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Characteristics of Dry Matter Production and Partitioning of Dry Matter to Panicles in High Yielding Semidwarf Indica and Japonica-Indica Hybrid Rice Varieties

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Abstract : A field experiment was carried out to investigate the dry matter production characteristics before and after heading, the partitioning of dry matter to panicles, and some related factors in high yielding semidwarf indica (SDI) and japonica-indica hybrid (JI) varieties in comparison with those of japonica panicle weight (JP) and panicle number (JN) type varieties transplanted in early and late cropping seasons (ET and LT). Leaf area indices (LAIs) of the JI and SDI varieties in both ET and LT were higher at full heading, but decreasing percentages were much more prevalent in these varieties after heading, which resulted in much lower LAIs than those of japonica varieties at maturity. Total top dry weights at full heading of SDI and JI varieties were higher than those of JP and JN varieties in ET and LT, except for Akenohoshi in LT. However, the difference in dry matter increment during the period from full heading to maturity (HM) among the varieties were not found to be significant. Crop growth rates (CGR) during HM of SDI varieties both in ET and LT were the lowest among the varietal groups due to the highest decreasing percentage of LAIs and SPAD readings at the later grain filling stage. Panicle dry weights of SDI and JI varieties were about 125～190 gm^{-2} (20～31%) and 105～115 gm^{-2} (18～20%) higher than those of japonica varieties in ET and LT, respectively. Mean ratios of panicle dry weight to total top dry weight at maturity of the SDI and JI varieties in both ET and LT were about 56%, which were significantly superior to the corresponding mean ratios of JP and JN varieties (i.e., about 47%). These higher mean ratios resulted in panicle weight differences between the high yielding varieties and japonica varieties. The shoot dry matter partitioning percentages to panicles of SDI and JI varieties were more than two times higher in ET, and those of SDI varieties were about four times higher than those of the japonica varieties in LT. The panicle dry weight at full heading (sink capactiy) was found to be closely related to the panicle dry weight at maturity. When the sink capactiy was high, the increment in top dry weights during HM tended to be lower. It was also observed that the partitioning ratios of the accumulated assimilates in shoot to panicles were closely related to the sink capacity.

Key words : Dry matter production, Harvest index, Japonica-indica hybrid variety, Panicle weight, Rice plant, Semidwarf indica variety, Translocation.

多収性半矮性インド型および日印交雑型水稲品種の乾物生産特性と穂への乾物分配 : Mohammad Noor Hossain MIAH・吉田徹志*・山本由徳*・新田洋司*（愛媛大学大学院連合農学研究科・*高知大学農学部）

要　旨 : 多収性の半矮性インド型水稲品種（桂朝2号，IR 36 ; SDI）と日印交雑型水稲品種（アケノホシ，水原258号 ; JI）の乾物生産特性と穂重に対する出穂期前後に生産された乾物の分配率などについて，日本型水稲品種［農林22号，コガネマサリ ; 穂重型（JP），金南風，中生新千本 ; 穂数型（JN）］を対照品種として，作期を2回［移植日1992年5月15日（ET），6月9日（LT）］設けて圃場試験を行い検討した．多収性品種（JI,SDI）の穂揃期の葉面積指数（LAI）は両作期ともJP，JNより高かったが，登熟期間での減少割合が大きく，収穫期には低い値を示した．SDIとJIの穂揃期地上部乾物重は，LTのアケノホシを除いて，両作期ともJP，JNより高かったが，登熟期間の乾物重の増加量に有意差はみられなかった．特にSDIでは登熟期間のLAIの減少割合が大きく，また，登熟期後半のSPAD値が大きく低下したことと相まって，登熟期間の個体群生長速度は最も低くなった．SDIおよびJIの収穫期の穂重はJP，JNと比較してETでは20～30%，LTでは18～20%高かった．また，両作期のSDIとJIの収穫期の地上部乾物重に対する穂重の割合は，JP，JNと比較して有意に高く，この差が穂重差に反映されたものと考えられた．穂重に対する出穂期までに茎葉に蓄積された乾物の分配率をみると，ETではJPとJNの平均値よりSDIとJIが約2倍，LTではSDIが約4倍それぞれ高い値を示した．穂揃期の穂重（シンク容量）は収穫期の穂重と有意な相関関係を示し，シンク容量の大きい品種は登熟期間の地上部乾物重増加量が少なくなる傾向がみられた．また，茎葉に蓄積された同化産物の穂重への分配率はシンク容量と関係が深いことが認められた．

キーワード : 乾物生産，収穫指数，水稲，転流，日印交雑型水稲品種，半矮性インド型水稲品種，穂重．

In Japan, the yielding ability of the existing rice varieties has already reached a plateau. Consequently, high yielding semidwarf indica varieties and japonica-indica hybrid varieties are being introduced to Japan from China, Korea and The Philippines (IRRI varieties) in order to increase productivity as well as improve existing varieties[4]. The green revolution in China, Korea and tropical countries was realized by semidwarf indica plant type with large panicle. These varieties can produce even 50% more spikelets per unit area than common Japanese varieties[4,7,30]. In previous studies it has been reported that semidwarf indica and japonica-indica hybrid varieties can produce even more than 900 kg/10 *a* of brown rice in the southern warmer districts of Japan[7,30]. Moreover, these varieties have a capactiy for producing more yield, which is evident from the existing large gap between the actual and the potential yield. This large gap is attributed mainly to a lower percentage of ripened grains[30]. To improve the lower percentage of ripened grains, thereby minimize the gap between the actual and potential yield, it is very important to clarify the characteristics of dry matter production and the partitioning of dry matter to grain of these high yielding rice varieties.

A large number of researchers have investigated the dry matter production patterns[2,6,8~10,12~17,19~21,23~26,28,30,31] and the relevant factors such as LAI[11,27] and photosynthesis[3,18] of semidwarf indica and japonica-indica hybrid varieties so far. However, these reports are not sufficient to make a general conclusion for the large number of varieties available. Most of the studies compared a few varieties at a time, with or without variations in heading time. Moreover, it is reported that the yield responses of these high yielding varieties to climatic conditions are more sensitive than that of conventional japonica varieties[5,7,8,14,16,23,26]. Therefore, the present experiment was conducted to investigate dry matter production characteristics before and after heading, its partitioning to panicles, and some related factors, such as changes in leaf area index, crop growth rate, and net assimilation rate of the high yielding semidwarf indica and the japonica-indica hybrid varieties, which have almost same heading time[30], in comparison with those of the japonica panicle weight and number type varieties during early and late cropping seasons.

