Plant Prod. Sci. 9(4) : 435 — 445 (2006)

Growth of Three Rice Cultivars (*Oryza sativa* L.) under Upland Conditions with Different Levels of Water Supply
2. Grain Yield

Yoichiro Kato[1], Akihiko Kamoshita[2] and Junko Yamagishi[1]

([1]Field Production Science Center, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Midori-cho 1-1-1 Nishitokyo, Tokyo 188-0002, Japan;
[2]Asian Natural Environmental Science Center, The University of Tokyo, Midori-cho1-1-1 Nishitokyo, Tokyo 188-0002, Japan)

Abstract : Upland rice production has great potential as a water-saving form of agriculture if yield can be increased and stabilized across a range of environments with different levels of water supply. The objective of this study was to clarify the effects of water supply and plant characteristics on grain yield of rice (*Oryza sativa* L.) grown under upland conditions. We compared grain yield (ranging from 346-685 g m^{-2}) and yield components of three rice cultivars ('Yumeno-hatamochi', YHM; 'Lemont', LMT; 'Nipponbare', NPB) grown under upland conditions with three water regimes (rain-fed, RU; irrigated, IU; and water deficit during the panicle-formation stage, WD) with those of rice grown under flooded lowland (FL) conditions (ranging from 394-649 g m^{-2}) from 2001 to 2003 at Nishitokyo, Japan. Grain yield and each yield component of NPB in RU were comparable to those in FL when there was ample rain during the 40 days before heading in 2003. However, grain yield of NPB decreased with decreasing water supply during the period of 20-40 days before heading under upland conditions ($r = 0.93$) as a result of reduced number of spikelets per unit area and reduced harvest index. Water productivity (grain yield per unit water supply) in rice in RU and IU ranged from 0.43 to 1.05 kg m^{-3} in the three cultivars across the 3 years, and was more than twice the corresponding value in FL. We found a cultivar – water regime interaction for grain yield within each year and a cultivar × environment interaction across all the 5 upland conditions in 2002 and 2003. In FL, NPB and LMT had higher yields than YHM, while LMT had the highest yield under all upland conditions and NPB grain yield under the suboptimal upland environments (i.e. RU and IU in 2002) decreased to the largest extent compared with that under optimal upland environment, i.e. IU in 2003 among the three cultivars. The reasons for the highest grain yield of LMT across upland conditions were maintenance of large panicle and high harvest index. Maximum yield was lowest in YHM. In WD, yield potential and growth recovery, rather than crop growth during water stress, affected the cultivar ranking in terms of grain yield. We conclude that water supply during panicle development is important for maintenance of high yield and that a high potential yield and harvest index, as well as yield stability under different water regimes, are important putative plant characters for developing new elite varieties for water-saving upland rice production.

Key words : Grain yield, Harvest index, Upland rice, Water productivity, Water supply, Yield potential.

Upland rice (*Oryza sativa* L.) production has great potential as a water-saving form of agriculture (Bouman, 2001) because it requires less water (irrigation plus rainfall) than flooded lowland rice production systems. Studies of upland rice grown with irrigation ("aerobic rice") have recently begun in China (Yang et al., 2005) and at the International Rice Research Institute (IRRI) (Lafitte et al., 2002; Bouman et al., 2005), and the extent of the success in reducing water consumption is being quantified in terms of water productivity, which is defined as grain yield per unit of water supply as a measure of the efficiency of water use in rice production (Borrell et al., 1997; Bouman and Tuong, 2001; Tabbal et al., 2002; Belder et al., 2004; Hayashi et al., 2006; Kamoshita et al., 2007).

For use in flooded lowlands, IRRI has developed semi-dwarf varieties of rice that have contributed to yield increases by enhancing the harvest index and the number of spikelets per unit area (Peng et al., 1999; Peng and Khush, 2003). A high harvest index with a large panicle is also characteristic of high-yielding lowland varieties that have been developed in Japan (Jiang et al., 1988; Saito et al., 1991; Kumura, 1993; Kushibuchi, 1997). Also, high harvest index were regarded as an important character to enhance yield potential of rain-fed lowland rice (Fischer et al., 2003), but the corresponding characteristics have not yet been demonstrated in upland rice. In the regions where late-season drought frequently occurs such as in Northeast Thailand, earlier flowering germplasms are preferred in breeding programs because of their drought escape mechanisms (Fukai et al., 1999), but phenology requirement in water limited upland

Received 1 September 2005. Accepted 11 April 2006. Corresponding author: A. Kamoshita (akamoshita@anesc.u-tokyo.ac.jp, fax +81-42-463-1696).

fields in temperate regions such as in Japan, might be different, as is expected from the different rainfall pattern, and worth investigation. Information required to develop new rice varieties with high yield potential under water-saving upland conditions is limited.

In upland rice production, water supply is the main limiting factor in many Asian countries (Widawsky and O'Toole, 1996; Tsunoda, 1997; Nemoto et al., 1998). Grain yield and the yield components of upland rice may be affected in different manners by the patterns of water supply (Boonjung and Fukai, 1996). Especially, rice plants are susceptible to water deficit during meiosis stage or around flowering in pot experiments (Reyniers et al., 1982; Tajima, 1990), but the demonstration at field levels are not much reported. In tropical upland rice, Lafitte et al. (2002) tried to identify the particular stages that had the most detrimental effects on yield reduction, but they could not. In addition, a large cultivar × water regime (C × W) interaction exists for grain yield in upland rice (Lafitte and Courtois, 2002; Lafitte et al., 2002), since differences in plant characteristics such as panicle size, tillering, rooting, and phenology may cause differences in dry matter production (Kato et al., 2006a) and yield formation under different water regimes. These plant characteristics are not yet well-understood (Price et al., 2002). Therefore, we should clarify not only the causes of yield reduction from the yield formation processes under water limiting upland fields, and identify the important stages of water supply, but also the desirable plant characteristics adapted to upland conditions.

In the present paper, we analyzed the grain yield, yield components, and water use of three rice cultivars under upland conditions with different levels of water supply to clarify the effects of water supply and plant characteristics on rice yield. We also discuss the water availability suitable for upland rice production as an alternative to flooded lowland rice production.

