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

1. Nitrogen Content and Dry Matter Production

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Abstract: The total water supply (irrigation plus rainfall) would determine biomass production. This study aimed to elucidate the effects of water supply and cultivar differences on the dry matter production of rice grown under upland conditions. Three rice cultivars ('Yumeno-hatamochi', YHM; 'Lemont', LMT; 'Nipponbare', NPB) were used on an upland site with three water regimes (rain-fed, RU; irrigated, IU; water deficit during the panicle-formation stage, WD) and in a flooded lowland (FL) in Japan from 2001 to 2003. The total amount of aboveground dry matter (TDM) of NPB in RU (1101 g m⁻²) was 15% lower than that in FL (1302 g m⁻²) in 2001, when dry spells occurred frequently, but was comparable to FL in 2003 (1313 vs. 1324 g m⁻²) under favorable soil water conditions with ample rainfall before heading. The nitrogen (N) content of the aboveground part at maturity in RU in 2003 was similar to that in FL, but the growth duration was 9 days longer in RU. The amount of total water supply during the crop growth differed greatly (419 to 1132 mm) among water regimes and years under upland conditions, where TDM and aboveground N content generally increased with increasing water supply. We detected a cultivar – water regime interaction in TDM at maturity in both 2002 and 2003. In FL and under the upland conditions with adequate water supply in 2003, TDM was the largest for NPB, but it was the smallest in this cultivar in 2002 when rainfall was less frequent. The small TDM of NPB in 2002 resulted from a smaller amount of N uptake associated with shallower root system development. In contrast, YHM had a deeper root system and thus the amount of N uptake was larger and TDM was smaller under upland conditions with limited water supply. Our results indicate that the three cultivars responded differently to the water conditions, and that the total water supply greatly affected TDM in uplands through its effects on the amount of N uptake, which was associated with the depth of root development.

Key words: Biomass production, Deep rooting, Nitrogen uptake, Water-use efficiency.

More than 70% of available fresh water worldwide is used for agriculture, and the availability is now decreasing (Baker et al., 1999). Recently, degradation of the quality of fresh water by chemical pollution and salinization and reduction of the quantity of available water (e.g., a falling water table) have become serious problems not only in arid and semi-arid areas, but also in some tropical and temperate areas, partly owing to greater competition from urban and industrial water uses (Baker et al., 1999). Therefore, there is a need to develop a more efficient water use system in agriculture.

For the increase of rice production using the limited water resource, there are two major options. One is to enhance and stabilize current rainfed rice production systems. Rainfed rice occupies 45% of the total rice area (IRRI, 2002), and partly because of its complex and heterogeneous environmental conditions, its yield increase has been much less than that in the irrigated rice for the past 30 years (Hossain, 1995; Wade, 1999). Great efforts have been made to characterize the target environments, and to clarify the physio-morphological adaptation to these rainfed environments (Wade et al., 1998; Courtois and Lafitte, 1999; Fukai et al., 1999).

The other option is to develop new water-saving rice production systems. Growers of irrigated lowland rice are the main users (more than 50%) of irrigation in Asia (Baker et al., 1999), but this practice may not be sustainable if fresh water resources continue to decline. Several water-saving rice production technologies...
have recently been developed (Tabbal et al., 2002; Kamoshita, 2003; Belder et al., 2004; Hayashi et al., 2006; Kato et al., 2006c). Among them, rice production without constant standing water in non-puddled soils, sometimes referred to as “aerobic rice”, is considered to be one of the most promising technologies in terms of saving water (IRRI, 2002; Wang et al., 2002). Studies on such new production systems for upland rice under favorable and intensive management conditions, with adequate water and nutrient supply, have just begun in some Asian countries (Bouman et al., 2005; Yang et al., 2005). In Japan, researchers have attempted to increase the grain yield of traditional upland rice by supplying supplementary irrigation (Hasegawa, 1962; Nakagawa and Goto, 1963), as well as by means of genetic improvement (e.g., drought resistance and blast resistance; Nemoto et al., 1998). However, average yields of upland rice in Japan (MAFF, 2005) and in the world (IRRI, 2002) are still much lower (less than 50%) than those of flooded lowland rice.