Materials and Methods

The experiment was conducted at the experimental farm of the Faculty of Agriculture, Kochi University, from May to October, 1992. Eight varieties belonging to four varietal groups were used, viz. (i) Semidwarf Indica type (SDI) - Gui Zhao 2 and IR 36 ; (ii) Japonica-Indica hybrid type (JI) - Akenohoshi and Suweon 258 ; (iii) Japonica panicle weight type (JP) - Norin 22 and Koganemasari ; and (iv) Japonica panicle number type (JN) - Kinmaze and Nakateshinsenbon. The first two varietal groups were chosen as high yielding, and the other two groups as control. All the selected varieties have almost the same heading time[30]. Transplanting was performed in early and late cropping seasons with two replications. The early one was transplanted on May 20 and the late one on June 9, and from onwards would be represented by ET and LT, respectively. Seedlings were raised in seedling boxes after treating seeds with pesticides. The seedlings at the 3.5 leaf stage were transplanted at a rate of three seedlings per hill. Planting spacing between and within rows was 30 cm and 18 cm, respectively. Dates of heading, maturity and top dressing of fertilizer during ET and LT are shown in Table 1. Four days before transplanting, at puddling, basal doses of nitrogen (as N), phosphorus (as P_2O_5), and potassium (as K_2O) were applied at a rate of 5.5 kg, 11.4 kg and 6.4 kg per 10 *a* from the commercial fertilizers ammonium chloride, super phosphate and potassium chloride, respectively. The whole amount of phosphorus was applied as basal, while top dressing of N and K was done two times during panicle formation stage at a rate of 1.7 kg N and 1.7 kg K_2O per 10 *a*. The first top dressing was done when panicle length was about 2～5 mm and the second top dressing was done 8 or 10 days after the first top dressing in ET and LT, respectively (Table 1).

Samplings were done six times in both ET and LT, i.e., 10 days before heading, at heading, 10 days after heading (DAH), 20 DAH, 30 DAH, and at maturity. During each sampling, 10 hills from each plot were counted for productive tillers and from the average of

Table 1. Dates of heading, maturity and top dressing of fertilizer.[a]

Crop	Varietal group	Variety	Full heading[b]	Maturity[b]	Date of fertilizer top dressing[c] PI stage I (July 15)	PI stage II (July 25)
Early transplanted crop (ET)	Japonica panicle weight type (JP)	Norin 22	Aug. 8(85)	Sept. 11(119)	−20	−10
		Koganemasari	〃 5(82)	〃 16(124)	−22	−12
	Japonica panicle number type (JN)	Kinmaze	〃 3(80)	〃 10(118)	−19	−9
		Nakateshinsenbon	〃 1(78)	〃 10(118)	−17	−7
	Japonica-Indica hybrid (JI)	Akenohoshi	〃 3(80)	〃 11(119)	−19	−9
		Suweon 258	〃 6(83)	〃 16(124)	−22	−12
	Semidwarf indica (SDI)	Gui Zhao 2	〃 11(88)	〃 21(129)	−27	−17
		IR 36	〃 7(84)	〃 16(124)	−23	−13
					PI stage I (July 28)	PI stage II (August 5)
Late transplanted crop (LT)	Japonica panicle weight type (JP)	Norin 22	Aug. 22(74)	Oct. 1(114)	−25	−17
		Koganemasari	〃 24(76)	Sept. 24(107)	−27	−19
	Japonica panicle number type (JN)	Kinmaze	〃 24(76)	Oct. 3(116)	−27	−19
		Nakateshinsenbon	〃 21(73)	Sept. 30(113)	−24	−16
	Japonica-Indica hybrid (JI)	Akenohoshi	〃 21(73)	〃 30(113)	−24	−16
		Suweon 258	Sept. 1(84)	Oct. 9(122)	−35	−27
	Semidwarf indica (SDI)	Gui Zhao 2	Aug. 25(77)	〃 3(116)	−28	−20
		IR 36	〃 28(80)	〃 7(120)	−31	−23

a : Dates of sowing and transplanting of ET and LT were April 27 and May 15, and May 20 and June 9, 1992, respectively.

b : Numericals within parentheses indicate days after transplanting.

c : PI=Panicle initiation stage and numericals with minus (−) indicate days before full heading.

these hills, three hills were sampled, i.e., six hills from two replications of the same variety. Sampled hills were washed in tap water to remove soils and one hill from each plot was randomly selected for the measurement of the leaf area by an automatic area meter (Hayashi Denko Co. Japan, AAM-7). The leaf areas of the other two hills were calculated from the ratio of leaf area to leaf dry weight of the hill used for the leaf area measurement. Dry weights of plants were measured after drying in oven, first at 95°C for two hours and subsequently at 65°C for 48 hours. Data of LAI for all six samplings of the four representative varieties of four varietal groups were used for comparing the leaf area changing pattern during the period from 10 days before heading to maturity in both ET and LT (Fig. 2). Measurements of SPAD readings and photosynthetic rates in the flag leaf in ET were performed four times at intervals of about 10 days by means of a SPAD-501 (Minolta) meter and a portable CO_2 gas analyzer (KIP-8510, Koito Kogyo Co., Japan), respectively during the period from full heading to maturity (HM). The meteorological data such as daily temperature, sunshine hours and light intensity during the whole experimental period were taken from the monthly reports of the Faculty of Agriculture, Kochi University (Table 2). Using the leaf area and dry weight data of different plant organs at heading and maturity, dry matter production characteristics, and relevant factors were analyzed. The obtained data were subjected to statistical analyses and comparisons were done by using Duncan's New Multiple Range Test (DNMRT)[1].

Table 2. Ranges of temperatures (mean, minimum, maximum and accumulated), daily mean light intensity (DMLI) and daily mean sunshine hours (DMSH) of each variety during the crop growth period from transplanting to full heading, full heading to maturity and transplanting to maturity (April～October, 1992).

Crop	Mean temp. (°C)	Min. temp. (°C)	Max. temp. (°C)	Accum. temp. (°C)	DMLI ($MJ\ m^{-2}\ d^{-1}$)	DMSH (hd^{-1})
			Transplanting to full heading			
Early transplanted crop (ET)	22.5～22.9	18.7～19.2	26.2～26.5	1774～2037	15.6～15.9	9.8～10.0
Late transplanted crop (LT)	24.3～24.6	21.1～21.3	27.6～27.9	1800～2092	14.2～14.4	9.0～ 9.1
			Full heading to maturity			
ET	25.7～26.4	22.2～23.2	29.3～29.6	1027～1093	14.5～14.8	8.6～ 8.8
LT	22.4～25.4	19.5～21.7	27.6～29.1	813～1022	13.6～14.8	8.6～ 8.9
			Transplanting to maturity			
ET	24.3～24.5	20.2～20.2	27.3～27.4	2853～3118	15.1～15.3	9.3～ 9.9
LT	24.5～24.9	21.8～21.0	27.8～28.1	2692～3007	14.0～14.6	8.8～ 9.0

Results and Discussion

1. Effects of temperature, light intensity and daily sunshine hours on growth duration

Dates of heading, maturity and top dressing of fertilizer are presented in Table 1. The period from transplanting to heading was 78 (Nakateshinsenbon) to 88 (Gui Zhao 2) days in ET, and 73 (Nakateshinsenbon and Akenohoshi) to 84 (Gui Zhao 2) days in LT. In LT, each variety headed 4～11 days earlier, i.e., its vegetative phase was shorter than that in ET, except for Suweon 258. The period from transplanting to maturity was 118 (Kinmaze and Nakateshinsenbon) to 129 (Gui Zhao 2) days in ET, while it was 107 (Koganemasari) to 122 (Suweon 258) days in LT. The periods from full heading to maturity (HM) in ET and LT were 38～41 days and 31～40 days, respectively.