Materials and Methods

1. Experimental design

The rice plants were cultivated at the Field Production Science Center of The University of Tokyo, at Nishitokyo (Japan) under nine experimental conditions, from 2001 to 2003. Table 1 shows the experimental design and weather conditions. For details, see Kato et al. (2006a). Our experiments were conducted under rain-fed upland conditions (RU in 2001–2003), irrigated upland conditions (IU in 2002 and 2003 only), upland conditions with a water deficit during the panicle-formation stage (WD, 88-106 days after sowing (DAS) and 116-145 DAS in 2003), and flooded lowland conditions (FL in 2001–2003). In 2002, plant establishment was poor in IU owing to lower initial soil moisture in the experimental field. In FL in 2002, nitrogen uptake and dry matter production were smaller than expected owing to the lack of any top-dressing. In 2001, rainfall in July and early-August (late-vegetative and panicle-formation stage) was much less than the average (15 mm), but there was ample rain before heading in 2003. In IU, supplementary irrigation was applied from July to September, with the total amount of irrigation being 60 mm in 2002 and 125 mm in 2003. Three cultivars (the upland cultivar 'Yumeno-hatamochi', YHM; the lowland cultivar 'Lemont', LMT; and the lowland cultivar 'Nipponbare', NPB) were used in our study, but only NPB in 2001.

2. Measurements

The harvested area in each treatment that was used for yield determination ranged from 0.54 to 0.90 m^2 (12 to 18 hills), depending on the treatment and year (Kato et al., 2006a). We selected three to six hills with an average number of panicles as a subsample for measuring the yield components. We hand-threshed the panicles in the subsample and separated filled spikelets that sank in tap water from unfilled spikelets. The filled and unfilled spikelets were then oven-dried at 80°C for at least 3 days, and their numbers and weights were determined. The number of spikelets per panicle and their fertility (the number of filled spikelets divided by the total spikelet number) were then calculated. Grain yield was determined by multiplying the weight of the dried panicles in the bulksample by the the ratio of the weight of the dried grains to the weight of the panicles in the subsample, then adjusting the grain yield to a moisture content of 14% and assuming that the moisture content of dried grain was 3% (IRRI, 1996). We calculated the harvest index by dividing the dry weight of grains by the total weight of the above ground dry matter. Water productivity was determined by dividing grain yield by the total water supply (irrigation plus rainfall) during the period of crop growth. Compared with water use efficiency (dry matter production per transpiration or evapotranspiration), water productivity is regarded as a more suitable index for quantifying the effects of water management or evaluating the effectiveness of cultivation methods designed to save water (Bouman and Tuong, 2001). In 2003, we also counted the number of spikelets per panicle and the number of primary and secondary rachis branches, as well as panicle length on the longest culm on three plants. Data for all treatments in a given year were analyzed using analysis of variance using Systat 10.0 (SPSS, 2000). Combined analysis on the C × W interaction and comparison among the water regimes were also conducted by the statistical model of the interaction between cultivar and location (IRRI, 1999). We used the least-significance difference at $P = 0.05$ or 0.10 (marginally significant) when comparing cultivar differences within a treatment. The coefficients of correlation between grain yield (and the yield

Table 1. Summary of the upland and flooded lowland conditions in 2001, 2002 and 2003.

Year	Temperature and solar radiation	Treatment[(a)]	Water regime	Water supply[(b)] until H (mm)	Water supply[(b)] until M (mm)
2001	Above normal level during panicle-formation stage	FL	Continuous flooding	NA[(c)]	NA[(c)]
		RU	Rainfed; scarce rainfall during panicle-formation stage	431	895
2002	Normal	FL	Continuous flooding	NA[(c)]	NA[(c)]
		RU	Rainfed; normal level of rainfall	622	992
		IU	Total of 60 mm irrigation during panicle-formation stage	676	1052
2003	Below normal level during panicle-formation stage	FL	Continuous flooding	NA[(c)]	NA[(c)]
		RU	Rainfed; ample rainfall until heading	794	1008
		IU	Total of 125 mm irrigation during panicle-formation stage	899	1132
		WD	Water supply excluded during panicle formation and early ripening stage	359	419

(a) FL, flooded lowland; RU, rainfed upland; IU, irrigated upland; WD, water deficit under upland conditions during the panicle-formation stage.
(b) Amount of irrigation plus rainfall. Data were those of Nipponbare. H = heading, M = maturity.
(c) Data were not available.

components) and the total water supply during various growth stages under six upland conditions (RU in 2001, 2002 and 2003, IU in 2002 and 2003, WD in 2003) were also calculated for NPB.

Results

1. Grain yield and yield components

In 2001, the grain yield and harvest index of NPB in RU were 25% and 14%, respectively, lower than that in FL (Table 2). Many small or infertile panicles were produced during grain-filling in RU. The numbers of spikelets per panicle and per unit area in NPB in RU were 32% and 29% lower, respectively, than those in FL.

In 2002, a nitrogen deficit occurred in FL during later growth stages owing to the lack of any top-dressing, and as a result, the grain yield of NPB in RU was not significantly different from that in FL (Table 2). Despite the use of supplementary irrigation, the grain yield of NPB was the lowest of all the cultivars in IU because of inferior initial plant establishment. There was a C × W interaction for grain yield among the three conditions (i.e., FL, RU and IU; Table 2), but there was no C × W interaction for grain yield between the two upland conditions (i.e., RU and IU; data not shown). Grain yield was not significantly different in FL, though NPB had the highest value. In RU and IU, LMT had the highest yield, followed by YHM. Harvest index was the highest in LMT in all treatments. In RU and IU, the number of spikelets per unit area was much lower in NPB than in the other cultivars, but did not differ among cultivars in FL. The fertility of YHM was 75% or lower in all treatments, but the weight in 1000 grains was the heaviest in YHM among the three cultivars (Table 2).