Rice plants may be continuously subjected to water stress under upland conditions (Lafitte and Bennett, 2002). The growth of rice cultivars is likely to differ between upland and lowland conditions, and it may also differ with the amount of water supply under upland conditions. Cultivars that could maintain water and nutrient uptake under less moist soils may produce larger amounts of dry matter, and these cultivars would thus become important as the water supply decreases. Dry matter production, one of the major determinants of grain yield, would result from resource acquisition (e.g., nitrogen (N) uptake and radiation absorption) and the conversion of these resources into plant biomass (Ladha et al., 1996). Pheno logical development (Yun et al., 1997), and plant morphological features such as tillering, leaf area expansion, and rooting (Kondo et al., 2003) may differ between upland and lowland cultivars, and between upland and lowland conditions. All of these differences may be associated with resource acquisition and dry matter production, as is suggested from the pot experiments (e.g. Wada et al., 2002), but validation at field levels is limited, particularly with a view of improving biological yield in high-input upland rice production systems. It is also not clear how cultivar differences in root system will be associated with resource uptake under different water supply in the upland fields, since the rhizosphere environments are totally different from those of pot systems. The physiology and morphology of rice cultivars and their resource acquisitions for dry matter production under upland field conditions need to be elucidated for breeding new rice varieties adapted to the water-saving agriculture (Lafitte et al., 2002). In the first study of the series, we examined the responses of two lowland and one upland rice cultivars to different degrees of water availability under upland conditions, and compared them with rice grown under flooded lowland conditions. The objective of this paper was to elucidate the effects of water supply on plant growth and dry matter production of rice and the differences among cultivars in dry matter production under different levels of water supply.

Materials and Methods

1. Experimental site and climatic conditions

The experiments were conducted at the Field Production Science Center of the University of Tokyo at Nishitokyo, Japan (lat. 35° 43´ N, long. 139° 32´ E), on Andosol fields in three summer seasons (from April to October) from 2001 to 2003. The topsoil layer (to a depth of 35 cm) was a dark, humic silty loam, and the subsoil layer (below 35 cm) was a red-brown silty clay loam (Yamagishi et al., 2003). The hydraulic properties of the experimental site were previously measured by H. Imoto, the University of Tokyo (unpublished data). Topsoil properties are: volumetric soil water content at saturation (0 MPa), 0.65 cm$^3$ cm$^{-3}$; at field capacity (−0.01 MPa), 0.55 cm$^3$ cm$^{-3}$; at wilting point (−1.5 MPa), 0.26 cm$^3$ cm$^{-3}$; bulk density, 0.77 g cm$^{-3}$; saturated permeability, 3.5 × 10$^{-5}$ cm s$^{-1}$. Subsoil properties are: volumetric soil water content at saturation, 0.72 cm$^3$ cm$^{-3}$; at field capacity, 0.65 cm$^3$ cm$^{-3}$; at wilting point, 0.48 cm$^3$ cm$^{-3}$; bulk density, 0.50 g cm$^{-3}$; saturated permeability, 1.1 × 10$^{-5}$ cm s$^{-1}$. Climatic data for the experimental periods are summarized in Table 1. Rainfall in April and July in 2001 was considerably lower than in the common year, with unusually high temperature and high levels of solar radiation in July. In 2002, the total rainfall was the same as in the common year after May, but there were two dry spells of more than 10 days in August. Rainfall was ample until August in 2003, with no dry spells and with low temperature and solar radiation.

2. Experimental design

Experiments were conducted under rainfed upland (RU) and flooded lowland (FL) conditions in 2001 (2 trials); under RU, irrigated upland (IU), and FL conditions in 2002 (3 trials); and under RU, IU, and water deficit conditions during the panicle-formation stage (47 days) in upland (WD) and FL conditions in 2003 (4 trials). One trial plot was sufficiently distant from the others (at least 4 m) so that the water regime in each trial should not affect the others. Areas of one plot were 12 to 16 m$^2$, depending on the year and treatment, for RU, IU, and FL, and were 7.7 m$^2$ in WD in 2003. The whole plot area in each trial was 36 to 144 m$^2$ in RU, IU, FL, and WD, and the total area of the trials was 92 m$^2$ in 2001, 360 m$^2$ in 2002 and 393 m$^2$ in 2003. In IU, the total amounts of irrigation (using sprinklers) were 60 mm (9 times in August and once in September, about 6 mm each) in 2002 and 125 mm (once in June, twice in July, twice in August and...
once in September, about 20 mm each) from July to September in 2003. Plant establishment was inferior in IU in 2002 owing to the lower initial soil moisture in the experimental field. Flooded conditions were maintained in FL, except for 1 week during the mid-vegetative stage and immediately before maturity. In WD, rice plants were grown under a rainout shelter, a permanently installed arch-shaped polyvinyl mulch of 4.5 m height and 5.5 m width that excluded rainfall (an area of 18 × 5.5 m). Irrigation was applied twice per week (15 mm each) until July 17 (87 days after sowing, DAS), then stopped from July 18 to September 15 (57 days from 88 to 145 DAS). However, unusually heavy storms affected the WD area on August 6 and 14. The actual soil drying periods were thus from 88 to 106 DAS (18 days) and from 116 to 145 DAS (29 days) in WD. Irrigation was resumed on September 16 and continued until maturity (every 4 days, 15 mm each). Table 2 shows the amount of rainfall and irrigation during crop growth. The amount of the unexpected storms on 6 and 14 August in 2003 (192 mm in total) was not included for the calculation of water supply in WD, since it was difficult to estimate the percentages of rainfall affecting the plots in WD.

