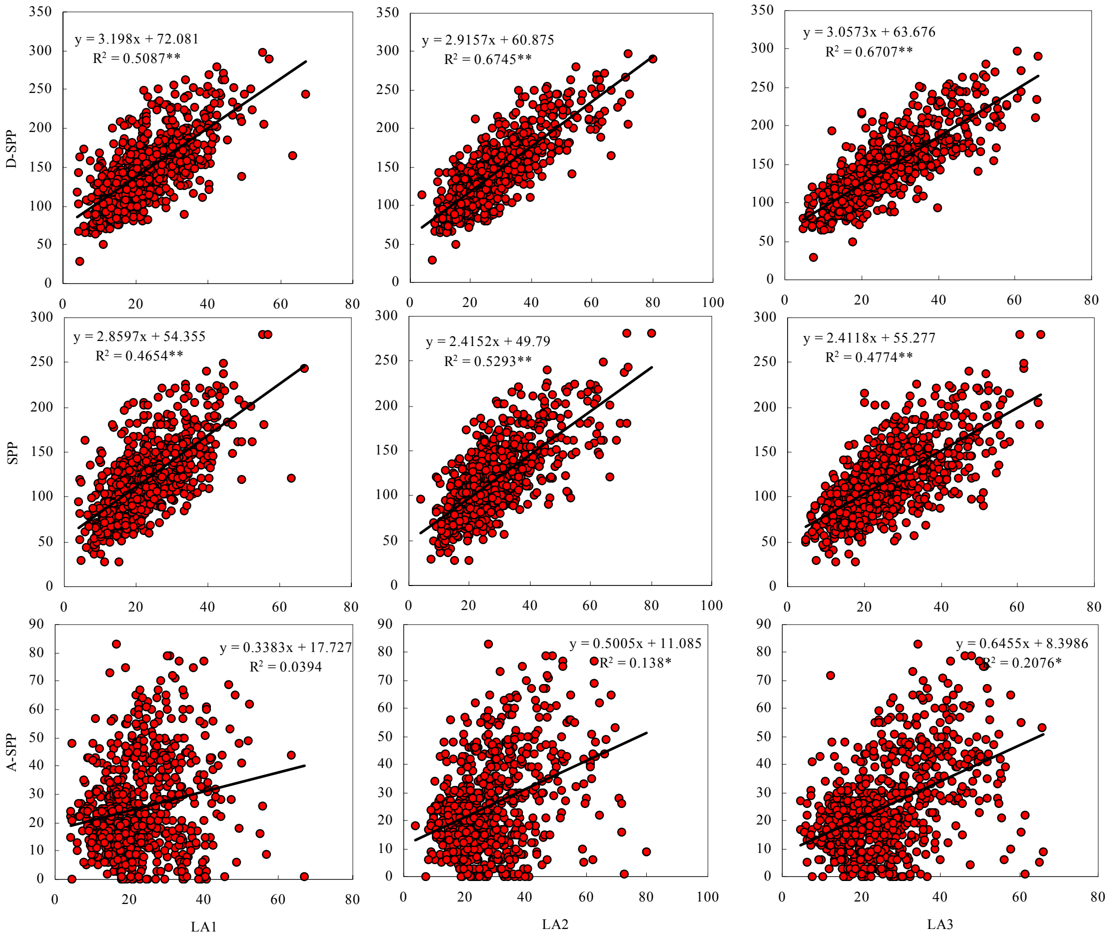


Fig. A The relations between the D-SPP, SPP and A-SPP to the leaf area. LA1: flag leaf; LA2: down next to the flag leaf; LA3: the third leaf from the top. *and ** indicated the significant level at 0.05 and 0.01 respectively.