In 2003, the grain yield of NPB in RU was only 6 % lower than that in FL (Table 2). Among the upland conditions, the grain yields of NPB in IU and WD were 9% higher and 37% lower, respectively, than in RU. There was a C × W interaction for grain yield among all the 4 treatments (Table 2), though there was no C × W interaction for grain yield among the 3 upland conditions (data not shown). NPB had the highest yield in FL, but LMT (followed by NPB) under all upland conditions. The mean harvest index of these cultivars was the greatest in IU (0.45), followed by FL and RU. The harvest index in WD (0.37) was considerably lower. The harvest index was the highest in LMT in all treatments, as was the case in 2002. Panicle number and spikelets number per panicle were significantly lower in WD than in RU. Supplementary irrigation in IU significantly increased spikelets number per panicle than in RU. Thus, the mean number of spikelets per unit area was the highest in IU, but considerably lower in WD. LMT also had the highest number of spikelets per unit area under all upland conditions, but NPB had the highest number per unit area in FL. Mean fertility was the highest in IU followed by RU, and decreased slightly in WD (the average of the three cultivars was 0.77, Table 2). The

Table 2. Grain yield and yield components for three cultivars (Yumeno-hatamochi [YHM], Lemont [LMT] and Nipponbare [NPB]) grown under flooded lowland, rainfed upland, irrigated upland and water deficit upland from 2001 to 2003. Least significant difference at P = 0.05 (*) and 0.10 (†) were also shown.

	Grain Yield ($g\ m^{-2}$)	Harvest Index	Panicle number (m^{-2})	Spikelets number ($panicle^{-1}$)	Spikelets number per area ($\times 10^3\ m^{-2}$)	Fertility (%)	1000 grains weight (g)
2001							
Flooded lowland							
NPB	627	0.43	313	97	30.4	84	24.5
Rainfed upland							
NPB	468	0.37	335	66	21.7	82	26.4
LSD	*91**	*0.05**	*20†*	*9**	*4.9**	*n.s.*	*0.9**
2002							
Flooded lowland							
YHM	436	0.43	221	85	18.8	75	32.0
LMT	492	0.49	151	137	20.7	88	26.7
NPB	497	0.40	226	89	20.0	92	26.4
LSD	*n.s.*	*0.02**	*20**	*13**	*n.s.*	*3**	*0.4**
Rainfed upland							
YHM	562	0.37	294	126	37.1	59	28.7
LMT	637	0.48	170	190	32.0	88	22.3
NPB	480	0.39	262	80	21.1	91	25.7
LSD	*87**	*0.04**	*36**	*32**	*4.8**	*4**	*2.7**
Irrigated upland							
YHM	504	0.40	255	129	32.8	59	27.8
LMT	631	0.49	150	230	34.3	82	23.6
NPB	453	0.41	237	86	20.2	91	26.6
LSD	*102**	*0.02**	*48**	*21**	*4.4**	*11**	*2.0**
Water regime							
Flooded lowland	475	0.44	199	104	19.8	85	28.3
Rainfed upland	560	0.42	242	132	30.1	79	25.6
Irrigated upland	529	0.43	214	148	29.1	77	26.0
LSD	*63†*	*n.s.*	*22**	*13**	*3.7**	*4**	*0.4**
Cultivar	*	*	*	*	*	*	*
Cultivar × Water	*	*	n.s.	*	*	*	*
2003							
Flooded lowland							
YHM	394	0.34	318	81	25.7	55	29.0
LMT	638	0.51	196	173	33.8	84	23.4
NPB	649	0.43	314	114	35.7	84	24.2
LSD	*62**	*0.04**	*40**	*14**	*3.9**	*8**	*1.9**
Rainfed upland							
YHM	484	0.37	330	85	28.2	64	27.7
LMT	655	0.47	171	200	32.2	89	23.0
NPB	607	0.41	294	106	31.2	85	25.0
LSD	*87**	*0.03**	*37**	*28**	*n.s.*	*8**	*0.8**
Irrigated upland							
YHM	595	0.43	314	101	31.7	75	28.5
LMT	685	0.48	181	206	37.4	90	22.6
NPB	662	0.43	279	123	34.3	85	25.1
LSD	*65**	*0.02**	*27**	*24**	*n.s.*	*7**	*1.2**
Water Deficit							
YHM	346	0.34	244	87	21.4	64	26.9
LMT	440	0.43	131	202	26.3	85	21.4
NPB	380	0.34	224	98	22.0	83	22.7
LSD	*55**	*0.05**	*27**	*34**	*3.3†*	*14†*	*1.0**
Water regime							
Flooded lowland	561	0.43	276	122	31.7	75	25.5
Rainfed upland	582	0.42	265	130	30.5	80	25.2
Irrigated upland	647	0.45	258	143	34.4	83	25.4
Water deficit upland	389	0.37	200	129	23.2	77	23.7
LSD	*57**	*0.01**	*23**	*11**	*3.0**	*5**	*0.5**
Cultivar	*	*	*	*	*	*	*
Cultivar × Water	*	*	†	n.s.	n.s.	n.s.	†

n.s. means difference in the same column was not statistically significant.

Table 3. Spikelet number per panicle, panicle length, number of primary rachis branches (PR) and secondary rachis branches (SR), and the ratio of the number of SR to that of PR of the longest culm for three cultivars (Yumeno-hatamochi [YHM], Lemont [LMT] and Nipponbare [NPB]) grown under flooded lowland, rainfed upland, irrigated upland and water deficit upland in 2003. Least significant difference at P = 0.05 (*) was also shown.

	Spikelets number (panicle^{-1})	Panicle length (cm)	PR	SR	SR/PR
Cultivar					
YHM	139	22.6	9.8	25.2	2.6
LMT	244	26.0	14.4	43.8	3.0
NPB	144	22.2	12.2	24.6	2.0
LSD	*13**	*0.8**	*0.4**	*2.6**	-
Water regime					
Flooded lowland	165	24.4	11.0	29.8	2.7
Rainfed upland	180	23.6	12.5	31.9	2.5
Irrigated upland	184	23.5	12.3	33.5	2.7
Water deficit upland	173	22.9	12.7	29.6	2.3
LSD	*6**	*0.5**	*0.5**	*1.5**	-
Cultivar × Water	n.s.	*	n.s.	*	-

n.s. means difference in the same column was not statistically significant.