We used one cultivar (‘Nipponbare’, NPB) in 2001, and three cultivars (‘Yumeno-hatamochi’, YHM; ‘Lemont’, LMT; and NPB) in 2002 and 2003, with three replicates in each treatment arranged in a randomized block design. The area of one replicate was 12 to 48 m$^2$ depending on the number of cultivars used in each treatment in each year. In RU, IU, and WD, the width of each row was 50 cm in 2001 and 2002 and 35 cm in 2003. Plants were thinned to 24 hills m$^{-2}$ at 28 DAS in 2001, to 26 hills m$^{-2}$ at 43 DAS in 2002 and to 29 hills m$^{-2}$ at 45 DAS in 2003 (one plant per hill). In FL, plants were transplanted at a density of 22 hills m$^{-2}$ (one plant per hill, 30 × 15 cm) at 17, 23, and 31 DAS in 2001, 2002, and 2003, respectively, because transplanting is preferred in lowland systems in Japan (over 95%) and in most of rice growing Asian countries (86-88% on average) (Pandey and Velasco, 2002). YHM is an upland japonica cultivar with a deep root system, which has been recently bred in Japan, and often performs better than other upland cultivars under upland conditions in dry years in Japan (Hirasawa et al., 1998). LMT is a lowland japonica cultivar developed in the United States (Bollich et al., 1985), and has a deep root system under flooded lowland conditions in Japan (Morita et al., 1995). NPB is a lowland japonica cultivar with a shallower root system than the other two cultivars. The sowing dates were May 9 in 2001 and April 30 in 2002, but were staggered in 2003 in order to more closely match the heading dates of each cultivar; NPB was sown on April

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**Table 1.** Monthly means of daily solar radiation (MJ m$^{-2}$ d$^{-1}$), mean air temperature (°C) and monthly rainfall (mm) in the summer season in 2001, 2002 and 2003. The averages of 11 years (1993 to 2003) at the experimental farm were also shown as the value in a common year.

| Solar radiation | Mean temperature | Rainfall |
|----------------|------------------|----------|
| 2001 2002 2003 Common year | 2001 2002 2003 Common year | 2001 2002 2003 Common year |
| April | 14.9 12.9 n.a. 16.3 | 14.4 15.2 13.8 14.1 | 44 63 122 126 |
| May | 13.8 13.8 n.a. 14.0 | 18.8 17.9 17.7 18.4 | 169 85 167 126 |
| June | 11.7 11.5 n.a. 11.6 | 22.5 20.9 22.7 21.7 | 70 157 88 144 |
| July | 17.2 14.5 8.8 13.1 | 28.8 27.6 22.5 25.9 | 15 181 187 194 |
| August | 10.0 15.1 11.1 12.6 | 25.9 27.4 25.8 26.8 | 200 196 341 203 |
| September | 9.0 9.3 11.0 9.7 | 22.1 22.0 23.6 23.0 | 285 200 142 243 |
| October | 8.5 9.5 8.8 8.6 | 17.0 17.4 16.5 17.4 | 220 240 121 129 |

n.a. means data were not available.

**Table 2.** Cumulative amount of irrigation and rainfall (mm) from sowing to heading [H] and to maturity [M] in rainfed upland, irrigated upland and upland with water deficit during panicle formation stage (cv. Nipponbare) in 2001, 2002 and 2003.

| Year | Rainfed upland | Irrigated upland | Water deficit upland |
|------|----------------|------------------|---------------------|
| 2001 | 431 895 | 676 1052 | 359 419 |
| 2002 | 592 1008 | 794 1132 | 359 419 |
| 2003 | 794 1132 | 1008 1419 | 359 419 |
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21, whereas LMT and YHM were sown 4 and 11 days later, respectively, in all treatments. For simplicity, we counted days after sowing (DAS) in 2003 from the sowing date of NPB.