The meteorological data such as ranges of mean, minimum and maximum temperature, light intensity and mean daily sunshine hours during the two growth periods are summarized in Table 2. The mean temperature during the period from transplanting to full heading in LT was about 2°C higher than that in ET, while light intensity and sunshine hours in ET were 1.5 $MJ\ m^{-2}d^{-1}$ and 0.1 $h\ d^{-1}$ higher than that in LT, respectively (Table 2). The mean temperature during HM in ET was 1～3°C higher than that in LT. Although a slightly higher light intensity was observed in ET, no difference in the daily mean sunshine hours was observed in both the crops. During the entire period from transplanting to maturity, the mean temperature in LT was 0.2～0.4°C higher than in ET, whereas the accumulated temperature, light intensity and daily mean sunshine hours in ET were 111～161°C, 0.5～0.9 $MJ\ m^{-2}\ d^{-1}$, and 0.7～1.1 $h\ d^{-1}$ higher than in LT, respectively.

It is obvious from the above results that the period from transplanting to maturity in LT was about 2～17 days shorter, particularly 17 and 13 days shorter in Koganemasari and Gui Zhao 2 than in ET. It was also observed that full heading time in LT was about 4～11 days earlier than in ET, except for Suweon 258. These changes in heading time with the shifting of transplanting time might be due to the difference in sensitivity to meteorological conditions, especially temperature and day length. These conditions caused a shorter vegetative phase in LT, resulting in a lower dry matter production until heading than in ET. But there was almost no difference in the periods from full heading to maturity between ET and LT, exclusive of Koganemasari in LT (Table 1).

2. Changes in leaf area index (LAI)

The LAI at full heading and maturity and its decreasing percentage during HM are illustrated in Fig. 1. Significant differences were observed among the varieties in both ET and LT at heading. LAIs ranged from 7.8 (IR 36) to 5.2 (Nakateshinsenbon) in ET and from 6.4 (Suweon 258) to 3.4 (Nakateshinsenbon and Akenohoshi) in LT. LAIs of all varieties in ET, except for Suweon 258, were 0.4～2.7 higher than those in LT. This was mainly due to the difference in number of panicles during the cropping seasons. The varietal group orders of LAI at heading in ET and LT were SDI (7.4) >JP (6.0) >JI (5.7) >JN (5.5), and SDI (5.6) >JI (5.2) >JN (4.8) >JP (4.6), respectively. Yamamoto *et al.*[30] have reported that the LAIs of JI and SDI varieties at heading time were higher than those of japonica varieties. The present results are in agreement with the reported ones. However, Maruyama *et al.*[11] have reported that the LAI at full heading of SDI varieties was the same as those of japonica varieties, but the LAI of JI varieties was lower than in japonica varieties. On the other hand, Motomatsu *et al.*[13] have reported that the LAI at heading of both JI and SDI varieties was smaller than japonica varieties, which were inconsistent with the results of the present study.

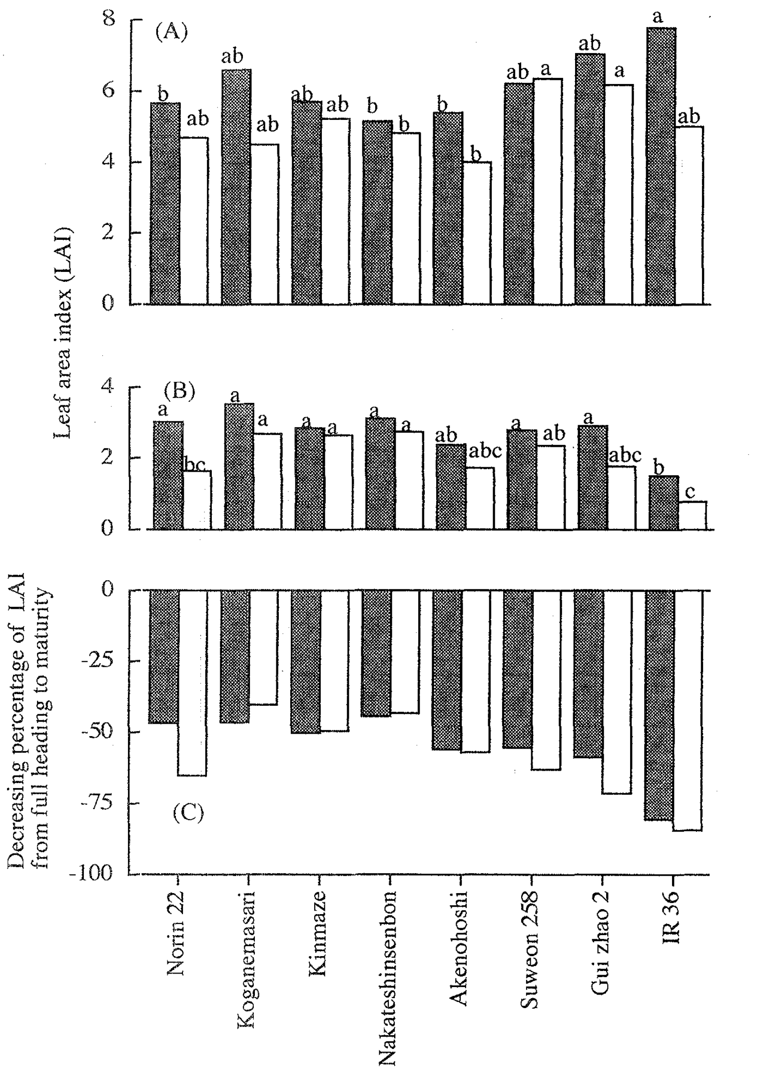

Fig. 1. Leaf area index (LAI) at full heading (A), at maturity (B), and decreasing percentage of LAI during the period from full heading to maturity (C). Columns followed by the same letter (s) is or are not statistically different from each other at 5% level of significance among the varieties within the same crop according to Duncan's New Multiple Range Test (DNMRT). ▩: Early transplanted crop (ET), □: Late transplanted crop (LT).

At maturity, the ranges of the LAIs were from 3.5 (Koganemasari) to 1.5 (IR 36) in ET and from 2.7 (Nakateshinsenbon) to 0.8 (IR 36) in LT. LAIs at maturity in ET were 0.2 (Nakateshinsenbon) to 1.4 (Norin 22) higher than those in LT. The varietal group orders in ET and LT were JP (3.3) >JN (3.0) >JI (2.6) >SDI (2.2), and JN (2.7) >JI (2.0) >JP (1.6) >SDI (1.3), respectively. Thus the LAI of the SDI group in both ET and LT at maturity were the lowest compared to the full heading time.

Decreasing percentages of LAIs of IR 36 during HM in both ET and LT were the highest, 80.6 and 84.4%, respectively, while the lowest decreasing percentage was 39.7% of Nakateshinsenbon in ET and 40.4% of Koganemasari in LT. The leaf area reduction patterns during the period from 10 days before full heading to maturity are shown in Fig. 2. It can be seen from this figure that the leaf area reduction patterns in japonica varieties Koganemasari and Nakateshinsenbon were less than those of the high yielding varieties, Akenohoshi and Gui Zhao 2. It was also observed that there was sharp reduction in LAI in the high yielding varieties[13].

