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Analysis of the Dry Matter Production Process Related to Yield and Yield Components of Rice Plants Grown under the Practice of Nitrogen-Free Basal Dressing Accompanied with Sparse Planting Density

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Abstract : Experiments were carried out in 1999, 2000 and 2001 on the field of Iwate University, Japan to examine the effect of nitrogen-free basal dressing accompanied with sparse planting density (BNo) on the dry matter production (DMP) of 12 rice cultivars or lines belonging to the early, medium and late-maturing genotypes. During the period from transplanting to panicle initiation (PI), DMP was lower in BNo than in the conventional cultivation (CONT) in all 3 years. The DMP during the period from PI to full heading (FH) was also lower in BNo than in CONT, particularly in the high solar radiation year of 1999, because of the small leaf area index. During the ripening stage, leaf area index in BNo was smaller, but crop growth rate in BNo was similar to or higher than that in CONT due to the large net assimilation rate, which resulted from the large flag leaf and 2nd leaf, and the heavy specific leaf weight in BNo. The DMP per panicle during the period from PI to FH positively and significantly correlated with the number of spikelets panicle^{-1}. The percentage of ripened grains (PRG) was also closely related with the amount of carbohydrates from stems ($-\triangle S$) and photosynthesis after FH ($\triangle W$) contributed to a spikelet during the early ripening period (during 20 days after FH). The higher DMP per panicle in BNo compared with CONT during the period from PI to FH, therefore, resulted in a larger number of spikelets panicle^{-1} in the former. On the other hand, the large amount of carbohydrate supply per spikelet during the early ripening period could also secure a high and stable PRG in BNo, especially under unfavorable weather conditions.

Key words : Dry matter production, Nitrogen-free basal dressing, Rice cultivars, Sparse planting density, Weather conditions.

Yield of rice is a result of the dry matter production (accumulation and translocation) before and after heading. The potential size of yield (the product of the number of spikelets per unit land area and grain size) is primarily determined before heading. Ultimate grain yield, or the weight of filled grains, is mainly determined by the amount of carbohydrates stored in plants before heading and those produced by photosynthesis after heading (Yoshida, 1981; Weng et al., 1982). The dry matter production process varies with the genotype, environmental condition and cultivation practice. Thus, understanding the difference in dry matter production among cultivars, environmental conditions and cultivation practices is an essential step in the development of high and stable-yielding cultivars or cultivation practices.

We have examined the effect of nitrogen-free basal dressing accompanied with sparse planting density (BNo), which has been used to overcome the cool weather damage to rice in the Tohoku region of Japan (Murata, 1994; Hirano et al., 1997), on yield and yield components of various rice cultivars belonging to the early, medium and late-maturing genotypes (Pham et al., 2004a and b). We found that BNo reduced the number of panicles m^{-2}, but often increased the number of spikelets panicle^{-1}, the percentage of ripened grain and 1,000-grain weight as compared with the conventional cultivation (CONT), especially in the years with unfavorable weather. The grain yield in BNo was slightly lower in the years with favorable weather, but was similar to or higher than that in CONT in the years with unfavorable weather. In those studies, however, the dry matter production related to yield and yield components was not elucidated. In the present study, therefore, we examined the dry matter production of 12 rice cultivars or lines belonging to

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Abbreviations : BNo, the practice of nitrogen-free basal dressing accompanied with the sparse planting density of 16.7 hills m^{-2}; CONT, the standard cultivation with the planting density of 22.2 hills m^{-2}; DMP, dry matter production; ($-\triangle S$), a decrease in stem weight; ($\triangle W$), an increase in total weight; FH, full heading stage; PI, panicle initiation stage; PRG, percentage of ripened grains.

the early, medium and late-maturing genotypes grown in BNo, and compared it with that in CONT in 3 years (1999, 2000 and 2001). Furthermore, the effects of dry matter production during various growth periods on yield and yield components in years with different weather were also examined and discussed.

Materials and methods

Experiments were conducted in the paddy field of the Faculty of Agriculture, Iwate University, in 1999, 2000 and 2001. Materials, experimental design and management are reported separately (Pham et al., 2004a and b). Briefly, 12 cultivars or lines belonging to the early (Iwate43, Hananomai, Ouu339 and Fukei149), medium (Akitakomachi, Hatajirushi, Fukuhibiki and Iwanan7) and late (Menkoina, Okiniiri, Ouu316 and Hitomebore)-maturing genotypes were cultivated in a split random block designed experiment with two replications. In BNo, the planting density was 16.7 hills m^{-2} (30 × 20cm) and the amount of nitrogen fertilizer was 9g m^{-2} (3.0 g at the 8th leaf-age stage, 2.0g at the neck-node initiation, 2.0g at about 25-20 days before heading and 2.0 g at the heading stage). In CONT, planting density and nitrogen application regimes were the same as in the standard practice in Iwate Prefecture; the planting density was 22.2 hills m^{-2} (30 × 15cm) and the total nitrogen fertilizer was 11.0 g m^{-2} (6.5 g as basal dressing, 2.5g at about 25-20 days before heading and 2.0g at the heading stage). Phosphorus and potassium fertilizers at 14.0g m^{-2} and 12.8g m^{-2}, respectively, were applied as basal dressing in both CONT and BNo.

For investigating dry matter production (DMP), we randomly sampled nine hills from each replication at the panicle initiation (PI), full heading (FH), mid-ripening (20 days after FH) and full ripening stages (40 days after FH). Plants were washed to remove soil, and the above ground organs were separated from roots. Of the nine hills, one was used for measuring leaf area, and the five hills with average growth were selected and then separated into different categories : the dead parts, leaf blade, stems + leaf sheaths and panicles. All samples were oven-dried at 90°C for over 48 hours and then weighed.