3. Cultural details

We applied a mixed fertilizer (high-analysis compound fertilizer A907, COOP Chemical Inc., Tokyo) at the time of sowing at a rate of 50 g m\(^{-2}\) (N, P, K = 60, 39, 67 kg ha\(^{-1}\)) in RU, IU, and FL, and at a rate of 60 g m\(^{-2}\) in WD (N, P, K = 72, 47, 80 kg ha\(^{-1}\)). In RU and IU, no top-dressing was applied in 2001; 14.3 (N = 30 kg ha\(^{-1}\)) g m\(^{-2}\) of ammonium sulfate was applied at 50 DAS in 2002; and 14.3 g m\(^{-2}\) (N = 30 kg ha\(^{-1}\)) at both 53 DAS and the panicle-initiation stage in 2003. In FL, there was no top-dressing in 2001 and 2002, since this represents the conventional cultural practice at our experimental site. Nitrogen uptake and dry matter production were smaller than expected in the later growth stages in 2002 because the experimental area in 2002 was found to be less fertile. In 2003 in FL, we top-dressed ammonium sulfate at a rate of 14.3 g m\(^{-2}\) (N = 30 kg ha\(^{-1}\)) at 53 DAS, 9.5 g m\(^{-2}\) (N = 20 kg ha\(^{-1}\)) at the panicle-initiation stage, and 4.8 g m\(^{-2}\) (N = 10 kg ha\(^{-1}\)) at the heading stage. In WD, the top-dressing of ammonium sulfate was applied at a rate of 22.9 g m\(^{-2}\) (N = 48 kg ha\(^{-1}\)) at 53 DAS. Weeds were controlled by means of hand weeding and herbicide application (Clincher Bas ME, Nissan Chemical Industries, Ltd., Tokyo, cyhalofop-butyl 3.0 % and bentazon 20.0 %). No serious disease problems and bird damage were observed.

4. Measurements

(1) Soil water content

We measured the volumetric soil water content of the surface 10 cm layer of soil at five spots per plot in the inter-row and inter-hill spaces in 2001 but only at a 10-cm distance from the rows in 2003 by means of time-domain reflectometry (HydroSense, Campbell Scientific Inc., Logan, Utah, USA) in RU, IU, and WD. Soil water content was measured two times in July, once in August and once in October in 2001 (RU only), but nine times in RU and IU in 2002 and 2003, and every few days in WD from June to September in 2003. In IU, each measurement was conducted just before irrigation to monitor the minimum soil water content. The value provided by time-domain reflectometry \((x)\) was converted into a soil water content \((y)\) from an equation calibrated in 2003 according to the manufacturer’s instructions:

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y = 0.004693x + 0.2744 \quad (n = 33, r = 0.96, P < 0.001) \quad (1)
\]

(2) Phenological development

The dates of heading and maturity were recorded. Heading date was defined as the date the top of the panicle appeared from at least one stem in each of five to six plants in 2001 and in more than 50% of 10 to 15 plants per plot in 2002 and 2003. Maturity was defined as the date when more than 90% of the grains had turned yellow.

(3) Plant height, tiller number and radiation interception

We measured plant height and tiller number at 69 and 134 DAS in 2002, and at 67 and 142 DAS in 2003. Photosynthetically active radiation was measured

Table 3. Phenological development (heading [H] and maturity [M]) from sowing in three cultivars (Yumeno-hatamochi [YHM], Lemont [LMT] and Nipponbare [NPB]) under flooded lowland, rainfed, irrigated and water deficit upland trials in 2001, 2002 and 2003.

| Water regime        | 2001(a) | 2002 | 2003 |
|---------------------|---------|------|------|
|                     | H DAS(b) | M DAS | H DAS | M DAS | H DAS | M DAS |
| Cultivar            |         |      |      |      |      |      |
| YHM                 | – –     | 107 155 | 118 164 |
| LMT                 | – –     | 117 163 | 129 173 |
| NPB                 | 116 161 | 121 165 | 128 174 |
| Water regime        |         |      |      |      |      |      |
| Flooded lowland     | 110 153 | 109 153 | 117 163 |
| Rainfed upland      | 122 168 | 117 165 | 127 173 |
| Irrigated upland    | – –     | 119 165 | 128 173 |
| Water deficit upland| – –     | – –   | 128 172 |

(a) data on water regime were those of NPB in 2001, because YHM and LMT were not grown.
(b) days after sowing. DAS was counted from the sowing date of NPB in 2003.
at ground level in each plot and above the plant canopy, between 11:00 and 13:30 every 1 to 2 weeks in 2002 and 2003 using a quantum sensor (LI-191SA, LI-COR, Lincoln, Nebraska, USA). We obtained three measurements in each plot. Then the fraction of radiation interception by the plant canopy was determined. We measured it in advance and confirmed that fraction of interception by the plant canopy on a measurement date was not affected by the fluctuation of photosynthetically active radiation between 11:00 and 13:30.