2. The spikelet number per panicle of plants with the root restriction

In order to investigate the function of below ground part to the spikelet number per panicle and the response to panicle number per hill, the root restriction experiment was designed (Chapter 3). According to the results, the spikelet number per panicle was increased due to the improved nitrogen uptake, which would promote the dry matter production and increase the spikelet number per panicle. The root restriction treatment limited the nitrogen uptake greatly, and dry matter was small, so the spikelet number per panicle was small. It was clearly shown that there was closely positive relation between the nitrogen absorption and spikelet number per panicle in both cultivars, Akihikari and IRAT109 (Fig. 3-4). Kobayasi (2001) had reported the positive relation between the shoot nitrogen concentration and spikelet production. However, in the present study, the spikelet number per panicle was not improved efficiently with higher shoot nitrogen concentration, and this was genotype dependence. In IRAT109 with the root restriction in low planting density, the shoot nitrogen concentration was higher than the controls, but the spikelet number per panicle was less than the control in low planting density (Fig. B and Table 3-8). But this was different in Akihikari which had higher nitrogen concentration in plats of controls than that with root restrictions in low planting density (Fig. B). This might be explained by the nitrogen use efficiency was limited by the root restriction because the nitrogen use efficiency for dry matter production was reciprocal of the nitrogen concentration. It was reported the leaf expansion and shoot growth activity could drive the nitrogen uptake (Lemaire, et al., 2007; Peng, Y., 2010). So it might be that the shoot growth was limited by the root restriction and influenced on the leaf expansion and dry matter production. However, the physiological process of the root restriction influencing on shoot growth was not clear. Hormones such as Abscisic Acid (ABA) was reported to reduce the spikelet number per panicle under water stress condition (Morgan, J.M., 1980), and it was also reported the influence only happened after the anthesis (Setter, T.L., et al., 2001). Cytokinins could improve the grain production due to the promotion of dry matter, GA was reported to improve the spikelet number per panicle through the improvement of SAM (shoot apical meristem), plant height and dry matter production (Motoyuki, A., et al., 2005; Wang, Y., et al., 2006; Mu, S., et al., 2001; Yamagishi, J., et al., 1994). ABA and Cytokinins are mainly produced by the root. So the restriction on root development would be regenerate the response of these hormones and result into the small plant size and lower dry matter production.

Both in Akihikari and IRAT109, The plants in low planting density had higher nitrogen concentration than plants in the higher planting density, this was because of the high nitrogen use efficiency due to the more quickly and earlier roots proliferation in high planting density than in low planting density (Fig. B).