Results

1. DMP, crop growth rate (CGR), leaf area index (LAI) and net assimilation rate (NAR) during various growth periods

Since the difference between BNo and CONT in the DMP was nearly the same in all cultivars in a year, only the DMP of Menkoina and Okiniiri (the two high yielding potential cultivars) is presented in Fig. 1. From transplanting to PI, the DMP was clearly lower in BNo than in CONT in both cultivars and in all 3 years. The DMP in the period from PI to FH was significantly lower in BNo than in CONT in the high solar radiation year of 1999, but was only slightly lower in BNo than CONT in the low solar radiation year of 2001. During the early ripening period, DMP was also lower in BNo than in CONT in the high solar radiation condition of 2000, but was higher in the former than in the latter in the low solar radiation condition of 1999. During the late ripening period, DMP in BNo was similar to or higher than that in CONT.

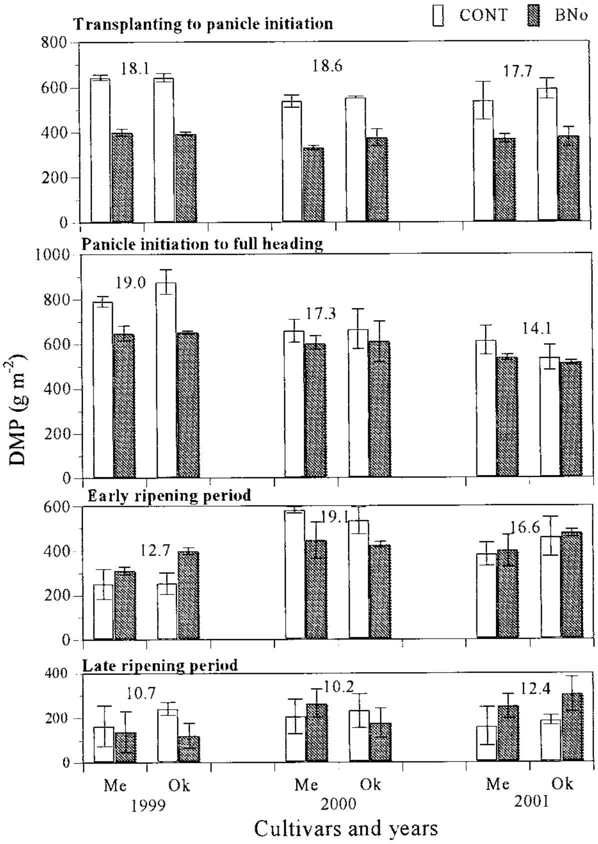

Fig. 1. Dry matter production (DMP) during different growth periods of two rice cultivars Menkoina (Me) and Okiniiri (Ok) in 1999, 2000 and 2001.
Numerals above bars indicate solar radiation (MJ m^{-2} day^{-1}). Error bars indicate standard error.

For further understanding the difference between BNo and CONT, and among cultivar groups in DMP during various growth periods, some growth parameters (CGR, LAI and NAR) are presented in Table 1, 2 and 3. During the period from PI to FH, CGR was often lower in BNo than in CONT, and the CGR averaged over cultivars and years was 22.7 g m^{-2} day^{-1} in BNo and 25.3 g m^{-2} day^{-1} in CONT. The difference between BNo and CONT in CGR did not vary with the cultivar (interaction between cultivar and cultivation practice was not significant), but varied with the year (interaction between cultivation practice and year was significant at the 0.01 probability level). The difference was large in 1999, when solar radiation and air temperature were rather high (18.4 MJ m^{-2} day^{-1} and 25.7°C, respectively), but was small in 2000 and

Table 1. Air temperature (T), solar radiation (SR), crop growth rate (CGR), leaf area index (LAI) and net assimilation rate (NAR) during the period from panicle initiation to full heading of different cultivar groups under CONT and BNo in 1999, 2000 and 2001.

Years	Cultivar	T	SR	CGR ($\mathrm{g\ m^{-2}\ day^{-1}}$)			LAI ($\mathrm{m^{2}\ m^{-2}}$)			NAR ($\mathrm{g\ m^{-2}\ day^{-1}}$)		
	groups	°C	$\mathrm{MJ\ m^{-2}\ day^{-1}}$	CONT	BNo	%3)	CONT	BNo	%	CONT	BNo	%
1999	Early	24.6	18.1	27.7a1)	22.4b	81	5.2b	2.9c	56	5.4a	7.8a	145
	Medium	26.0	18.1	28.5a	25.5a	90	5.9a	3.5b	59	4.8b	7.4a	153
	Late	26.4	19.1	28.5a	24.4a	86	6.2a	4.0a	64	4.6b	6.2b	135
	Ave 2)	*25.7*	*18.4*	*28.2*	*24.1*	*85*	*5.8*	*3.5*	*60*	*4.9*	*7.1*	*145*
2000	Early	23.7	16.9	24.5a	22.3b	91	5.1a	3.8a	73	4.8a	5.9b	124
	Medium	24.6	17.8	24.6a	24.2a	97	5.1a	3.7a	73	5.0a	6.6a	131
	Late	24.9	17.3	23.6a	22.0b	93	5.4a	4.0a	75	4.4a	5.5b	125
	Ave	*24.4*	*17.3*	*24.3*	*22.8*	*93*	*5.2*	*3.8*	*74*	*4.7*	*6.0*	*127*
2001	Early	23.1	15.5	24.ab	20.6b	85	4.6b	3.2b	69	5.2a	6.4a	123
	Medium	22.7	15.5	25.5a	22.0a	86	5.6a	3.7a	66	4.6b	6.1ab	132
	Late	22.2	14.2	21.7b	20.7b	95	5.3a	3.7a	69	4.1b	5.6b	138
	Ave	*22.7*	*15.0*	*23.8*	*21.1*	*89*	*5.2*	*3.5*	*68*	*4.6*	*6.0*	*130*
	AVE4)			**25.3**	**22.7**	**90**	**5.4**	**3.6**	**67**	**4.8**	**6.4**	**134**
ANOVA	Cultivar (C)				*			**			**	
	Cultivation practice (CP)				**			**			**	
	Year (Y)				**			**			**	
	C × CP				ns			ns			ns	
	C × Y				ns			**			**	
	CP × Y				**			**			**	
	C × CP × Y				ns			ns			ns	