(4) Dry matter production and nitrogen content

We harvested the above-ground parts of the plant as follows: at maturity in RU and FL in 2001, at the late-vegetative stage (71 DAS), heading and maturity in RU, IU and FL in 2002, and at around the panicle-initiation stage (91 DAS), heading and maturity in RU and IU in 2003, at around the panicle-initiation stage (80 DAS), heading and maturity for FL in 2003. In WD, aboveground parts of the plant were harvested at one day before the beginning and at one week before the end of the water-deficit period (87 and 138 DAS) and at maturity. The harvested plant parts were used to calculate the total aboveground dry matter per unit area (TDM). The harvested area in each plot ranged from 0.54 to 0.90 m², depending on the treatment and year. The leaf area index at 71 DAS was also determined in 2002. We selected four plants, each of which had an average number of tillers, as a subsample, and measured the leaf area of one plant from each subsample with an automatic area meter (LI-3100 Area Meter, LI-COR, Lincoln, Nebraska, USA) to determine specific leaf area. The rest of a subsample was also separated them into stems and leaves. All the leaves and stems of the subsample, and the bulk sample were weighed after drying in an oven at 80°C for at least 3 days. The ratio of leaf weight to total aboveground weight (leaf plus stem) of the subsample was calculated, and the leaf area index (LAI) was estimated by dividing TDM by specific leaf area and the ratio of leaf weight to total aboveground weight (leaf plus stem).

For the determination of the N content of the aboveground part, the dried subsamples of leaves and stems were ground together and the N concentration was analyzed by combusting the 5.0-10.0 mg of dried material with an automated NC analyzer (Sumigraph NC-90A, SCAS, Oosaka, Japan) in 2002 and 2003.

The daily radiation interception in each plot was estimated in 2002 and 2003 by multiplying the fraction of radiation interception by the daily total solar radiation recorded at the weather station of Field Production Science Center about 200 m away from the experimental areas. Cumulative radiation interception was calculated from the sums of daily radiation interception from the first plant harvest (late-vegetative to panicle-initiation stages depending on years and treatments) for each treatment in each year. The radiation-use efficiency was calculated by dividing

| Cultivar | 2002 | | 2003 | |
|----------|------|------|------|------|
|          | Plant height (cm) | Tiller number (m²) | Plant height (cm) | Tiller number (m²) |
| YHM | 52.8 | 109.1 | 287 | 285 |
| LMT | 51.2 | 95.4 | 147 | 180 |
| NPB | 46.3 | 93.0 | 180 | 280 |
| LSD | 2.8* | 3.0* | 24* | 36* |

Water regime

| Water regime | 2002 | | 2003 | |
|--------------|------|------|------|------|
| Flooded lowland | 55.1 | 95.2 | 262 | 258 |
| Rainfed upland | 51.4 | 103.8 | 201 | 252 |
| Irrigated upland | 45.8 | 98.5 | 150 | 235 |
| Water deficit upland | — | — | 4.3 | 102.1 |
| LSD | 4.7* | 3.0* | 45* | n.s. |

| Cultivar×Water | 2002 | | 2003 | |
|----------------|------|------|------|------|
| LSD | 2.2* | 4.8* | 25* | 27* |

n.s. means difference in the same column was not statistically significant.
the dry matter increase between the first harvest and the time of heading by the cumulative radiation interception during the same period, assuming that there is a linear response of canopy productivity to intercepted radiation.

(5) Root system

In order to compare the root system among the treatments, we estimated root biomass and root length by the core sampling method (Kondo et al., 2003). Root samples were collected from each plot in RU and IU in 2002. At 122 DAS, two soil cores (50-mm diameter) per plot were extracted at a distance of 10 cm from a row, to a depth of 65 cm using a liner soil sampler (DIK-110B, Daiki Rika Kogyo, Saitama, Japan). The 30 to 35 cm soil layer was not included for technical reasons. The soil cores were divided into 0–15, 15–30 and 35–65 cm segments and carefully washed to extract the roots. The total root length was determined using a Comair Root Length Scanner (Commonwealth Aircraft, Melbourne, Australia), and measured total root dry weight after drying the samples in an oven at 80°C for 3 days. These root characteristics were examined on a unit area basis (i.e., root length density; cm cm⁻² or root weight density; mg cm⁻²) for relative comparison among the cultivars, but may not indicate the real values, because the cores were taken at limited positions (10 cm from the row).