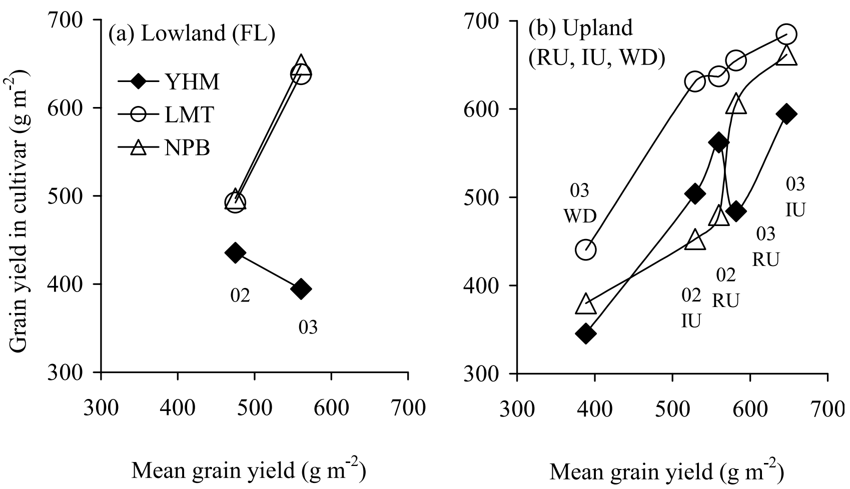

Fig. 1. Relationship between mean grain yield of three cultivars and the grain yield of each cultivar under different environmental conditions (flooded lowland, FL; rain-fed upland, RU; irrigated upland, IU; and water-deficit upland, WD) in 2002 and 2003. Cultivars used were ('Yumeno-Hatamochi', YHM; 'Lemont', LMT; and 'Nipponbare', NPB). Years are indicated as follows: 02 = 2002, 03 = 2003. Mean grain yield on the x-axis indicates average grain yield among the three cultivars in each environment.

fertility of YHM was 75% or less in all treatments, as was the case in 2002.

The number of spikelets per panicle on the longest culm was the highest in LMT in all treatments (Table 3). Though the C × W interaction for this variable was not significant, the number of spikelets per panicle on the longest culm was relatively stable in LMT, whereas this value decreased by 17% and 9%, respectively, in NPB and YHM in WD compared with the value in IU. Panicle length on the longest culm of NPB was also shorter in WD than in IU. In WD, the number of secondary rachis branches on the longest culm of YHM and NPB was lower, but that of LMT was not, compared with the corresponding values in IU. When we compared the ratio of the number of secondary rachis branches to that of primary rachis branches (Table 3) in order to eliminate any bias caused by the number of primary rachis branches, we found that the

Table 4. Coefficients of correlation between grain yield (and yield components) of Nipponbare and the amount of water supply (rainfall plus irrigation) among six upland conditions.

	Total	Until heading	During 20 d before heading	During 20-40 d before heading	During 40 days before heading	During 40-60 d before heading	During 60 days before heading
Grain yield	0.724	0.899 *	0.709	0.926 **	0.934 **	0.382	0.906 *
Harvest index	0.914 *	0.977 **	0.746	0.913 *	0.947 **	0.673	0.989 **
Panicle number	0.399	0.106	0.724	0.072	0.444	-0.559	0.247
Spikelets per panicle	0.141	0.665	−0.004	0.810	0.471	0.546	0.545
Spikelets per unit area	0.410	0.763	0.425	0.876 *	0.747	0.293	0.722
Fertility	0.473	0.371	0.122	0.202	0.186	0.785	0.356
1000 grain weight	0.777	0.298	0.796	0.097	0.498	0.035	0.442

Significance at P = 0.01 (**), 0.05 (*) was |r| = 0.917, 0.811, respectively.

ratio did not differ between IU and WD in LMT, but that the ratios were lower in WD than in IU or FL in YHM and NPB.

In a combined analysis of the data of 2002 and 2003, there was a cultivar-environment interaction in grain yield across all the 7 treatments as well as across all the 5 upland conditions (data not shown). The relationship between mean yield and grain yield of each cultivar is shown for two lowland conditions (Fig. 1a) and five upland conditions (Fig. 1b). LMT had the highest grain yield under all upland conditions. NPB achieved a high yield (more than 600 g m^{-2}) in upland environments with the most favorable conditions (i.e., in 2003), but its yield declined sharply in environments with only moderately favorable conditions (i.e., in 2002). YHM had the lowest yield in 2003, partly because its fertility was reduced by low temperatures during panicle development. However, YHM tended to have a higher yield than NPB under suboptimal upland conditions in 2002.

2. Relationship of water supply to grain yield under upland conditions

Table 4 shows the coefficients of correlation between grain yield (and the yield components) and the total water supply during various growth stages of NPB under upland conditions. Grain yield and harvest index were strongly and significantly correlated with the water supply during the 40 days before heading (r = 0.934 and 0.947, respectively) and during the 20 to 40 days before heading (r = 0.926 and 0.913, respectively). Among the yield components, the number of spikelets per unit area was significantly correlated with the water supply during the 20 to 40 days before heading (r = 0.876); no other components were significantly correlated with water supply during any period before heading (Table 4) or during any post-heading stage (data not shown).

Water productivity in RU, IU, and WD ranged from 0.43 to 1.05 kg m^{-3} among the three cultivars. Water productivity was much higher in WD than under other conditions (Table 5). LMT achieved the highest water productivity in both years. C × W interaction did not exist in water productivity in both 2002 and 2003. With supplementary irrigation, water productivity did not decrease compared with RU in both years.

Table 5. Water productivity (kg m^{-3}; grain production per unit volume of water suppy) for three cultivars (Yumenohatamochi [YHM], Lemont [LMT] and Nipponbare [NPB]) grown under rainfed, irrigated and water deficit upland trials in 2001, 2002 and 2003.

	2001[(a)]	2002	2003
Cultivar			
YHM	-	0.55	0.65
LMT	-	0.63	0.77
NPB	0.52	0.46	0.70
LSD	-	*0.06**	*0.05**
Water regime			
Flooded lowland[(b)]	-	-	-
Rainfed upland	0.52	0.58	0.59
Irrigated upland	-	0.51	0.59
Water deficit upland	-	-	0.94
LSD	-	*n.s.*	*0.06**
Cultivar × Water	-	n.s.	n.s.

(a) Data in 2001 was that of NPB in rainfed upland.
(b) Though water productivity was not determined in flooded lowland in this study, the other study (Kamoshita et al., 2007) showed that water productivity of NPB in flooded lowland in 2002 at the same experimental site was 0.18 kg m^{-3}, when grain yield was 535 g m^{-2}.

Discussion

1. Grain yield and water productivity between upland and lowland conditions

In upland conditions, rice yield is prone to be lower than in flooded lowland conditions, but it

Table 6. Comparison of grain yield and water productivity between flooded lowland (F) and favourable upland condition (U) from various references.