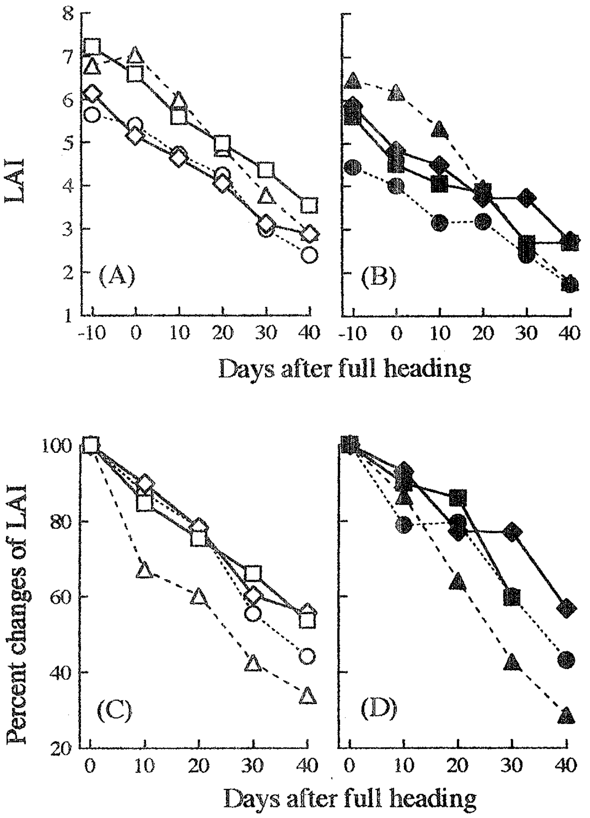

Fig. 2. Changes of LAI during the period from 10 days before full heading to maturity in ET (A), in LT (B), and percent changes of LAI during the same period in ET (C) and in LT (D), respectively, of four rice varieties.
ET : Koganemasari —□—, Nakateshinsenbon —◇—, Akenohoshi ···○···, Gui Zhao 2--△--.
LT : Koganemasari —■—, Nakateshinsenbon —◆—, Akenohoshi ···●···, Gui Zhao 2--▲--.

At full heading, the correlation between LAIs of different varieties in ET and LT was not significant (r=0.369 ns), but at maturity, a significant correlation (r=0.817*) was found between LAIs in ET and LT.

3. SPAD reading and photosynthetic rate of flag leaf

The SPAD reading and photosynthetic rates of flag leaf during HM in ET are illustrated in Figs. 3 and 4, respectively. It shows that in japonica varieties of the JN and JP groups, SPAD readings were about 38 and 42, respectively, at about full heading time, whereas around 35 days after heading, very little change occurred and the readings were about 34 and 41, respectively (Fig. 3(A) and (B)). During the same period, SPAD readings of the JI and SDI varieties declined from about 46 to 42, and from 40 to 26, respectively (Fig. 3(C)

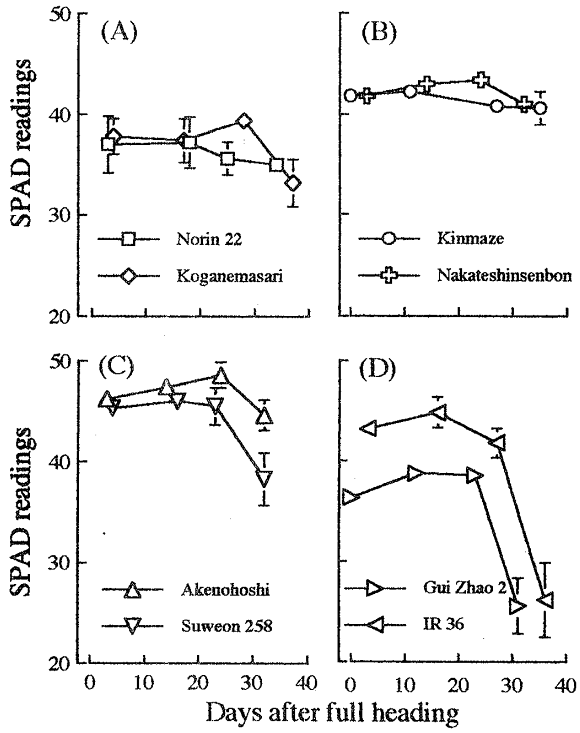

Fig. 3. Changes of SPAD readings of different varieties during the period from full heading to maturity in ET. Bars over the symbols for standard deviation (n=5), if not shown, fall within symbols.

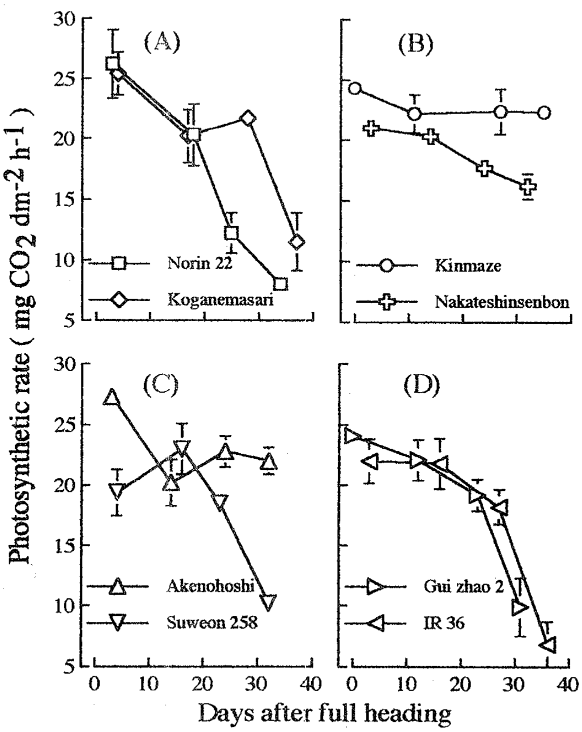

Fig. 4. Changes of photosynthetic rates of flag leaves of different varieties during the period from full heading to maturity in ET. Bar over the symbols are for standard deviation (n=5), if not shown, fall within symbols.

and (D)). These figures also depict that in the JI varieties, SPAD readings declined after about 25 days of heading with a minimum value of 35, whereas in SDI varieties the SPAD readings started declining from the same time as in JI, but it fell below 25.