5. Statistical analyses

We compared data from all treatments in a given year using the analysis of variance using Systat 10.0 (SPSS, 2000). Combined analysis on the cultivar-water regime interaction and comparison among the water regimes were also conducted by the statistical model of the interaction between cultivar and location (IRRI, 1999). We tested the least-significant difference at $P = 0.05$ or 0.10 (marginally significant) to compare cultivars within a treatment.
Table 5. Leaf area index (LAI), total aboveground dry matter (TDM; g m⁻²) and aboveground nitrogen (N) content (g m⁻²) in three cultivars (Yumeno-hatamochi [YHM], Lemont [LMT] and Nipponbare [NPB]) under flooded lowland, rainfed, irrigated and water deficit upland trials in 2002 (at 71 days after sowing (DAS) and maturity) and 2003 (at maturity only). Least significant difference (LSD) at P = 0.05 (*) and 0.10 (†) was also shown.

| Cultivar | 2002  | 2003  |
|----------|-------|-------|
|          | 71 DAS | Maturity | 71 DAS | Maturity |
|          | LAI    | TDM    | N content | TDM    | N content |
| Flooded lowland |       |       |       |       |       |
| YHM      | 1.49   | 128    | 3.6   | 891    | 6.9     |
| LMT      | 1.38   | 124    | 3.2   | 889    | 6.3     |
| NPB      | 1.79   | 142    | 4.1   | 1092   | 6.8     |
| LSD      | n.s.   | n.s.   | n.s.  | 115*   | n.s.    |
| Rainfed upland |       |       |       |       |       |
| YHM      | 1.59   | 117    | 4.1   | 1342   | 16.4    |
| LMT      | 1.28   | 103    | 3.9   | 1165   | 13.8    |
| NPB      | 1.07   | 82     | 3.0   | 1077   | 12.3    |
| LSD      | 0.24*  | 11*    | 0.5*  | 150*   | 1.8*    |
| Irrigated upland |       |       |       |       |       |
| YHM      | 1.36   | 93     | 3.1   | 1130   | 13.5    |
| LMT      | 1.13   | 91     | 2.9   | 1133   | 13.2    |
| NPB      | 0.79   | 67     | 2.2   | 989    | 11.2    |
| LSD      | 0.35*  | 19†    | 0.7*  | n.s.   | 1.9*    |
| Water deficit upland |       |       |       |       |       |
| YHM      | —      | —      | —    | —     | —      |
| LMT      | —      | —      | —    | —     | —      |
| NPB      | —      | —      | —    | —     | —      |
| LSD      | —      | —      | —    | —     | 58†    |
| Water regime |       |       |       |       |       |
| Flooded lowland | 1.55  | 132    | 3.6   | 957    | 6.6     |
| Rainfed upland | 1.31  | 101    | 3.7   | 1195   | 14.2    |
| Irrigated upland | 1.09  | 84     | 2.7   | 1084   | 12.6    |
| Water deficit upland | —     | —      | —    | —     | 933    |
| LSD      | 0.24*  | 18*    | 0.5*  | 122*   | 1.1*    |
| Cultivar | *      | *      | *    | n.s.  | *      |
| Cultivar × Water | *  | *      | *    | *     | n.s.   |

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

Results

1. Soil water content

In 2001, when July rainfall was very scarce, soil water content of the surface 10 cm in RU decreased from July to 0.33 cm⁻³ cm⁻³ in early-August at 81 DAS (data not shown). In contrast, soil water content in 2003 was kept at 0.41 cm⁻³ cm⁻³ or higher in RU and IU and decreased to 0.36 cm⁻³ cm⁻³ at the end of the water-deficit period (145 DAS) in WD (data not shown).

2. Phenological development

In FL, the duration of crop growth was 10 to 15 days shorter than in RU across the three cultivars (Table 3). In all treatments, YHM headed earliest, and its growth duration was the shortest. In WD, no cultivar delayed heading markedly compared with RU and IU.

3. Plant height, tiller number, and radiation interception

Since similar trends were observed in 2002 and 2003, we presented here the plant height and tiller number in 2002 and 2003 (Table 4) and the radiation interception in 2002 (Fig. 1). Both plant height and tiller number in FL were the highest at 69 and 67 DAS in 2002 and 2003, respectively, but those in RU and
IU were not significantly lower than those in FL at 134 and 142 DAS in 2002 and 2003, respectively (Table 4). In WD in 2003, plant height and tiller number were the lowest at 142 DAS. In general, the mean square of cultivar was larger than that of the interaction between the cultivar and water regime (C×W) for plant height and tiller number. The tendency of a C×W interaction was observed. In FL, plant height and tiller number tended to be higher in NPB, but in RU and IU, they tended to be higher in YHM, compared with other cultivars in both years (data not shown). Tiller number of LMT was much lower than that of YHM or NPB in all treatments at 134 and 142 DAS in 2002 and 2003, respectively.

The radiation interception in FL was higher than in RU and IU during the early vegetative stages although the difference was not significant (Fig. 1a).