Reference	Country	Grain yield ($g\ m^{-2}$) F	Grain yield ($g\ m^{-2}$) U		Water productivity ($kg\ m^{-3}$) F	Water productivity ($kg\ m^{-3}$) U	Cultivar [a]	Information about aerobic condition
Hasegawa, 1962	Japan	448	373	(17) [b]	-	-	2 U and 1 L	Over -50 kPa (10 cm depth)
Yun et al., 1997	Japan	556	499	(10)	-	-	1 U and 3 L	Rainfed (rainfall was about 900 mm)
Yang et al., 2005	China	700	476	(32)	0.50	0.74	2 UxL and 1 L	Soil water content in root zone at 80-90 %
McCauley, 1990	USA	636	507	(20)	-	0.48	14 L	Water supply more than evapotranspiration
Westcott and Vines, 1986	USA	785	590	(25)	-	-	6 L	Over -30 kPa (15 cm depth)
Blackwell et al., 1985	Australia	687	581	(15)	0.07	0.34	1 L	28 % more than pan evaporation
Bouman et al., 2005[c]	Philippines	494	349	(29)	0.28	0.44	1 UxL and 2 L	Over -30 kPa (15 cm depth); Dry season
Bouman et al., 2005[c]	Philippines	510	416	(18)	0.29	0.46	1 UxL and 2 L	Over -30 kPa (15 cm depth); Wet season

(a) U, L and UxL mean upland, lowland and upland x lowland cultivars respectively.
(b) Values in parentheses were yield reducitions (%) under upland condition compared with flooded lowland.
(c) Data were the first year (2001) of the three years due to yield decline as a result of monocropping of upland rice in the subsequent years.

could be comparable to or higher than in the lowland conditions under adequate rainfall or irrigation (i.e., RU and IU in 2003). NPB, an elite lowland cultivar in Japan with its potential yield over 600 g m^{-2} under flooded lowland conditions (e.g., FL in 2001 and 2003), yielded 25% less grain in RU than in FL in a dry year (2001), due to small harvest index and spikelet number per area, and yielded less than 500 g m^{-2} in RU even in a normal year with approximately 1000 mm of rainfall during crop growth (2002). The grain yield and each yield component in RU in a year with adequate and frequent rainfall (2003) were comparable to the values in FL (Table 2). This favourable water availability in uplands in 2003 allowed greater amounts of nitrogen uptake and higher total dry matter production than in FL (Kato et al., 2006a), which would have lead to high grain yield under RU and IU in 2003. There are not many studies experimentally assessing the productivity of rice under both lowland and upland conditions. Among the 7 studies that compared grain yield of rice between favourable upland and flooded lowland conditions (Hasegawa, 1962; Blackwell et al., 1985; Westcott and Vines, 1986; McCauley, 1990; Yun et al., 1997; Bouman et al., 2005; Yang et al., 2005) we found yield disadvantages of 10% to 32% under upland conditions (Table 6), even though there were no obvious environmental stresses and crop management was adequate. The yield reduction under upland conditions was due to a reduction in the number of spikelets per panicle in one of the studies listed in Table 6 (Peng, 2003; Bouman et al., 2005). However, a few studies done in temperate climates with favorable water supply revealed smaller reductions or even similar grain yields in uplands compared with flooded lowlands (Yun et al., 1997). Studies in the Philippines have shown that the reduction in grain yield under upland conditions compared with yields in a flooded lowland was smaller during the wet season than during the dry season (Bouman et al., 2005).

The water productivity of NPB under upland conditions in the present study ranged from 0.43 to 0.91 kg m^{-3}, or 2.4 to 5.1 times the value for this cultivar in our flooded lowland (0.18 kg m^{-3}; Hayashi et al., 2006; Kamoshita et al., 2007), and other studies have also reported higher water productivity under upland conditions (Table 6). Upland rice production is a promising alternative to lowland rice production with insufficient water to permit flooding. Further testing at the basin level will be necessary in order to extrapolate our results at the field level and demonstrate superior resource use of upland rice over lowland rice; at the basin level, various factors such as rainfall, evapotranspiration, the water-holding capacity of soil, and the amount of available irrigation affect the water balance. Furthermore, the additional beneficial roles of paddy fields, such as the maintenance of biodiversity and landscape, and "externalities" such as

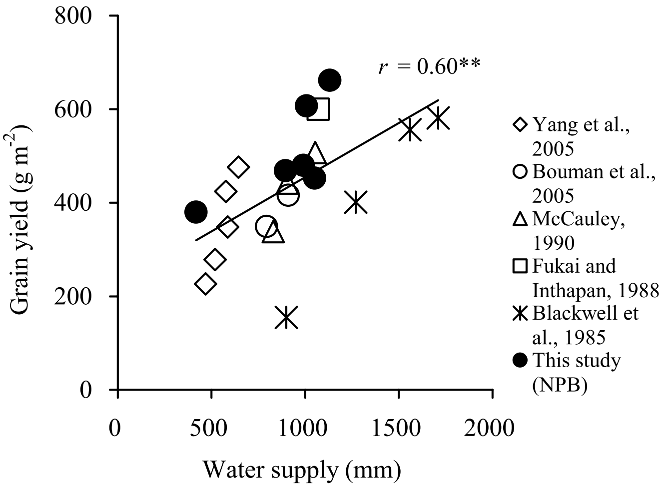

Fig. 2. Relationship between the water supply during crop growth (rainfall plus irrigation) and grain yield under upland conditions based on data cited in the literature. **, P = 0.01.

reducing air temperature (Kamoshita, 2003), should not be neglected. Adopting upland rice production as an alternative to production in flooded lowlands may depend on which aspect of the rice production system is most important in respective local situation.