The photosynthetic rate in flag leaves of almost all the varieties immediately after heading was about 25 mg CO_2 dm^{-1} h^{-1}, but the reduction pattern in the JN varieties, Kinmaze and Nakateshinsenbon, and the JI variety, Akenohoshi, were different from the others (Fig. 4). The photosynthetic rate of Kinmaze, Nakateshinsenbon and Akenohoshi remained higher even after about 30 days of heading, and did not decrease below 20 mg CO_2 dm^{-2} h^{-1}. However, in other varieties, it even decreased below 10 mg CO_2 dm^{-2} h^{-1} (Fig. 4(A), (C) and (D)). Jiang *et al.*[3] have reported that the flag leaf photosynthetic rate in JI variety, Akenohoshi, was higher than that of the japonica variety, Nipponbare, during HM. The result of the SPAD readings and photosynthetic rates (Figs. 3 and 4) in ET during HM indicates that the drastic decrease in leaf chlorophyll in SDI varieties[7] was responsible for lower photosynthetic rates at the later period of maturity, resulting in a small increase in top dry weight during that period than seen in the japonica varieties. On the other hand, the high photosynthetic rates for a longer period after heading in the JN varieties were responsible for a greater dry matter increment in these varieties. Saitoh *et al.*[18] have reported that the photosynthetic rate reduction with leaf aging in the JI and SDI varieties was higher than that in japonica varieties.

4. Dry matter production pattern

Top dry weights at heading and maturity, and increases in top dry weight during HM are presented in Fig. 5. The highest and the lowest total top dry matters until heading were 1114 (Gui Zhao 2) and 813 g m^{-2} (Nakateshinsenbon) in ET, and 836 (Gui Zhao 2) and 641 g m^{-2} (Akenohoshi) in LT, respectively (Fig. 5(A)). Thus, in both seasons, Gui Zhao 2 produced the highest top dry matter among the varieties, although it was lower in LT than in ET. The varietal group orders were SDI (1079) > JP (976) > JI (907) > JN (843) and SDI (804) > JN (752) > JP (738) > JI (713 g m^{-2}) in ET and LT, respectively.

The crop growth rate (CGR) during the period from transplanting to full heading ranged from 12.64 (Gui Zhao 2) to 10.40 g m^{-2} d^{-1} (Nakateshinsenbon) in ET, and from 10.84 (Gui Zhao 2) to 8.76 g m^{-2} d^{-1} (Akenohoshi) in LT. The ranges of net assimilation rate (NAR) during the same period, on the other hand, were from 14.23 (Koganemasari) to 9.78 g m^{-2} d^{-1} (IR 36) in ET, and from 12.93 (Nakateshinsenbon) to 8.33 g m^{-2} d^{-1} (Suweon 258) in LT.

The correlation between CGR and LAI during the period from transplanting to full heading in ET and LT together was positively significant ($r=0.618^*$), but individually it was not found to be significant either in ET or in LT. However, the correlation coefficient in ET ($r=0.625$ ns) was higher than that in LT ($r=0.340$ ns). No significant correlations between CGR and NAR were obtained either in ET and LT, taken separately or taken together, for the same period. These results show that the difference in CGR between ET and LT was brought about by the difference in LAIs[6].

The ranges of total top dry weights at maturity were from 1539 (Gui Zhao 2) to 1243 gm^{-2} (Akenohoshi) in ET, and from 1293 gm^{-2} (Suweon 258) to 1157 (Akenohoshi) in LT, respectively. A significant difference was observed among the varieties in respect of total top dry weight at maturity in ET only but not in LT (Fig. 5(B)). The varietal group orders were SDI (1435) > JP (1392) > JI (1296) > JN (1296) and JI (1225) > SDI (1200) > JN (1197) > JP (1152 gm^{-2}) in ET and LT, respectively.

The increase in top dry weight during HM showed no significant differences among the varieties either in ET or in LT (Fig. 5(C)). The ranges were from 490 (Nakateshinsenbon) to 286 gm^{-2} (IR 36) in ET and from 515 gm^{-2} (Akenohoshi) to 384 gm^{-2} (Gui Zhao 2) in LT. However, within the same variety, Akenohoshi and IR 36 showed differences in the increment of dry weight between ET and LT and the increment of these varieties was higher in LT than in ET. Jiang *et al.*[2] have reported that increase in dry weight of JI hybrid varieties during the ripening period was higher than that of the japonica varieties. These findings are in agreement with those of the present experimental results in LT, though the increment of dry weight in ET was slightly higher in japonica than in the JI and SDI varieties[6].

The correlations between top dry weights in ET and LT at full heading as well as maturity were not significant ($r=0.452$ ns and $r=0.228$ ns, respectively). The correlation of increase in top dry weights during HM between ET and LT was also not significant ($r=0.177$ ns). These results showed the different responses to meteorological conditions of the varieties to their performances.

CGR of the most varieties in LT during HM was higher than that in ET. When the varietal groups were considered, the SDI varieties in both ET (10.38~7.15 $gm^{-2}\ d^{-1}$) and LT (9.62 ~9.25 $gm^{-2}\ d^{-1}$) had the lowest CGR during HM. On the other hand, the japonica varieties had similar CGR within the same crop, which were higher in LT (14.01~10.13 $gm^{-2}\ d^{-1}$) than that in ET (12.25~9.17 $gm^{-2}\ d^{-1}$). Although the JI varieties had lower CGR (11.09~8.32 $gm^{-2}\ d^{-1}$) than the japonica varieties in ET, the trend was reverse in LT (13.75~12.35 $gm^{-2}\ d^{-1}$). According to Motomatsu *et al.*[13] and Saitoh *et al.*[17], CGR during ripening period of SDI varieties was similar to that of the japonica varieties, which are inconsistent to the present results. However, the present findings in LT are consistent with those of Takeda *et al.*[24], Jiang *et al.*[2], and Saitoh *et al.*[17] who reported that the CGR of JI varieties during ripening period were higher than those of the japonica.

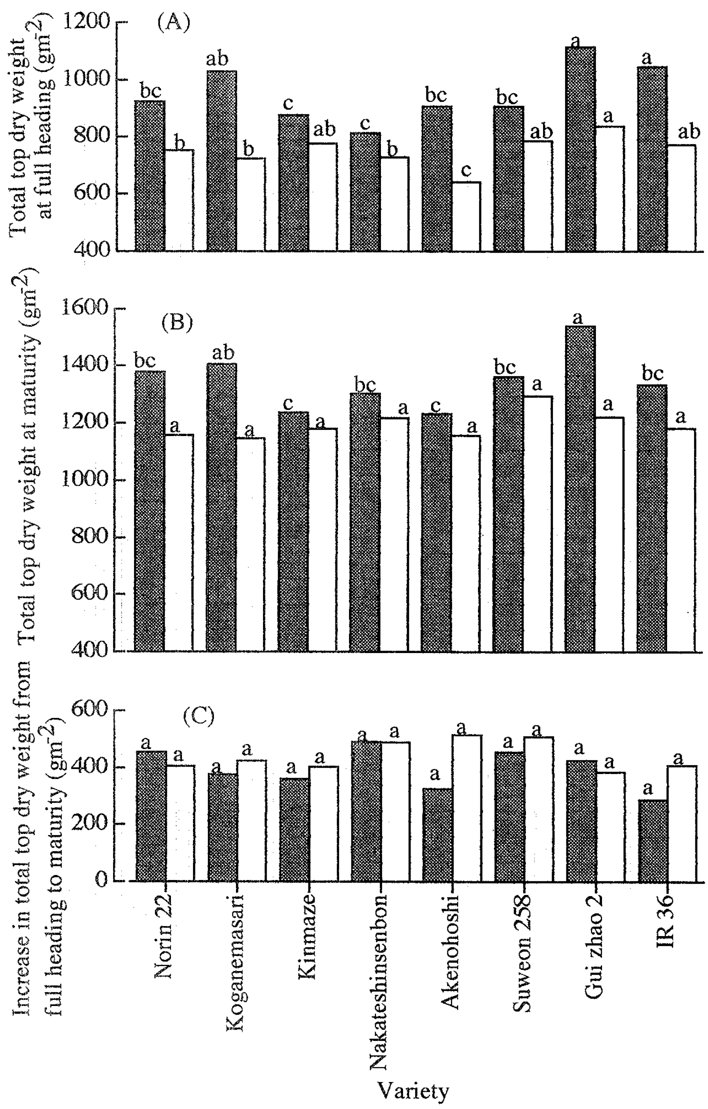

Fig. 5. Total top dry weights at full heading (A), at maturity (B), and increase in total top dry weight during the period from full heading to maturity (C). Columns followed by the same letter (s) is or are not statistically different from each other at 5% level of significance among the varieties within the same crop according to DNMRT. Column symbols are the same at those of Fig. 1.