Table 6. Total aboveground dry matter (TDM; g m⁻²) and aboveground nitrogen (N) content (g m⁻²) of three cultivars (Yumeno-hatamochi [YHM], Lemont [LMT] and Nipponbare [NPB]) under water deficit upland trial at the onset and the end of water deficit period in 2003 (87 and 139 days after sowing, respectively). Least significant difference (LSD) at P = 0.05 (*) among cultivars was also shown.

| Treatments | Stress onset | Stress end | Stress onset | Stress end |
|------------|--------------|------------|--------------|------------|
| YHM        | 114          | 813        | 3.7          | 12.5       |
| LMT        | 80           | 666        | 2.6          | 10.7       |
| NPB        | 93           | 681        | 2.7          | 9.9        |
| LSD        | 19*          | 86*        | 0.3*         | 1.5*       |

In IU, radiation interception during the early stages (until 100 DAS) tended to be lower than in RU. In FL, radiation interception was greatest in NPB, but in RU and IU, the values in YHM increased faster than those in NPB (Figs. 1b–d).

4. **LAI, biomass production and nitrogen content**

In 2001, TDM at maturity was significantly lower in RU than in FL (1101 vs. 1302 g m⁻²; P < 0.05).

In 2002, LAI of three cultivars on the average was higher in FL than in RU, and was the lowest in IU at 71 DAS (Table 5). There was a C×W interaction in LAI. LAI was not different among the cultivars in FL, whereas it was the largest in YHM in RU and IU at 71 DAS. There was also a C×W interaction in TDM. TDM was the largest in NPB in FL while it was the largest in YHM at 71 DAS and maturity in RU, despite the shorter growth duration of YHM. The N content at maturity was lower in FL than in RU, probably because of the lack of top-dressing (Table 5). The N content was lower in IU than in RU at both 71 DAS and maturity. There was a C×W interaction in N content at both 71 DAS and maturity. In FL, NPB tended to have larger N content than the other cultivars, whereas in RU and IU, YHM had the largest N content and NPB had the lowest.

In 2003, TDM in RU was larger than that in FL at maturity (Table 5). TDM at maturity tended to be larger in IU than in RU (though not significant), and that in WD was significantly smaller than that in the other treatments. Although there was a significant C×W interaction, TDM was the largest in NPB in all treatments at maturity. This differed from the results in 2002. The N content at maturity was not different
among the plants in RU, IU and FL, but it was significantly lower in WD (Table 5). In FL, NPB had the largest N content at panicle initiation and heading stages (significant at P=0.05, data not shown), while YHM tended to have larger N content at the panicle-initiation stage in IU and RU (though not significant at P=0.10, data not shown).

Dry matter production during the period from 87 to 138 DAS in WD was the largest in YHM and consequently, YHM had the largest TDM at the end of the water-deficit period in WD (Table 6). The similar trend was observed for N content; YHM had larger N content at the end of the water-deficit period than the other cultivars.

Radiation-use efficiency during the panicle-formation stage (from around panicle initiation to heading) was higher in 2003 (1.9 g MJ\(^{-1}\)) than in 2002 (1.1 g MJ\(^{-1}\)), possibly due to the differences in fertilizer management and weather conditions. Radiation-use efficiency generally differed little among water regimes and cultivars in both years (data not shown), possibly due to the lower frequency of our measurements of radiation interception and TDM.

Fig. 2 shows the relationships between mean TDM of these cultivars at maturity in each environment (lowland versus upland) and TDM of each cultivar at maturity to permit a comparison of cultivar responses to environmental conditions. In FL, TDM was the largest in NPB and the lowest in YHM (Fig. 2a). Under the largest yielding upland environment (i.e., very favorable upland conditions, 03 IU), TDM was the largest in NPB (Fig. 2b), but under lower yielding but not least yielding upland environments (i.e., suboptimal upland conditions, 02 RU, 02 IU), TDM was much larger in YHM than in NPB.

There was a positive correlation between N content and TDM at maturity in each cultivar across different water regimes in different years, except in FL in 2002.