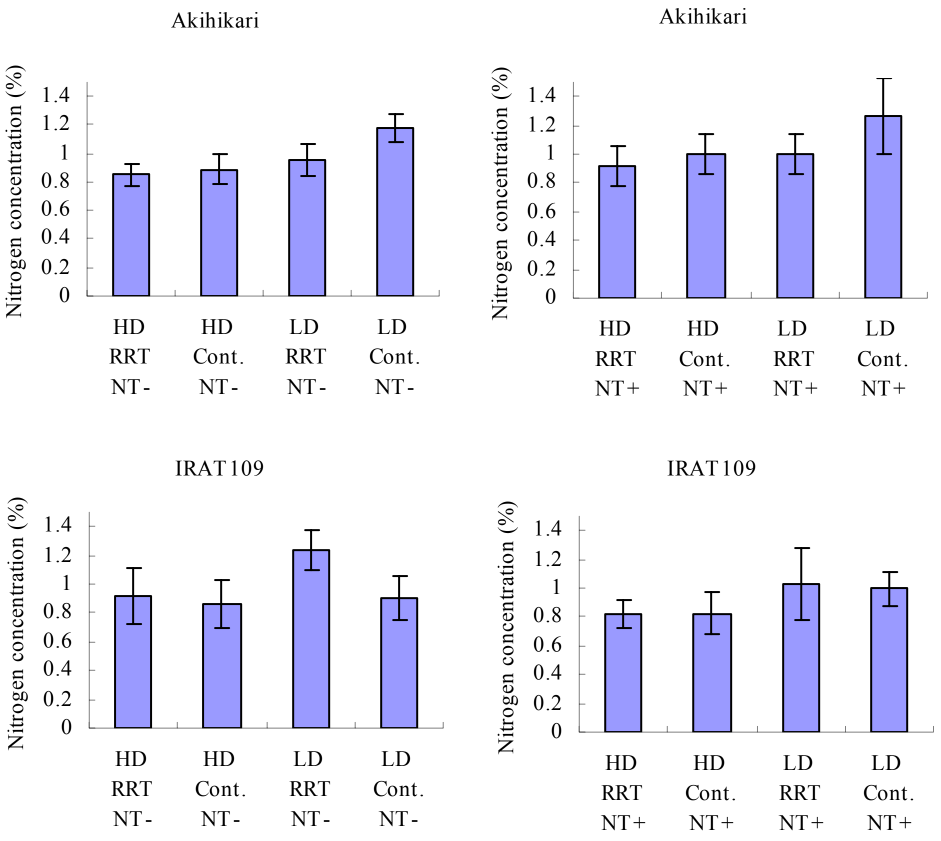


Fig.B. Nitrogen concentration (%) under two planting densities (HD and LD) and two nitrogen topdressing levels (NT+ and NT-) with or without root restriction (RRT and Cont.) in Akihikari (upper) and IRAT109 (below) at heading in 2008.

Abstract

The yield in cereals is determined by the yield components, panicle number, spikelet number per panicle, percentage of ripened grain and 1000-grain weight, and the achievement for high yield in rice is necessary and effectively through the improvement in these yield components. However, the relations among the components always have the strains each other on the achieving high yields, especially the relation between the panicle number (tiller number) and grain (spikelet) number per panicle. Spikelet number per panicle was affected by panicle number and spikelet number per panicle would influence on the grain ripening and single grain weight. So it is essential that to clarify the relations among the yield components, specially the relations between the tiller number and the spikelet number per panicle before heading stage since the panicle number per m^2 and spikelet number per panicle have been determined before anthesis. The spikelet number per panicle is the difference between differentiated spikelet number per panicle and aborted spikelet number per panicle before anthesis. The increase of differentiated spikelet number per panicle and decrease of aborted spikelet number per panicle are necessary to increase the spikelet number per panicle. So the response of differentiated or aborted spikelet number per panicle to panicle number should be studied in rice. On the other side, the variation of spikelet number per panicle within a plant is another factor influencing on the average spikelet number per panicle, since the differences about the spikelet number per panicle among the tillers exist. In this thesis, the determination of spikelet number per panicle in relation to panicle number was studied from (1) the response of spikelet number per panicle on each panicle within a plant to panicle number variation; (2) the response of spikelet number per panicle on each panicle within a plant relating to transplanting density; (3) the effects of spikelet number per panicle on the grain yield and yield components

Chapter 1. The spikelet number per panicle and its variation within a plant in 16 rice cultivars

The average spikelet number per panicle (SPP), differentiated spikelet number per panicle (D-SPP), and aborted spikelet number per panicle (A-SPP) in a plant, and their variations within plant on the each panicle were investigated in 16 rice cultivars in 2005 and 2006. There was magnificent genetic difference about SPP, D-SPP, and A-SPP on both averages and main stems. The cultivars with larger panicle on main stems always had larger panicle on average in SPP, D-SPP and A-SPP, indicating that there were closely positive relations between the main stem and tillers about SPP, D-SPP, and A-SPP. The negative relationships were observed in panicle number hill $^{-1}$ and SPP, D-SPP, and A-SPP. According to the relative SPP on tillers to SPP on main stem, D-SPP were declined, however, the spikelet abortion percentages were increased with the panicle order increased. Panicles on tillers showed greater variation in SPP than D-SPP, due to the high variation in A-SPP. Larger SPP on main stem increased the variation of SPP within hill, but not D-SPP, and the lower A-SPP on main stem reduced the variability of A-SPP in tillers. This indicated that the assimilates supplying relations among the tillers would effect the spikelet number per panicle.

Chapter 2 The response of spikelet number per panicle to transplanting density and its influence on yield in rice

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 under 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 higher D-SPP in lower order panicles. D-SPP declined as panicle order increased 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 (D-SPP or SPP per leaf area) of each tiller was higher in IR65564-44-51 (NPT65) and Akihikari than other cultivars, indicating a greater capacity of tillers to produce spikelet or support spikelet growth. In each cultivar except NPT65, spikelet production efficiency for D-SPP increased as panicle order increased, whereas spikelet production efficiency for SPP remained constant or decreased. This finding indicates that, irrespective of planting density, higher 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 decreased with panicle order increase.