The NAR of all the varieties in LT (2.66~4.77 $gm^{-2}\ d^{-1}$) was higher than those in ET (1.87 ~3.01 $gm^{-2}\ d^{-1}$) during HM, and the difference between Akenohoshi and Koganemasari was greater. NAR of Akenohoshi in LT (4.77 $gm^{-2}\ d^{-1}$) on an average 40% higher than in the japonica varieties (3.34 $gm^{-2}\ d^{-1}$) when compared within the same crop. Takeda *et al.*[24] and Jiang *et al.*[2] have reported that the NAR of JI hybrid varieties during the ripening period was 20% higher than those of the japonica varieties, which is in good agreement with the present results in LT. But Saitoh *et al.*[16] have reported that the NAR of JI hybrids and SDI varieties were lower than those of the japonica varieties. Those results are in agreement with the NAR in ET, but are different from that in LT. In the present experiment, NAR in LT was superior to NAR in ET due to the lower LAI of the former (Fig. 1(A)), which utilized solar energy properly, resulting in better NAR. But clear cut results were not yet obtained regarding the differences in NAR between japonica and high yielding varieties during the period from full heading to maturity. This was due to the weather conditions of the cropping season, the method and amount of fertilizer applications, and the cultivation procedures, such as planting density, which might have affected the LAI and light reception of the crop canopy[15,16].

CGR and NAR during HM in ET and LT together showed a significant positive correlation ($r=0.618^*$). Separately, they showed a significant positive correlation ($r=0.887^{**}$) in ET only. However, CGR and LAI did not show any significant correlation either separately, in ET or in LT, or in ET and LT taken together. These results clearly indicate that CGR during HM is mainly governed by the NAR.

5. The panicle weight and its constituent factors

The number of panicles per unit area of all the varietal groups was higher in ET than in LT, except for JI. The range of panicle numbers of JP, JN, JI and SDI varieties in ET were 376～457, 543～617, 311～454, and 348～513, respectively. In LT, they were 309～348, 413～583, 309～478, and 357～487, respectively.

(1) Panicle and straw weight

The panicle and straw dry weight, and the ratio of panicle dry weight to total top dry weight expressed as percentages (harvest index) at maturity are depicted in Fig. 6. Significant differences were observed among the panicle dry weights of the varieties at maturity. The highest and the lowest panicle dry weights were 854 (Gui Zhao 2) and 594 gm^{-2} (Kinmaze), respectively, in ET and 700 (Suweon 258) and 520 gm^{-2} (Koganemasari), respectively in LT (Fig. 6 (A)). The varietal group orders were SDI (812) >JI (743) >JP (628) >JN (611 gm^{-2}) in ET and JI (676) >SDI (655) >JN (586) >JP (538 gm^{-2}) in LT. The panicle dry weights (i.e., rough yield), of all the varieties and the varietal groups, were higher in ET than those in LT due to the greater single panicle dry weight and panicle number, except for the JI of the latter. A larger number of panicles were produced as a result of the greater number of tillers caused by the low temperature and more sunshine hours (Table 2) during the period from transplanting to heading in ET[7,29]. Komatsu *et al.*[7], Tezuka and Ito [26] and Nonoyama *et al.*[14] have reported that the earlier transplanting of SDI and JI varieties produce more yield owing to the larger number of spikelets and the increase in the percentage of ripened grains. Those findings are in agreement with the present results. It was observed that the panicle dry weights of high yielding varieties (SDI and JI) were about 125～190 gm^{-2} (20～31%) and 105～115 gm^{-2} (18～20%) higher than those of japonica varieties (JN and JP) in ET and LT, respectively (Fig. 6). However, the mean number of panicles of JN varieties was higher than that of the SDI and JI varieties in both ET and LT, and that of the JP was higher than JI in ET only. These results coincided with the differences of brown rice yields among these varietal groups of a previous report[30], in which the yield differences were attributed to the larger number of spikelets per panicle as well as per unit area of the SDI and JI compared to the JN and JP varieties. The high yields of the JI and SDI varieties compared to the japonica varieties have been reported by several researchers[2,5,7,8,13,14,17,19,20,23,24,26,31]. The straw dry weight at maturity showed significant differences among the varieties in both ET and LT (Fig. 6 (B)). The ranges of straw dry weights were from 769 (Koganemasari) to 521 gm^{-2} (Akenohoshi) in ET, and from 626 (Koganemasari) to 506 gm^{-2} (Akenohoshi) in LT. The varietal group orders were JP (764) >JN (658) >SDI (623) >JI (553 gm^{-2}) in ET and JP (614) >JN (612) >JI (549) >SDI (535 gm^{-2}) in LT.

Significant differences were also observed in the ratio of panicle weight to total top dry weight at maturity (harvest index) among the varieties in both ET and LT (Fig. 6 (C)). In ET, the highest and the lowest ratios were 57.8% in IR 36 and 44.9% in Norin 22, respectively, while in LT, they were 56.3% in Akenohoshi and 44.5% in Koganemasari, respectively. Among the varietal groups, the SDI and JI varieties (56%) were superior to JP and JN varieties (47%) in both ET and LT. These results are in good agreement with the previous findings[2,6,7,13,17,23,30,31], and thereby suggest that the harvest index is an inherent characteristic of the varietal groups which does not change markedly with cropping seasons.

Large differences in panicle dry weight between the high yielding varieties and the japonica varieties were observed. To clarify the reason of differences, the correlation analysis between the panicle dry weight and the total top dry weight at maturity was investigated. It revealed a positive significant correlation (r=0.707**) when all the varieties in ET and LT were taken together. Further the panicle dry weight and the ratio of panicle dry weight to the total top dry weight at maturity in ET and LT together showed a high positive correlation (r=0.928**), while they had significant positive correlation coefficients: r=0.818* and r=0.759*, respectively, when taken separately (Table 3).