1) : Comparison of the average value of different cultivar groups within a year and cultivation practice; values followed by the same letter are not significantly different from each other at 0.05 probability level. 2) : The average value of all cultivar groups within a year and cultivation practice. 3) : The ratio (%) of values in BNo to those in CONT. 4) : The values averaged over cultivars and years. ANOVA : Results of analysis of variance; * and ** : significant at 0.05 and 0.01 probability levels, respectively; ns : not significant.

Table 2. Air temperature (T), solar radiation (SR), crop growth rate (CGR), leaf area index (LAI) and net assimilation rate (NAR) during the early ripening period of different cultivar groups under CONT and BNo in 1999, 2000 and 2001.

Years	Cultivar	T	SR	CGR ($\mathrm{g\ m^{-2}\ day^{-1}}$)			LAI ($\mathrm{m^{2}\ m^{-2}}$)			NAR ($\mathrm{g\ m^{-2}\ day^{-1}}$)		
	groups	°C	$\mathrm{MJ\ m^{-2}\ day^{-1}}$	CONT	BNo	%3)	CONT	BNo	%	CONT	BNo	%
	Early	26.8	17.3	22.1a1)	22.5a	104	5.7b	3.5c	60	3.9a	6.5a	171
1999	Medium	25.3	15.1	15.8ab	17.5ab	114	5.9a	3.7b	64	2.7b	4.7b	180
	Late	24.1	12.3	12.6b	15.7b	130	5.8a	3.9a	68	2.2c	4.0c	189
	Ave 2)	*25.4*	*14.9*	*16.8*	*18.6*	*116*	*5.8*	*3.7*	*64*	*2.9*	*5.1*	*180*
	Early	24.5	19.5	26.0a	24.2a	94	5.8a	4.4a	76	4.5b	5.6a	124
2000	Medium	24.1	19.2	28.1a	25.2a	90	5.3a	4.4a	82	5.3a	5.7a	109
	Late	24.0	18.7	25.9a	22.8a	89	5.7a	4.5a	79	4.6ab	5.1a	114
	Ave	*24.2*	*19.1*	*26.7*	*24.1*	*91*	*5.6*	*4.4*	*79*	*4.8*	*5.5*	*116*
	Early	22.2	16.4	19.5a	19.4a	100	5.2a	3.8a	73	3.8a	5.1a	135
2001	Medium	22.8	15.8	15.9a	18.3a	116	5.2a	3.8a	73	3.1a	4.9a	158
	Late	22.8	16.4	18.6a	19.2a	104	4.8a	4.0a	83	3.8a	4.8a	126
	Ave	*22.6*	*16.2*	*18.0*	*19.0*	*106*	*5.1*	*3.9*	*76*	*3.6*	*4.9*	*140*
	AVE4)			**20.5**	**20.6**	**100**	**5.5**	**4.0**	**73**	**3.8**	**5.2**	**137**
ANOVA	Cultivar (C)				ns			**			*	
	Cultivation practice (CP)				ns			**			**	
	Year(Y)				**			**			**	
	C × CP				ns			ns			ns	
	C × Y				ns			**			*	
	CP × Y				*			**			**	
	C × CP × Y				ns			ns			ns	

1) : Comparison of the average value of different cultivar groups within a year and cultivation practice; values followed by the same letter are not significantly different from each other at 0.05 probability level. 2) : The average value of all cultivar groups within a year and cultivation practice. 3) : The ratio (%) of values in BNo to those in CONT. 4) : The values averaged over cultivars and years. ANOVA : Results of analysis of variance; * and ** : significant at 0.05 and 0.01 probability levels, respectively; ns : not significant.

Table 3. Air temperature (T), solar radiation (SR), crop growth rate (CGR), leaf area index (LAI) and net assimilation rate (NAR) during the late ripening period of different cultivar groups under CONT and BNo in 1999, 2000 and 2001.