Spikelet number per panicle was larger in LD than in HD. This was because of the larger tiller size in leaf area, shoot dry matter in LD than in HD. There was clear compensation of spikelet number per panicle increase to the panicle number m^{-2} reduction. So the spikelet number per m^2 and grain number per m^2 kept stability on varying transplanting density. The filled grain percentage was constant. There was a little higher yield production in HD than in LD, because of higher 1000 grain weight. The yield and its components showed clearly higher on primary rachis branch than on secondary rachis branches. As a conclusion, although the grain number per m^2 kept constant, the more grain production on the secondary rachis branch should be responsible for the lower yield in low transplanting density.

Chapter 3 The response of spikelet number per panicle and yield to transplanting density with root restriction in rice

As the indication of Chapter 2, the smaller tiller size in terms of tiller height, leaf area per tiller and dry matter per tiller due to the dense planting density resulted into the smaller spikelet number per panicle in high transplanting density (HD) than in low transplanting density (LD), so the possible root function in this response was studied by the root restriction treatment (RRT), a horizontal restriction treatment on root rhizosphere size. .The spikelet number per panicle, yield and nitrogen accumulation were examined under two planting density with RRT using two Japonica cultivars, Akihikari and IRAT109, in 2007 and 2008. The above ground dry matter, yield, nitrogen accumulation per unit area were not differed in both planting density without RRT. However, RRT reduced above ground dry matter, yield, nitrogen accumulation, and panicle number per unit area evidently in LD, though the reductions were very weak in HD. Spikelet number per panicle was decreased significantly by RRT in LD than in HD, through the reduction in differentiated spikelet number per panicle (D-SPP). These reductions of above ground dry matter, yield and spikelet number per panicle were elucidated by the reduction of nitrogen accumulation. Therefore, it is indicted that the effects of planting density on spikelet number per panicle and yield were by the nitrogen accumulation through below ground parts than the light shading on aerial parts. The different responses were observed in two cultivars in yield related characteristics in LD with RRT indicated that the strategies to limited nitrogen availability were dependent on cultivars.

Chapter 4 QTLs analysis for spikelet number per panicle under two nitrogen conditions

As the indications from Chapter 2 and 3, the planting density had effects on the spikelet per panicle, mainly through effecting on the nitrogen accumulations from soil. And also, in Chapter 3, it was verified that there was genetic difference in the response of spikelet per panicle to nitrogen condition in the soil. So in this Chapter, by using BC_1F_8 and BC_1F_9 of a 105BILs, inbred lines from a cross of temperate *Japonica* × tropical *Japonica***,** QTLs for spikelet number per panicle (SPP), and their components: primary rachis branch per panicle (BPP), spikelet number per primary rachis branch (SPB), and spikelet abortion percentage before flowering (A%) were identified under two nitrogen application conditions: low nitrogen (LN) and high nitrogen (HN) in 2006 and 2007. The results showed that totally, 11 QTLs and 12 QTLs were detected in LN and HN in two years. Among them, QTLs for SPP(3), BPP(7), SPB(2) and A% (6) were identified. Stable QTLs for SPP(2), BPP(1), and A% (2) were detected in two years under both nitrogen conditions, therefore, control mechanism of them were common under different nitrogen conditions. Co-location of QTLs on chromosome 6 was observed which could indicate strong relation between SPP and SPB under high nitrogen applied condition.

Therefore, in this study, it was shown clearly that (1) The spikelet number per panicle on each panicles within a plant were declined with the increasing of panicle orders. This is probably because of the decline of the leaf area, neck internode diameters and tiller height: (2) The spikelet production efficiency (spikelet number per leaf area) of each tiller within a plant for D-SPP increased as panicle order increased, whereas spikelet production efficiency for SPP remained constant or decreased, irrespective of the variation of tiller number per hill variation due to the planting density. Higher order panicles produce more spikelets than they can afford physiologically, but they were regulated downward to a nearly constant value: (3) Panicle number per hill had positive effects on the spikelet number per panicle through effecting on the differentiated spikelet number per panicle, this is mainly through the influencing on the nitrogen accumulation by roots from soil: (4) The genetic control mechanism of spikelet number per panicle response to nitrogen were common under different nitrogen application conditions.

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