(2) Panicle weight and assimilates before and after heading

In order to know the answer to the question of whether higher panicle dry weight of high yielding varieties was due to the accumulation of assimilates during HM or translocation of stored matter in shoot until heading, the relationships of panicle dry weight with the increase in top dry weight and decrease in shoot dry weight during HM were analyzed. The panicle dry weight and increase in top dry weight during the period did not show a significant correlation, but panicle dry weight and the decrease in shoot dry weight in ET showed a positive significant correlation (r=0.793*). Although the latter relationship was not significant in LT, its correlation coefficient was relatively high (r=0.595 ns). On the other hand, when the panicle dry weight and decrease in shoot dry weight in ET and LT were taken together, there was a significant positive correlation: r=0.802* (Table 3).

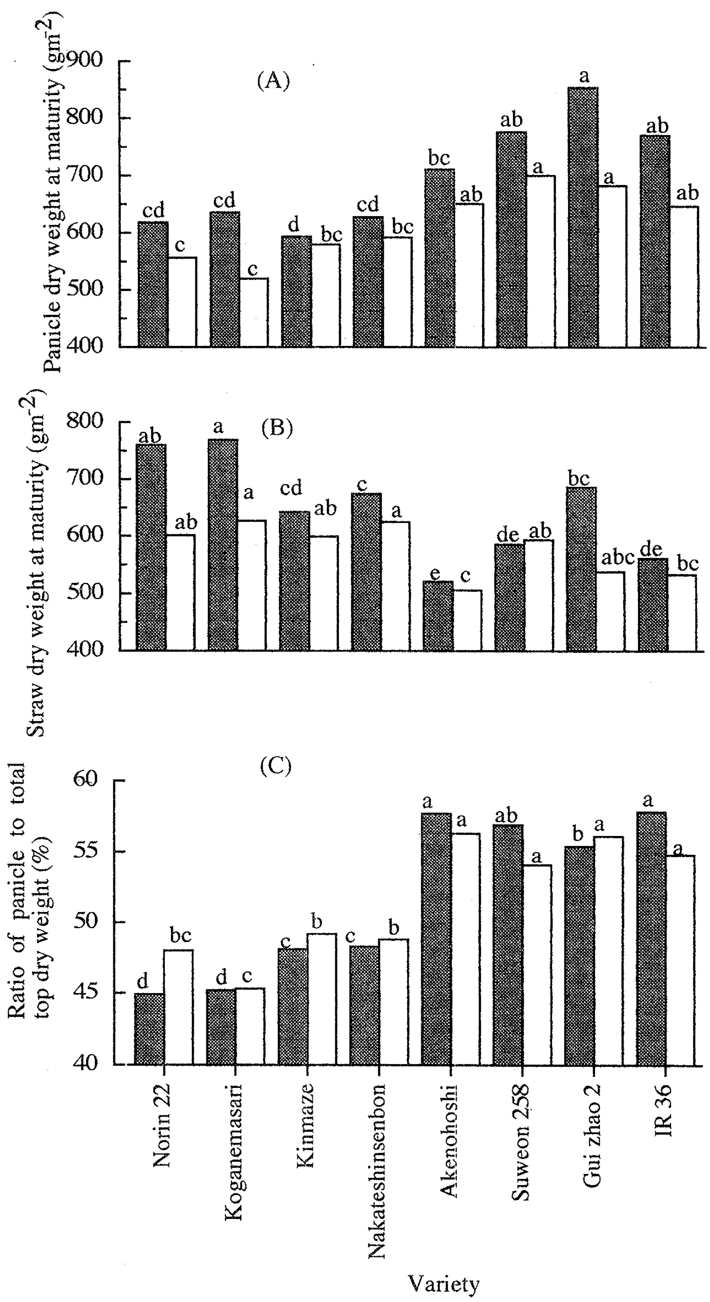

Fig. 6. Dry weights of panicle (A), straw (B), and ratio of panicle to total top dry weight at maturity (C). Column followed by the same letter (s) is or are not statistically different from each other at 5% level of significance among the varieties within the same crop according to DNMRT. Column symbols are the same as those of Fig. 1.

It was demonstrated that the high yielding varieties translocated more stored matter to the panicles than the japonica varieties, which ultimately resulted in higher decrease in shoot weight of high yielding varieties than the japonica varieties during the HM[20]. Kubota *et al.*[8] have reported that sufficient accumulated materials until the start of translocation to panicle were necessary for high yields. Weng *et al.*[28] have reported that the weight of panicles is largely dependent on the accumulated materials in shoots and their translocation to panicles during HM, i.e., the more accumulated materials of the varieties, the higher the panicle weights. The present study also reveals that the high yielding varieties had more accumulated materials in the shoot before heading than the japonica varieties, and more translocation of those materials occurred during HM[6].

As mentioned above, the increase in top dry weight during HM of the high yielding varieties was lower than that of the japonica varieties, but the translocation of accumulated materials from shoot to panicle was higher in the high yielding varieties. The partitioning of stored assimilates in shoot before heading and the current assimilates after heading to panicles during HM are shown in Fig. 7. Clearly, IR 36 had the highest partitioning of 53.1% and Nakateshinsenbon had the lowest of 7.2% in ET, whereas in LT, Gui Zhao 2 had the highest partitioning of 32.2%. On the contrary, a little contribution of translocatory materials from shoot to panicle was observed in Koganemasari (1.6%), Nakateshinsenbon (2.5%) and Akenohoshi (5.0%) in LT during HM. It should be noted that these values fluctuated with the cropping season within the same variety as well as among the varieties[30].

Table 3. Correlation matrix of different characters.

Correlation between-	Correlation coefficient	Regression line[a]
Total top dry weight (TTDW) and panicle dry weight (PDW) at maturity (gm^{-2})	ET : r=0.566 ns	—
	LT : r=0.700 ns	—
	ET+LT : r=0.707**	y=0.57x−64.26
Ratio of PDW to TTDW (%) and PDW at maturity (gm^{-2})	ET : r=0.818*	y=13.45x+1.58
	LT : r=0.759**	y=13.83x−57.79
	ET+LT : r=0.928**	y=13.99x−105.24
Increase in TTDW during the period from full heading to maturity and PDW at maturity (gm^{-2})	ET : r=0.128 ns	—
	LT : r=0.321 ns	—
	ET+LT : r=0.155 ns	—
Decrease in shoot dry weight (SDW) during the period from full heading to maturity and PDW at maturity (gm^{-2})	ET : r=0.793*	y=0.71x+579.96
	LT : r=0.595 ns	—
	ET+LT : r=0.802**	y=0.73x+571.67
PDW at full heading and increase in TTDW during the period from full heading to maturity (gm^{-2})	ET : r=0.436 ns	—
	LT : r=0.008 ns	—
	ET+LT : r=0.439 ns	—
PDW at full heading and decrease in SDW during the period from full heading to maturity (gm^{-2})	ET : r=0.870**	y=4.02x−377.92
	LT : r=0.670 ns	—
	ET+LT : r=0.873**	y=3.61x−321.40
PDW at full heading and PDW at maturity (gm^{-2})	ET : r=0.881**	y=3.65x+204.17
	LT : r=0.843**	y=3.78x+211.53
	ET+LT : r=0.896**	y=3.39x+246.37
PDW at full heading and total straw dry weight at maturity (gm^{-2})	ET : r=0.329 ns	—
	LT : r=0.643 ns	—
	ET+LT : r=0.018 ns	—
PDW at full heading (gm^{-2}) and ratio of PDW to TTDW at maturity (%)	ET : r=0.708*	y=0.18x+27.65
	LT : r=0.817*	y=0.24x+25.56
	ET+LT : r=0.593*	y=0.12x+36.75

a : Regression lines have shown for only significant relations. ET and LT are for the early and late transplanted crop, respectively. * and ** are significant at 5% and 1% levels, respectively.