Years	Cultivar groups	T °C	SR MJ m^{-2} day^{-1}	CGR (g m^{-2} day^{-1}) CONT	CGR BNo	CGR %[3]	LAI (m^2 m^{-2}) CONT	LAI BNo	LAI %	NAR (g m^{-2} day^{-1}) CONT	NAR BNo	NAR %
1999	Eealy	21.9	11.4	7.9a[1]	8.7a	111	4.4a	2.8b	63	1.8a	3.0a	170
	Medium	21.5	10.9	10.9a	11.3a	104	4.4a	2.9ab	67	2.5a	3.9a	158
	Late	21.2	10.8	9.3a	9.4a	101	4.2a	3.1a	75	2.3a	3.0a	132
	Ave[2]	*21.5*	*11.0*	*9.4*	*9.8*	*105*	*4.3*	*3.0*	*68*	*2.2*	*3.3*	*152*
2000	Eealy	22.7	12.8	12.3a	13.7a	111	4.4a	3.5a	79	2.9a	3.9a	136
	Medium	21.7	10.2	11.1a	11.3a	102	4.6a	3.8a	83	2.4a	2.9b	120
	Late	21.7	9.5	10.2a	12.1a	119	4.9a	3.7a	77	2.1a	3.2ab	157
	Ave	*22.0*	*10.8*	*11.2*	*12.3*	*110*	*4.6*	*3.7*	*80*	*2.5*	*3.4*	*137*
2001	Eealy	21.4	13.2	15.2a	17.3a	114	4.3a	3.4a	78	3.5a	5.2a	149
	Medium	20.8	12.4	10.8a	14.9a	138	3.7a	3.2a	87	2.9a	4.8a	164
	Late	20.3	12.3	11.6a	15.2a	132	3.9a	3.4a	87	3.0a	4.6a	152
	Ave	*20.9*	*12.6*	*12.5*	*15.8*	*126*	*4.0*	*3.3*	*83*	*3.1*	*4.9*	*155*
	AVE[4]			**11.0**	**12.7**	**115**	**4.3**	**3.3**	**77**	**2.6**	**3.8**	**148**
ANOVA	Cultivar (C)				ns			ns			ns	
	Cultivation practice (CP)				*			**			**	
	Year (Y)				**			**			**	
	C × CP				ns			ns			ns	
	C × Y				ns			ns			ns	
	CP × Y				ns			**			ns	
	C × CP × Y				ns			ns			ns	

1) : Comparison of the average value of different cultivar groups within a year and cultivation practice; values followed by the same letter are not significantly different from each other at 0.05 probability level. 2) : The average value of all cultivar groups within a year and cultivation practice. 3) : The ratio (%) of values in BNo to those in CONT. 4) : The values averaged over cultivars and years. ANOVA : Results of analysis of variance; * and ** : significant at 0.05 and 0.01 probability levels, respectively; ns : not significant.

2001, when solar radiation was lower (17.3 MJ m^{-2} day^{-1} in 2000 and 15.0 MJ m^{-2} day^{-1} in 2001). The lower CGR in BNo compared with CONT was mainly attributed to the small LAI in spite of the higher NAR in BNo.

During the early ripening period (from FH to 20 days after FH), CGR did not vary with the cultivation practice or the cultivar, but significantly varied with the year (Table 2). CGR, especially in CONT, was often higher in the high solar radiation and warm temperature year of 2000 than in the low solar radiation and high temperature year of 1999. The difference between BNo and CONT in CGR also varied with the year (interaction between cultivation practice and year was significant at 0.05 probability level). In the high solar radiation and warm temperature year of 2000, CGR was lower in BNo than in CONT, but in the low solar radiation and high temperature year of 1999, it was higher in BNo than in CONT, particularly in the late-maturing cultivars (BNo/CONT=130%). Although LAI was smaller in BNo than in CONT, NAR was higher in the former than in the latter. The higher NAR in BNo, especially in the low solar radiation and high temperature year of 1999, thus, could compensate for the small LAI, and consequently brought about the similar or higher CGR in BNo compared with CONT.

During the late ripening period (from 20 days to 40 days after FH), solar radiation was low (11.0 MJ m^{-2} day^{-1} in 1999, 10.8 MJ m^{-2} day^{-1} in 2000 and 12.6 MJ m^{-2} day^{-1} in 2001). During this growth period, CGR was also higher in BNo than in CONT in all cultivar groups and in all 3 years (Table 3). The higher CGR in BNo compared with CONT also resulted from the higher NAR in BNo. Among the years, the CGR averaged over cultivars in both BNo and CONT was also higher in the high solar radiation year of 2001 than in the low solar radiation year of 1999 or 2000.

2. Leaf area and specific leaf weight (SLW) of leaves at different positions on a stem

For the elucidation of plant factors that determine CGR, LAI and NAR, the leaf area and SLW of leaves at different positions on a stem of 12 cultivars in CONT and BNo were measured at FH in 2000 and 2001. Because obtained results were nearly the same in both two years, only the data in 2001 are presented in Fig. 2. The 3rd and 4th leaves counted from the flag leaf were smaller in BNo than in CONT, and the leaf area of these two leaves averaged over 12 cultivars was 25.2 and 16.9 cm^2, respectively, in BNo, and 29.5 and 21.1cm^2, respectively, in CONT (BNo/CONT=85 and 80%, respectively). The flag leaf and 2nd leaf in BNo, however, were similar to or slightly larger than those in CONT. The leaf area of the flag leaf averaged over 12 cultivars was 26.9 cm^2 in BNo and 25.3cm^2 in CONT (BNo/CONT=106%), and that of the 2nd leaf was 31.3 cm^2 in the former and 31.0 cm^2 in the latter

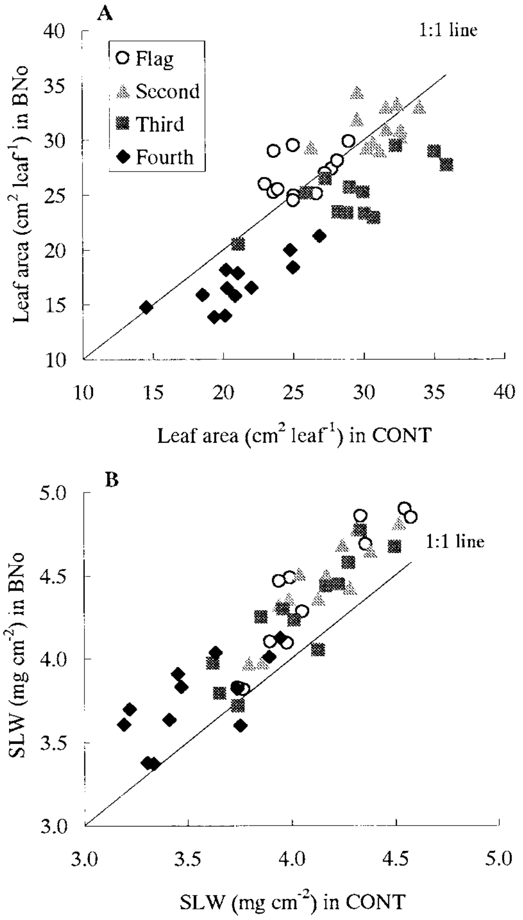

Fig. 2. Comparison between BNo and CONT for leaf area (A) and specific leaf weight (SLW) (B) of leaves at different leaf positions on a stem in 2001.