2. Water supply and grain yield under upland conditions

The grain yield of NPB, an elite lowland cultivar, under upland conditions increased with increasing water supply before heading (Table 2, 4). The water supply during panicle development, particularly during the 20-40 days before heading, was the most critical for panicle size and grain yield under the upland conditions in our study. The yield of NPB increased by 9% as a result of supplementary irrigation, without significantly reducing water productivity (Table 5). Although water productivity increased in WD, the grain yield of NPB decreased by 33%. The variation in grain yield under upland conditions was attributed primarily to the number of spikelets per unit area and to the harvest index (Table 4), as well as to biomass production and nitrogen uptake (Kato et al., 2006a). The water supply during panicle development affected the development of secondary rachis branch and each spikelet (Table 3), and consequently harvest index. Previous studies have also shown that grain yield under upland conditions generally increased as the water supply increased (Fig. 2; e.g., Fukai and Inthapan, 1988), although the amount of water supply was not determined in previous older works (Nakagawa and Goto, 1963; Puckridge and O'Toole, 1981; Aragon and De Datta, 1982). It should be also noted that within the range of yield levels in our trials for NPB cultivar (380-662 g m^{-2}), water supply during 20-40 days before heading was more important than during 0-20 days before heading. Although pot experiments identified the critical susceptible stage of rice plants to declining internal plant water status around meiosis stage (i.e. about 10 days before heading) or flowering stage (Reyniers et al., 1982; Tajima, 1990), we found that water supply during earlier stage during panicle development (i.e. 20-40 days before heading) was more important under the realistic water deficiency in the field experiments, through greater nitrogen uptake and biomass production (Kato et al., 2006a) and sink organ development. In Japan and temperate regions of Far East, ample rainfall is usually expected after the heading of rice plants (i.e. from late August and September; Table 1), whereas dry spells sometimes occur before heading (e.g., 2001). The present study indicated that supplementary irrigation supply during panicle development effectively minimized the reduction in growth and yield in dry years with scarce rainfall before heading. When greater amounts of water supply are available either from supplementary irrigation or rainfall, larger amounts of nutrient supply may be needed to achieve a higher potential yield of upland rice, and this aspect of nutrient in relation to water supply should be further studied.

3. Cultivar differences in grain yield under upland conditions

The yield of the upland cultivar YHM was lower than that of NPB and LMT in FL in both 2002 and 2003. NPB produced the largest biomass (Kato et al., 2006a), with many panicles, and LMT achieved a higher harvest index with larger panicles than the other cultivars. The reason for low yield of YHM was relatively short growth duration and low biomass production, with a small sink size (number of spikelets per unit area) and low fertility (Table 2). Since many of the current Japanese upland rice varieties mature earlier and produce lower yields than YHM (Hirasawa et al., 1998), they also may not produce high yield under flooded lowland conditions.

There was a cultivar × environment interaction for grain yield among upland conditions across years with different water regimes (data not shown). In uplands, LMT and NPB had the highest yield under optimal conditions (i.e., RU and IU in 2003). However, the yield of NPB declined sharply with suboptimal conditions (i.e., in 2002; Fig. 1b), with greater reduction in both panicle and spikelet number than Lemont. This was because NPB, a cultivar with shallower roots, had reduced nitrogen uptake and hence decreased the dry matter production (Kato et al., 2006a) and probably assimilate supply to developing panicles. More detailed experiments are needed to assess the role of deep roots in nutrient uptake under water limiting conditions.

The stress level in WD was not so severe in the present study (a 40% yield reduction in WD compared with IU) and the ranking of the cultivars in terms of grain yield in WD (i.e., LMT > NPB > YHM) was similar to the ranking of their maximum yield under favorable water conditions. Although nitrogen uptake and dry matter production of YHM were superior to those of the other cultivars at the end of stress, the later-maturing LMT and NPB had a correspondingly longer period of recovery growth and hence achieved higher yield than YHM. Under mild to moderate conditions, intermittent water deficits during panicle development, recovery growth seems to be significant. Importance of recovery growth was also recognized under the stress during seedling stage (Mitchell et al., 1998). Later-maturing germplasm may be useful in terms of resource use in humid temperate regions, where moderate levels of intermittent water deficit from the vegetative to the early-reproductive stage are expected and where rainfall is ample later in the growing season; the longer maturation period provides more time for recovery growth.

LMT had the highest grain yield under all upland conditions because it had a larger panicle and the highest number of secondary rachis branches (Table 3) and had the highest harvest index (Table 2). Producing a higher harvest index has been a major driving force for yield improvement in irrigated lowland rice both in tropical areas (Peng et al., 1999; Peng and Khush, 2003) and in temperate areas (Saito et al., 1991; Hiraoka et al., 1992). High harvest index and high potential yield were regarded as important characters in rain-fed lowland rice as well (Jearakongman et al., 1995; Romyen et al., 1998; Fukai et al., 1999; Pantuwan et al., 2002). Although YHM is a recently developed, improved upland cultivar with higher yield than traditional Japanese upland cultivars (Hirasawa et al., 1998; Nemoto et al., 1998) with high biomass production and nitrogen uptake (Kato et al., 2006a), its maximum yield was the lowest of the three cultivars in our study partly owing to its lower fertility. The flotation method we used to separate unfilled grains may not be appropriate for estimating the fertility of YHM, because partially filled grains in the huge husks of YHM may have been discarded as unfilled in our study. Nonetheless, the potential yield of the current upland rice varieties in Japan is still lower than that of lowland rice varieties, as is the case for many traditional upland varieties in other marginal areas of Asia. Further enhancing potential yield of upland rice by improving harvest index through the development of large panicles may be necessary, as was suggested by the present study and previous results (Aragon and De Datta, 1982; Lafitte et al., 2002).

In conclusion, in order to develop new elite varieties for water-saving rice production in upland systems, we should take higher potential yield, harvest index and sink size as well as plant characteristics adapted to uplands (Kato et al., 2006a; e.g., a deep root system and high N uptake, yield stability under different water regimes) into account. Further study is needed to compare grain yield under uplands with that under lowland conditions using more diverse germplasm (e.g., *indica* vs. *japonica*). As stress levels become more intense, putative drought resistance traits may become increasingly important for upland rice (Ludrow and Muchow, 1990; Fukai and Cooper, 1995; Nguyen et al., 1997). Some of the physio-morphological aspects of the cultivars in the present study, such as the role of the root system in extracting soil water and maintaining favorable plant water status, will be reported in another paper (Kato et al., 2006b).