The varietal group orders were SDI (45.5) >JI (36.7) >JP (16.7) >JN (16.0%) in ET and SDI (26.9) >JN (8.9) >JI (8.2) >JP (6.6%) in LT. Both in ET and in LT, the SDI varieties had a maximum partitioning. Thus, the shoot dry matter partitioning percentages to panicles of the SDI and JI varieties were more than two times in ET and about four times in the SDI than those of the japonica varieties in LT (Fig. 7(A) and (B)).

(3) Sink capacity and partitioning of reserved shoot matter

To elucidate the dominant factors responsible for the differences in shoot matter partitioning to panicles among the varieties, the relationships of the panicle weight at full heading (as an indicator of sink capacity) with the increase in total top dry weight, or with the decrease in shoot dry weight during HM, were examined. The first relationship showed no significant correlation either in ET and LT taken separately, or taken together, but the second relationship had a significant positive relation in ET ($r=0.870^{**}$) and also in the case of ET and LT taken together ($r=0.873^{**}$), while in LT, the correlation coefficient was relatively high ($r=0.670$ ns) but not significant.

The panicle dry weight at full heading stage (sink capacity) was found to be closely related to the partitioning of shoot matter to panicle during HM and yield at maturity. Further relationships between the panicle weight at full heading and the panicle dry weight at maturity, or the straw dry weight at maturity, or the ratio of panicle dry weight to total top dry weight at maturity were investigated. The first and the third showed positive significant correlations for either ET and LT together ($r=0.896^{**}$ and 0.593^{*}) or separately ($r=0.881^{**}$, 0.843^{**} ; $r=0.708^{*}$, 0.817^{*}, respectively) but the second relationship showed no significant correlation. These results indicated that the sink capacity plays an important role in shoot matter partitioning to panicles[9]. The present results also indicate that panicle dry weights at full heading were closely related to the yield and when the sink capacity was high, the increase in top dry weight during HM had a tendency to be lower[26]. This implies that the higher the panicle dry weight at heading (i.e., the higher the sink capacity), the higher the panicle dry weight at harvest[21]. Saitho *et al.*[19] have reported that the increase in top dry weight of JI variety during HM was somewhat smaller, but the yield was very high. This is because of a large sink capacity and a greater translocation of the accumulated materials to the panicles before heading and after heading compared to the japonica varieties. Takebe *et al.*[23] have reported that the active translocation of dry matter and nutrients from the lower leaves and culms to the grains were related to the high yield of the high yielding varieties. Tezuka and Ito[26] have reported that the assimilates translocation from the shoot to the panicles of the semidwarf indica cultivars

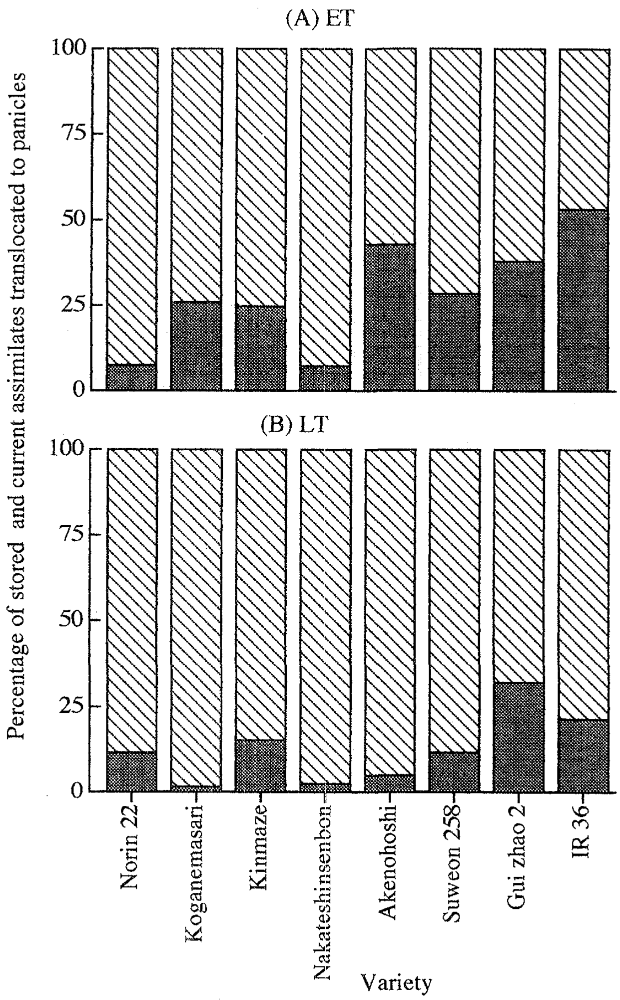

Fig. 7. Partitioning percentage of stored assimilates in shoot before heading and assimilates after heading to panicles in different varieties in ET (A) and LT (B). Column symbols are at follows :

▩ : Stored assimilates before full heading translocated to panicles,

▧ : Current assimilates translocated to panicles.

was higher due to large number of spikelets. Thus, both of them in combination produce high yields.

From the above results and discussion, it can be concluded that the panicle dry weights of the high yielding SDI and JI varieties were higher than those of the japonica varieties in both ET and LT. But the panicle dry weight differences among the varietal groups were affected by the cropping seasons, and were higher in ET than those in LT[5,7,8,14,26]. In ET, higher temperature and light intensity (Table 2) during HM positively affected the yield of the JI and SDI varieties[22]. The main factor responsible for the yield difference depends on the difference in the ratio of the panicle dry weight to total top dry weight rather than the differences in the total top dry weight increased during HM[6,31]. The higher ratios of panicles to total top dry weights at maturity of high yielding varieties were responsible for higher rate of translocation from shoot to panicles during HM as compared to the japonica varieties. It was demonstrated that this character was an inherent one, which does not change markedly with the cropping seasons and that the contribution ratio of accumulated assimilates in shoot to panicle was closely related to the sink capacity. This study also indicated that although the high yielding varieties under consideration had a large sink capacity, the increase in total top dry weights during HM were lower than those of the japonica varieties. This might be attributed to the faster leaf aging[13,23,27] and the rapid reduction in leaf photosynthesis[18] exclusive of Akenohoshi[3] during the same period. These are the factors associated with the lower percentage of ripened grains of the high yielding varieties, although many spikelets per unit area are produced[30]. The reasons for the fast leaf aging during HM might be due to the decrease in nutrient absorption and the large sink capacity, and/or the decrease in root activity. It is necessary to study further, the fertilizer management of these varieties, especially N management, for leaf photosynthesis and senescence during the grain ripening period[12] to improve the lower percentage of the ripened grains of the high yielding SDI and JI varieties.

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