(BNo/CONT=101%). The SLW, on the other hand, was heavier in BNo than in CONT in all leaves. The average SLW of 12 cultivars in the flag, 2nd, 3rd and 4th leaves was 4.4, 4.4, 4.3 and 3.8 mg cm^{-2} in BNo, and was 4.1, 4.1, 4.0 and 3.5 mg cm^{-2} in CONT, respectively (BNo/CONT=107, 107, 106 and 106%, respectively). The large flag and 2nd leaves with heavy SLW of rice plants in BNo could be the main reason for the high DMP in BNo in the ripening period, especially in the low solar radiation conditions.

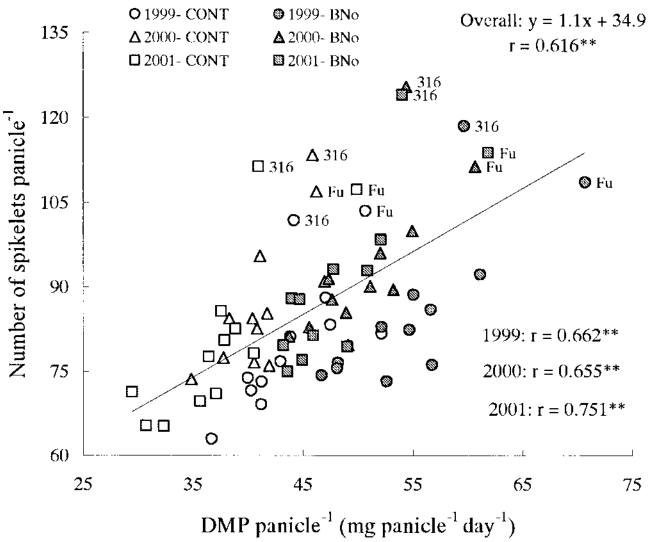

Fig. 3. Correlation of dry matter production per panicle (DMP panicle^{-1}) during the panicle formation period (4 weeks before full heading to full heading) with the number of spikelets panicle^{-1}.
** : significant at 0.01 probability level. Fu : var. Fukuhibiki, 316 : var. Ouu316.

3. Relationship between DMP in the period from PI to FH and the number of spikelets panicle^{-1}

To find the growth factors affecting the number of spikelets panicle^{-1}, we calculated the relationship between the DMP per panicle in the period from PI to FH and the number of spikelets panicle^{-1} (Fig. 3). The number of spikelets panicle^{-1} significantly correlated with the DMP per panicle. Overall, the DMP per panicle was higher in BNo than in CONT, and the DMP per panicle averaged over cultivars and years was 50.5 mg panicle^{-1} day^{-1} in BNo and 40.9 mg panicle^{-1} day^{-1} in CONT (BNo/CONT=126%). In 2001, when solar radiation was low, the DMP per panicle in CONT was very low (37.9 mg panicle^{-1} day^{-1}), and was 30% lower than that in BNo (49.0 mg panicle^{-1} day^{-1}). A higher DMP per panicle in BNo compared with CONT during the period from PI to FH, especially in 2001, thus, could have caused the larger number of spikelets panicle^{-1} in BNo. Among cultivars, Fukuhibiki and Ouu316 produced a larger number of spikelets panicle^{-1} than other cultivars with the same amount of

Table 4. Correlation coefficients (r) of the correlations between the percentage of ripened grains (PRG) with different growth parameters representing carbohydrate supply during different grain-filling periods.

Growth	Full heading — Full ripening				Full heading — Middle ripening				Middle ripening — Full ripening			
parameters	1999	2000	2001	Overall	1999	2000	2001	Overall	1999	2000	2001	Overall
△E*	100%	100%	100%		75~85%	75~85%	60~70%		15~25%	15~25%	30~40%	
△W-△S	-0.049ns	-0.158ns	-0.184ns	-0.223ns	0.250ns	-0.004ns	-0.248ns	0.201ns	-0.617*	-0.173ns	-0.061ns	0.174ns
(△W-△S)/SN	0.751**	0.779**	0.523*	0.421**	0.838**	0.859**	0.648**	0.714**	-0.255ns	0.106ns	0.224ns	0.341**

△E* : Indicates the ratio of panicle weight increase (%) during different grain-filling periods to that during the whole ripening period (100%); △S=the decrease or increase in stem weight (g m^{-2}); △W=the increase in total weight (g m^{-2}); SN=the number of spikelets m^{-2}. * and ** : significant at 0.05 and 0.01 probability levels, respectively; ns : not significant.

DMP per panicle.

Table 5. Correlation coefficients (r) of the correlations between the percentage of ripened grains (PRG) with the amount of carbohydrates from stems (−△S) and that produced after full heading (△W) contributed to a spikelet during the early ripening period.