Acknowledgments

We thank Mr. N. Washizu, Mr. K. Ichikawa, Ms. C. Sasaki, Ms. C. Yamazaki, Ms. S. Nakata, and Mr. H. Kimura (Field Production Science Center, The University of Tokyo) for their technical assistance in carrying out these experiments. We also thank Mr. K. Urasaki (Suntory Co., Ltd.) for his help in collecting data. Seeds of 'Yumeno-hatamochi' and 'Lemont' were provided by the Plant Biotechnology Institute, Ibaraki Agricultural Center, and the MAFF Genebank, National Institute of Agrobiological Sciences, Japan. This study was financially supported by the Moritani Foundation Scholarship and Inter-departmental Research Funds from the Graduate School of Agricultural and Life Sciences, The University of Tokyo.

References

Aragon, E.L. and De Datta, S.K. 1982. Drought response of rice at different nitrogen levels using line source sprinkler system. Irrig. Sci. 3 : 63-73.

Belder, P., Bouman, B.A.M., Cabangon, R., Lu, G., Quilang, E.J.P., Li, Y., Spiertz, J.H.J. and Tuong, T.P. 2004. Effect of water-saving irrigation on rice yield and water use in typical lowland conditions in Asia. Agric. Water Manage. 65 : 193-210.

Blackwell, J., Meyer, W.S. and Smith, R.C.G. 1985. Growth and yield of rice under sprinkler irrigation on a free-draining soil. Aust. J. Exp. Agric. 25 : 636-641.

Boonjung, H. and Fukai, S. 1996. Effect of soil water deficit at different growth stages on rice growth and yield under upland conditions. 2. Phenology, biomass production and yield. Field Crops Res. 48 : 47-55.

Borrell, A., Garside, A. and Fukai, S. 1997. Improving efficiency of water use for irrigated rice in a semi-arid tropical environment. Field Crops Res. 51 : 231-248.

Bouman, B.A.M. 2001. Water-efficient management strategies in rice production. Internat. Rice Res. Notes 16 : 17-22.

Bouman, B.A.M. and Tuong, T.P. 2001. Field water management to save water and increase its productivity in irrigated lowland rice. Agric. Water Manage. 49 : 11-30.

Bouman, B.A.M., Peng, S., Castañeda, A.R. and Visperas, R.M. 2005. Yield and water use of irrigated tropical aerobic rice systems. Agric. Water Manage. 74 : 87-105.

Fischer K.S., Fukai, S., Lafitte, H.R. and McLaren, G. 2003.

Know your target environment. In Fischer, K.S., Lafitte, H.R., Fukai, S., Atlin, G. and Hardy, B. eds., Breeding Rice for Drought-prone Environments. International Rice Research Institute, Los Baños, Philippines. 5-11.

Fukai, S. and Inthapan, P. 1988. Growth and yield of rice cultivars under sprinkler irrigation in south-eastern Queensland. 1. Effects of sowing time. Aust. J. Exp. Agric. 28 : 237-242.

Fukai, S. and Cooper, M. 1995. Development of drought-resistant cultivars using physio-morphological traits in rice. Field Crops Res. 40 : 67-86.

Fukai, S., Pantuwan, G., Jongdee, B. and Cooper, M. 1999. Screening for drought resistance in rainfed lowland rice. Field Crops Res. 64 : 61-74.

Hasegawa, S. 1962. Studies on the paddy rice growing on upland field. J. Cent. Agric. Exp. Sta. 1 : 109-156**.

Hayashi, S., Kamoshita, A. and Yamagishi, J. 2006. Effect of planting density on grain yield and water productivity of rice (*Oryza sativa* L.) grown in flooded and non-flooded fields in Japan. Plant Prod. Sci. (In review).

Hiraoka, K., Tatebe, M. and Yoneyama, T. 1992. Physiological characteristics of high-yielding rice varieties (4) : high productivity of Kanto 146 (Takanari) with special reference to nutrient partitioning and sink (panicle) structure. Jpn. J. Soil Sci. Plant Nutr. 63 : 517-523*.

Hirasawa, H., Nemoto, H., Suga, T., Ishihara, M., Hirayama, M., Okamoto, K. and Miyamoto, M. 1998. Breeding of a new upland rice variety "Yumenohatamochi" with high drought resistance and good eating quality. Breed. Sci. 48 : 415-419*.

IRRI. 1996. Quality Assurance Notebook of Measurements, International Rice Research Institute, Los Baños, Philippines. 49.

IRRI. 1999. Experimental design and data analysis for agricultural research. Volume 1. International Rice Research Institute, Los Baños, Philippines. 409.

Jearakongman, S., Rajatasereekul, S., Naklang, K., Romyen, P., Fukai, S., Skulkhu, E., Jumpaket, B. and Nathabutr, K. 1995. Growth and grain yield of contrasting rice cultivars grown under different conditions of water availability. Field Crops Res. 44 : 139-150.

Jiang, C.Z., Hirasawa, T. and Ishihara, K. 1988. Physiological and ecological characteristics of high yielding varieties in rice plants. 1. Yield and dry matter production. Jpn. J. Crop Sci. 57 : 132-138*.

Kamoshita, A. 2003. Recent status of irrigation water using and the strategies of water saving in paddy rice system in Japan. In Kim, Y.W. ed., Proceedings of International Symposium on Enhancement of Water Use Efficiency in Lowland Rice Cultivation, 15-19 September 2003, National Honam Agricultural Experiment Station, Rural Development Administration. Iksan, Korea. 93-121.

Kamoshita, A., Ishikawa, M., Abe, J. and Imoto, H. 2007. Development of water saving rice – winter crop production system in a suburb of Tokyo in the view of water productivity. Plant Prod. Sci. (In review).

Kato, Y., Kamoshita, A., Abe, J. and Yamagishi, J. 2006a. Growth of rice (*Oryza sativa* L.) cultivars under upland conditions with different levels of water supply. 1. Nitrogen uptake and dry matter production. Plant Prod. Sci. (In press)

Kato, Y., Kamoshita, A., Abe, J., Imoto, H. and Yamagishi, J. 2006b. Growth of rice (*Oryza sativa* L.) cultivars under upland conditions with different levels of water supply. 3. Root system development, water extraction and plant water status. Plant Prod. Sci. (In press).

Kumura, A. 1993. Physiology of high-yielding rice plants from the viewpoint of dry-matter production and its partitioning. In Matsuo, T., Kumazawa, K., Ishii, R., Ishihara, K., Hirata, H. eds., Science of the Rice Plant. 2. Physiology. Tokyo : Food and Agriculture Policy Research Center. 705-736.