Growth parameters	1999	2000	2001	Overall
△W/SN	0.758**	0.645**	0.623**	0.587**
-△S/SN	-0.195ns	0.457*	-0.356ns	-0.046ns

△ W, −△ S and SN are the same as Table 4. * and ** : significant at 0.05 and 0.01 probability levels, respectively; ns : not significant.

4. Relationship between the percentage of ripened grains (PRG) and some growth parameters representing carbohydrate supply during the ripening stage

For analyzing factors affecting PRG, the correlations of PRG with some growth parameters representing the amount of carbohydrates from stems (−△S) and the increase of total weight (△W) contributing to grains during the ripening stage are shown in Table 4. PRG did not correlate with the total carbohydrate supply (△W−△S) during the whole ripening period (r=−0.049, −0.158, −0.184 and −0.223 in 1999, 2000, 2001 and overall, respectively), but significantly correlated with the amount of carbohydrates contributing to a spikelet 〔(△W−△S)/spikelet number m^{-2} (SN)〕, and r was 0.751 (P<0.01) in 1999, 0.779 (P<0.01) in 2000, 0.523 (P<0.05) in 2001 and 0.421 (P<0.01) overall. Growth parameter that had the closest correlation with PRG was 〔(△W−△S)/SN〕 during the early ripening period, and r was 0.838 (P<0.01) in 1999, 0.859 (P<0.01) in 2000, 0.648 (P<0.01) in 2001 and 0.714 (P<0.01) overall. During this growth period, the relative increase in panicle weight (the ratio of panicle weight increase in this period to total panicle weight increase in the whole ripening period) was larger in 1999 or 2000 (75~85%) than in 2001 (60~70%).

To separate the effect of carbohydrates stored in stems from those produced by photosynthesis after heading on PRG, the correlations of PRG with −△S/SN and △W/SN during the early ripening period are presented in Table 5. PRG significantly correlated with △W/SN, and r was 0.758 (P<0.01) in 1999, 0.645 (P<0.01) in 2000, 0.623 (P<0.01) in 2001 and 0.587 (P<0.01) overall. PRG, however, did not statistically correlate with −△S/SN, except in 2000 (r=0.457, P<0.05).

The correlation of PRG with carbohydrate supply per spikelet 〔(△W−△S)/SN〕 during the early ripening period is detailed in Fig. 4. The amount of carbohydrate supply per spikelet during the late ripening period is also presented in this figure. During the early ripening period, the average amount of carbohydrate supply per spikelet over all cultivars and years was larger in BNo (0.68 mg spikelet^{-1} day^{-1}) than in CONT (0.58 mg spikelet^{-1} day^{-1}). The PRG averaged over cultivars and years was also higher in BNo (87%) than in CONT (77%). In 1999, when solar radiation was low and temperature was high, the average amount of carbohydrate supply per spikelet over 12 cultivars in CONT was small (0.53 mg spikelet^{-1} day^{-1}), and was significantly smaller than that in BNo (0.67 mg spikelet^{-1} day^{-1}). As a result, PRG was much higher in BNo (84%) than in CONT (70%) in this year. The amount of carbohydrate supply per spikelet during the late ripening period, on the other hand, was always larger in 2001 (≧0.195 mg spikelet^{-1} day^{-1}) than in 1999 or 2000 (<0.195 mg spikelet^{-1} day^{-1}) in both BNo and CONT (Fig. 4). Thus, at the same level of carbohydrate supply per spikelet during the early ripening period, PRG was higher in 2001 than in 1999 or 2000. Overall, the average PRG of 12 cultivars was also higher in 2001 (88% in BNo and 84% in CONT) than in 1999 (84% in BNo and 70% in CONT) and 2000 (87% in BNo and 78% in CONT).

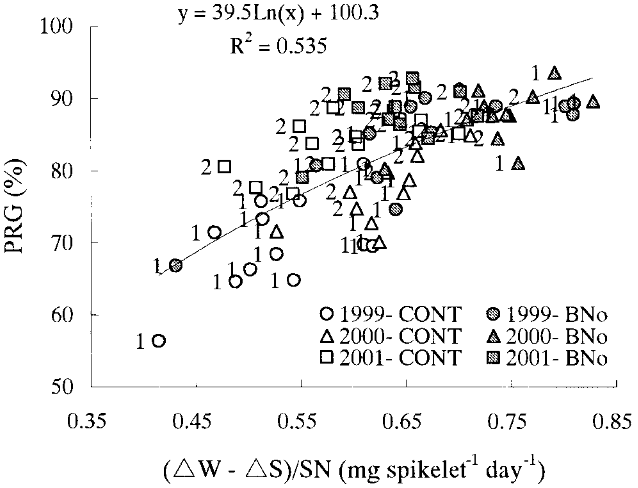

Fig. 4. Relationship between the percentage of ripened grains (PRG) and carbohydrate supply per spikelet during the early ripening period (during 20 days after full heading). Numerals beside symbols indicate the amount of carbohydrates supplied to a spikelet during the period from 20 to 40 days after full heading; 1 and 2 : the amount <0.195 and ≧ 0.195 mg spikelet^{-1} day^{-1}, respectively.

Discussion

1. Difference between BNo and CONT in DMP

In the present study, the DMP from transplanting to PI was clearly lower in BNo than in CONT (Fig. 1). This was because the numbers of tillers per m^2 were much smaller in BNo than in CONT (Hirano et al., 1997; Truong et al., 1998; Pham et al., 2004a).

The DMP of rice plants is affected by both plant factors, such as LAI, and environmental conditions, especially solar radiation (Yoshida, 1981). The optimum LAI for CGR in the period prior to heading is larger than that in the ripening period (Murata, 1976; Kumura, 1995). In the present study, LAI in the period from PI to FH was smaller in BNo than in CONT, and it might have caused the lower CGR in BNo, especially in 1999 when solar radiation was high (Table 1).

Truong et al. (1998) compared the DMP of rice grown in BNo and CONT, and reported that under the normal weather years, CGR in the early ripening period was higher in BNo than in CONT. The present study showed that during the whole ripening period, CGR was often higher in BNo than in CONT, especially in the low solar radiation conditions (Table 2 and 3). In the early ripening period of the late-maturing cultivars in 1999, and in the late ripening period of all cultivar groups in 1999, 2000 and 2001, CGR was significantly higher in BNo than in CONT. Under the low solar radiation conditions, the higher NAR might have totally compensated for the small LAI, and subsequently brought about the higher CGR in BNo. On the other hand, under the high solar radiations, particularly during the early ripening period in 2000, rice plants in CONT with a larger LAI could absorb more sunlight, and consequently showed the higher CGR than those in BNo (Table 2).

Canopy structure and photosynthetic activity of a single leaf are also the main plant factors affecting CGR (Kuroda and Kumura, 1990; Kumura, 1995). Hirano et al. (1997) studied the light intercepting characteristic of rice plants in BNo, and showed that at the heading stage, more sunlight was penetrated into the canopy of rice plants in BNo than in CONT. The present study showed that at FH, the leaf area of the 3rd and 4th leaves on a culm was smaller, but the flag leaf and 2nd leaf in BNo were similar to or slightly larger than those in CONT (Fig. 2a). The SLW, an important factor determining photosynthetic capacity (Tanaka and Matsushima, 1971; Bhagsari and Brown, 1986), on the other hand, was heavier in BNo than in CONT in all leaves at different positions on a culm (Fig. 2b). Kuroda and Kumura (1990), and Oritani (1995) demonstrated that photosynthetic activity and the contribution to grain yield of the two uppermost leaves (flag and 2nd leaves) were much higher than those of the two lower leaves (the 3rd and 4th leaves). The large flag leaf and 2nd leaf with heavier SLW, possibly resulted from the application of nitrogen fertilizer at the neck node initiation stage, and the better light intercepting characteristics of rice plants in BNo, thus, might have brought about a higher NAR thereby resulting in a higher CGR in BNo, especially in the low solar radiation conditions during the ripening stage.

2. Correlations of DMP with the number of spikelets panicle^{-1} and PRG

The number of spikelets panicle^{-1} is determined by two main factors : genetic traits and growth conditions. Kobayashi and Imaki (1997) demonstrated that the large number of spikelets in modern rice varieties resulted from the large number of secondary rachis branches. Yamagishi et al. (1992) studied the relation of the number of spikelets panicle^{-1} with the characteristics of shoot, and showed that the number of spikelets panicle^{-1} closely correlated with the diameter of young panicle base and that of the first internode. Yoshida (1973), on the other hand, stated that CO_2 enrichment during the period from the neck node initiation stage to heading increased photosynthetic rate thereby increasing the number of spikelets per panicle and per m^2. Heavy shading during this growth stage, however, reduces photosynthesis, and consequently causes the significant reduction in the number of spikelets per panicle and per m^2 (Yoshida and Parao, 1976). Ishii and Kumura (1987), furthermore, elucidated that low solar radiation during the period from 1 cm young panicle to FH caused a decrease in DMP, increasing the number of degenerated primordia, and subsequently reduced the number of spikelets panicle^{-1}. The present study showed that the number of spikelets panicle^{-1} significantly and positively correlated with the DMP per panicle during the period from PI (about 4 weeks before FH) to FH (Fig. 3). The higher DMP per panicle in BNo compared with CONT, especially in the low solar radiation year of 2001, thus, might have brought about the larger number of spikelets panicle^{-1} in BNo as shown in the accompanying paper by Pham et al. (2004b).

The effect of DMP on the number of spikelets panicle^{-1} also varied with the cultivar. At the same level of DMP, the number of spikelets panicle^{-1} was clearly larger in Fukuhibiki and Ouu316 than in other cultivars (Fig. 3). In the young panicle growth stage, a competition for photosynthates between young panicles and other parts, particularly stems and leaf sheaths, is less severe in the short-culm cultivars than in the long-culm ones (Fujita and Yoshida, 1984). On the other hand, Kuroda et al. (1989) showed that cultivars with a high plant-height had higher photosynthetic capacity than cultivars with a short plant-height. In the present study, Fukuhibiki and Ouu316 were two cultivars with a short-culm (Kuroda at al., 1997; Wang et al., 1997), but with a relatively high plant-height (data not shown). These two cultivars also possessed a large number of secondary rachis branches (Wang et al., 1997). The large number of secondary rachis branches, the high DMP per panicle and the possibly small competition for photosynthates among different plant parts might have caused the large number of spikelets panicle^{-1} in Fukuhibiki and Ouu316.

PRG is mainly affected by the amount of carbohydrates available for grain filling (Weng et al., 1982; Kobata et al., 2000) and the number of spikelets per unit land area (Wada, 1969; Kuroda et al., 1999; Pham et al., 2004b). Tsukaguchi et al. (1996) demonstrated that carbohydrates available per spikelet during the 10 days after FH positively and closely correlated with the filling percentage (the ratio of rough brown rice yield to the product of spikelet number per unit land area and the weight of a fully ripened grain). Nagata et al. (2001) also stated that PRG significantly correlated with the amount of carbohydrate supply per spikelet during the 10 to 20 days after heading. In the present study, among the growth parameters representing carbohydrate supply during the ripening stage, the amount of carbohydrates contributing to a spikelet during the 20 days after FH (the early ripening period) most closely correlated with the PRG (Table 4). These results indicate that the high PRG can be achieved only if the amount of carbohydrates is large enough to fill all spikelets during a certain growth period. In CONT, the combination of a large number of spikelets m^{-2} (Pham et al., 2004b) with a low CGR after heading, especially in 1999 when solar radiation was low, (Table 2) could result in a small amount of carbohydrate supply per spikelet, subsequently caused the low PRG. On the other hand, a large amount of carbohydrate supply for grain filling could secure the high and stable PRG as well as the stable yield in BNo.