Kushibuchi, K. 1997. Historical changes in rice cultivars. In Matsuo, T., Futsuhara, F., Kikuchi, F., Yamaguchi, H. eds., Science of the Rice Plant. 3. Genetics. Tokyo : Food and Agriculture Policy Research Center. 837-875.

Lafitte, H.R. and Courtois, B. 2002. Interpreting cultivar x environment interactions for grain yield in upland rice : Assigning value to drought-adaptive traits. Crop Sci. 42 : 1409-1420.

Lafitte, H.R., Courtois, B. and Arrandeau, M. 2002. Genetic improvement of rice in aerobic systems : progress from yield to genes. Field Crops Res. 75 : 171-190.

Ludrow, M.M. and Muchow, R.C. 1990. A critical evaluation of traits for improving crop yields in water-limited environments. Adv. Agron. 47 : 107-153.

McCauley, G.N. 1990. Sprinkler vs. flood irrigation in traditional rice production regions of Southeast Texas. Agron. J. 82 : 677-683.

Mitchell, J.H., Siamhan, D., Wamala, M.H., Risimeri, J.B., Chinyamakobvu, E., Henderson, S.A. and Fukai, S. 1998. The use of seedling leaf death score for evaluation of drought resistance of rice. Field Crops Res. 55 : 129-139.

Nakagawa, K. and Goto, Y. 1963. The relation of amount of irrigation water and growth stage of paddy and upland rice. Bull. Tokai Kinki Nat. Agric. Exp. Sta. 10 : 93-101**.

Nemoto, H., Suga, R., Ishihara, M. and Okutsu, Y. 1998. Deep rooted rice varieties detected through the observation of root characteristics using the trench method. Breed. Sci. 48 : 321-324.

Nguyen, H.T., Babu, R.C. and Blum, A. 1997. Breeding for drought resistance in rice : Physiology and molecular genetics considerations. Crop Sci. 37 : 1426-1434.

Pantuwan, G., Fukai, S., Cooper, M., Rajatasereekul, S. and O'Toole, J.C. 2002. Yield response of rice (*Oryza sativa* L.) genotypes to different types of drought under rainfed lowlands [sic] Part 1. Grain yield and yield components. Field Crops Res. 73 : 153-168.

Peng, S., Cassman, K.G., Virmani, S.S., Sheehy, J. and Khush, G.S. 1999. Yield potential trends of tropical rice since the release of IR8 and the challenge of increasing rice yield potential. Crop Sci. 39 : 1552-1559.

Peng, S. 2003. Comparison between aerobic rice and flooded rice in yield stability. In Kim, Y.W. ed., Proceedings of International Symposium on Enhancement of Water Use Efficiency in Lowland Rice Cultivation, September 15-19, 2003, National Honam Agricultural Experiment Station, Rural Development Administration. Iksan, Korea, 153-166.

Peng, S. and Khush, G.S. 2003. Four decades of breeding for varietal improvement of irrigated lowland rice in the International Rice Research Institute. Plant Prod. Sci. 6 : 157-164.

Price, A.H., Cairns, J.E., Horton, P., Jones, R.G.W. and Griffiths,

H. 2002. Linking drought-resistance mechanisms to drought avoidance in upland rice during a QTL approach : progress and new opportunities to integrate stomatal and mesophyll responses. J. Exp. Bot. 53 : 989-1004.

Puckridge, D.W. and O'Toole, J.C. 1981. Dry matter and grain production of rice, using a line source sprinkler in drought studies. Field Crops Res. 3 : 303-319.

Reyniers, F.N., Truong-Binh, Jacquinot, L. and Nicou, R. 1982. Breeding for drought resistance in dryland rice. In O'Toole, J.C. ed., Drought Resistance in Crops with the Emphasis on Rice. International Rice Research Institute, Los Baños, Philippines. 273-292.

Romyen, P., Hanviriyapant, P., Rajatasereekul, S., Khunthasuvon, S., Fukai, S., Basnayake, J. and Skulkhu, E. 1998. Lowland rice improvement in northern and northeast Thailand. 2. Cultivar differences. Field Crops Res. 59 : 109-119.

Saito, K., Kashiwagi, S., Kinoshita, T. and Ishihara, K. 1991. Characteristics of dry matter production process in high yielding rice varieties. 4. Dry matter accumulation in the panicle. Jpn. J. Crop Sci. 60 : 255-263*.

SPSS Inc. 2000. SYSTAT 10.0 : New Statistics. Chicago, USA.

Tabbal, D.F., Bouman, B.A.M., Bhuiyan, S.I., Sibayan, E.B. and Sattar, M.A. 2002. On-farm strategies for reducing water input in irrigated rice; case studies in the Philippines. Agric. Water Manage. 56 : 93-112.

Tajima, K. 1990. Occurrence and mechanism of drought damage. In Matsuo, T., Kumazawa, K., Ishii, R., Ishihara, K. and Hirata, H. eds., Science of the Rice Plant. 2. Physiology. Tokyo : Food and Agriculture Policy Research Center. 838-849.

Tsunoda, S. 1997. Drought resistance. In Matsuo, T., Futsuhara, F., Kikuchi, F. and Yamaguchi, H. eds., Science of the Rice Plant. 3. Genetics. Tokyo : Food and Agriculture Policy Research Center. 135-143.

Westcott, M.P. and Vines, K.W. 1986. A comparison of sprinkler and flooded irrigation for rice. Agron. J. 78 : 637-640.

Widawsky, D.A. and O'Toole, J.C. 1996. Prioritizing the rice research agenda for eastern India. In Everson, R.E., Herdt, R.W., Hossain, M. eds., Rice Research in Asia : Progress and Priorities. CAB International, Wallingford, Oxon, UK. 109-130.

Yang, X., Bouman, B.A.M., Wang, H., Wang, Z., Zhao, J. and Chen, B. 2005. Perfomance of temperate aerobic rice under different water regimes in North China. Agric. Water Manage. 74 : 107-122.

Yun, S., Wada, Y., Maeda, T., Miura, K. and Watanabe, K. 1997. Growth and yield of *japonica x indica* hybrid cultivars under direct seeding and upland cultivation conditions. Jpn. J. Crop Sci. 66 : 386-393*.

* In Japanese with English abstract.
** In Japanese with English summary.