The contribution of carbohydrates stored in stems before heading to grain carbohydrates ranges from 0~40% under most conditions (Yoshida, 1981). Many reports suggested that this source of carbohydrates did not regulate grain yield directly, but contributed to grain yield indirectly by increasing PRG, especially in unfavorable weather condition during the ripening stage (Tanaka and Matsushima, 1963; Yoshida, 1981; Hayashi, 1995). Nagata et al. (2001) studied the effects of stored carbohydrates (nonstructural carbohydrates) and dry matter produced after heading on grain filling, and reported that between the two factors, the latter had a stronger effect on PRG than the former. In the present study, the contribution of carbohydrates from stems to grain weight (panicle weight increased during the period from FH to full ripening) ranged from 8~25% (15.4% in average) in CONT, and 10~20% (14.4% in average) in BNo, and the average amount of carbohydrates from stems contributed to grains over all cultivars and years was 113.0 g m^{-2} in CONT and 98.9 g m^{-2} in BNo (data not shown). PRG significantly correlated with △W/SN, but did not correlate with -△S/SN, except in 2000, (Table 5). The larger effect of dry matter produced after heading on PRG and its higher contribution to grain yield, as compared with those of carbohydrates from stems, suggest that in rice cultivation it is necessary to maintain a high dry matter production during the ripening period to achieve a high PRG and therefore a high grain yield.

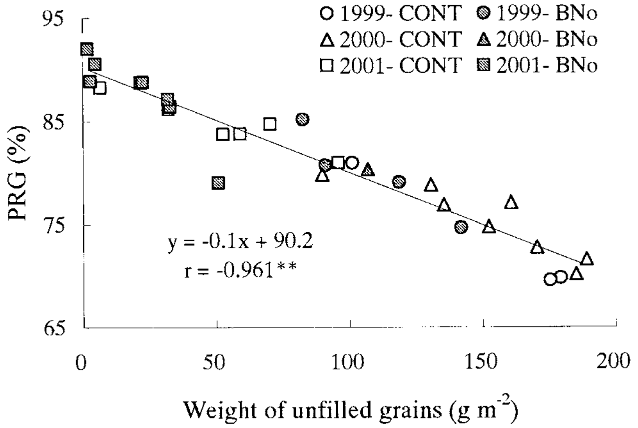

Fig. 5. Relationship between the percentage of ripened grains (PRG) and the weight of unfilled grains.
Note : calculation was for cultivars in which the amount of carbohydrates supplied to a spikelet during the early ripening period was in the range from 0.55~0.65 mg spikelet^{-1} day^{-1}.

The effect of carbohydrate supply per spikelet during the early ripening period on PRG varied with the year. The correlation coefficient (r) between PRG and carbohydrate supply per spikelet during the early ripening period was high in 1999 (r=0.838, P<0.01) or 2000 (r=0.859, P<0.01), when the temperature was high (Table 2), and the final panicle weight was almost determined during this period (Table 4). It was, however, low in 2001 (r=0.648, P<0.01), when temperature was mild (Table 2), and the increase of panicle weight (△E) during the early ripening period was only accounted for about 60~70% of total △E in the whole ripening period (Table 4). The high correlation coefficients (r) between PRG and carbohydrate supply per spikelet in 1999 and 2000 indicated that under the high temperature conditions, PRG was more dependent on the amount of carbohydrate supply during the early ripening period, and that a large amount of assimilate supply per spikelet during this period was important for achieving a high PRG. The higher PRG in BNo compared with CONT in 1999 and 2000, which resulted from a large amount of assimilate supply per spikelet during the early ripening period, suggested that BNo practice may be more effective for rice cultivation under unfavorable weather conditions such as high temperature or low solar radiation. On the other hand, in 2001, when temperature was mild and solar radiation was considerably high during the whole ripening period (Table 2 and 3), the large amount of photosynthates supplied to spikelets during the late ripening period (Table 3, 4 and Fig. 4) could also have affected the PRG, particularly in reducing the amount of unfilled spikelets thereby increasing the PRG (Fig. 5). The high PRG in all cultivars in CONT in 2001 compared with 1999 or 2000 indicates that a long ripening duration with high solar radiation is necessary for achieving the high PRG of rice plants in CONT that are characterized by a large number of spikelets per m^2 (Truong et al., 1998; Pham et al., 2004b).

As mentioned above, although DMP was significantly lower in BNo than in CONT during the period from transplanting to PI, resulting in the smaller number of panicles per m^2 in BNo, it was often higher in BNo than in CONT during the ripening stage. The high DMP per panicle during the period from PI to FH in BNo compared with CONT could increase the number of spikelets per panicle, so as to compensate for the small number of panicles per m^2 in BNo. The high DMP during the ripening stage, especially under the low solar radiation condition, on the other hand, could also bring about a high PRG thereby securing the high and stable grain yield in BNo. To further elucidate the effects of DMP on spikelet number and the PRG of rice plants grown under CONT and BNo conditions, we will analyze the partitioning and accumulation of carbohydrates during different growth periods in future studies.

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* In Japanese with English abstract or summary.

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