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**Table 7.** Root length density (RLD; cm cm\(^{-2}\))\(^{(a)}\) and root weight density (RWD; mg cm\(^{-2}\))\(^{(a)}\) at 0-65 cm depth and 35-65 cm depth, and DRL ratio (%) (ratio of RLD at 35-65 cm to that at 0-65 cm), in three cultivars (Yumeno-hatamochi [YHM], Lemont [LMT], and Nipponbare [NPB]) in rainfed and irrigated upland at 122 days after sowing in 2002. Least significant difference (LSD) at P = 0.05 (*) and 0.10 (†) was also shown.

| Cultivar | RLD at 0-65 cm | RLD at 35-65 cm | RWD at 0-65 cm | RWD at 35-65 cm | DRL ratio |
|----------|----------------|----------------|---------------|----------------|-----------|
| YHM      | 75             | 17             | 5.43          | 0.96           | 23        |
| LMT      | 73             | 11             | 6.23          | 0.71           | 14        |
| NPB      | 70             | 10             | 4.25          | 0.45           | 15        |
| LSD      | n.s.           | n.s.           | 1.12*         | 0.40*          | n.s.      |

| Water regime | RLD at 0-65 cm | RLD at 35-65 cm | RWD at 0-65 cm | RWD at 35-65 cm | DRL ratio |
|--------------|----------------|----------------|---------------|----------------|-----------|
| Rainfed upland | 83             | 14             | 5.65          | 0.73           | 17        |
| Irrigated upland | 63             | 12             | 4.95          | 0.67           | 18        |
| LSD          | 16†            | n.s.           | n.s.          | n.s.           | n.s.      |

| Cultivar × Water | RLD at 0-65 cm | RLD at 35-65 cm | RWD at 0-65 cm | RWD at 35-65 cm | DRL ratio |
|-----------------|----------------|----------------|---------------|----------------|-----------|
| n.s.            | n.s.           | n.s.           | n.s.          | n.s.           | n.s.      |

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

(a) The soil cores (50-mm diameter) were taken at a distance of 10 cm from a row, and the 30 to 35 cm soil layer was excluded for technical reasons.
where the nitrogen deficit was severer compared with the other treatments (Fig. 3). N-use efficiency (TDM per unit N content) was largest in NPB and lowest in YHM, probably due to the cultivar differences in growth duration for biomass production.

5. Root systems

Root length density (RLD) at 0-65 cm and root weight density (RWD) at 0-65 cm in 2002 were lower in IU than in RU owing to the inferior crop establishment that occurred in IU in that year (Table 7). The RLD and RWD values at 0-65 cm for NPB tended to be the lowest under both RU and IU conditions. RLD at 35-65 cm (though not significant) and RWD at 35-65 cm were the lowest in NPB and the largest in YHM. YHM also had the highest deep-root length (DRL) ratio (though not significant), which represents the ratio of root length at 35-65 cm to that at 0-65 cm.

Discussion

1. Dry matter production

Dry matter production of rice at maturity in upland conditions was lower than in flooded lowland conditions (by 11 – 26 %) when water supply was lower (e.g., 2001, WD in 2003), but it was comparable or superior to that in flooded lowland conditions when it rained amply and frequently before the heading stage (e.g., RU in 2003) (Table 5). The largest difference between RU and FL in this study was the phenological development of the plants. Though vegetative growth (as measured by plant height, tillering, and LAI) during the early growth stages in FL was superior to that in RU (Fig. 1, Tables 4), the duration of vegetative growth (i.e., days before heading) in RU was more than 10 days longer on average than in FL. This is considered to have increased N uptake and vegetative growth in RU to levels that were comparable or superior to those in FL, particularly in earlier maturing cultivars (Table 5). This also led to comparable cumulative amounts of radiation interception whereas radiation-use efficiency was similar between RU and FL (data not shown). Longer growth duration, particularly in the vegetative stage, enhances the amount of N uptake and hence dry matter production in lowland rice (Ladha et al., 1996; Inthapanya et al., 2000). The present study supports these observations under favorable upland conditions with adequate and frequent water supply. This longer growth duration in RU compared with FL would be in part due to the differences in the planting methods; growth duration can be lengthened in temperate region by direct seeding method than by transplanting method (Yun et al., 1997).

The higher N content resulted in a larger dry matter production for each cultivar across upland conditions with different water supply, and reduced water supply also reduced the amount of N uptake within a year (i.e., about 25% reduction in the amount of N uptake and total dry matter in WD compared with RU and IU in 2003). Prasertsak and Fukai (1997) showed that the reduction in dry matter production under water deficits in a upland field was associated with a reduction in the amount of N uptake. O'Toole and Baldia (1982) and Tanguiling et al. (1987) suggested that the transpiration of rice plants declined under water-deficit conditions, which reduced the amount of N uptake. Changes in surface soil moisture conditions from near saturation to water deficits may also reduce N availability (i.e., the amount of mineralized N in the rhizosphere soil) (Kumar and Goh, 2000), as is frequently observed in rainfed lowland rice (Wade et al., 1998). In the present study, reduction of water supply and amount of N uptake reduced vegetative plant growth (e.g., plant height and tillering) in WD compared with in RU in 2003, and consequently, decreased the cumulative amount of radiation interception and dry matter production.

The present study demonstrated that it was possible to achieve equally large TDM values under upland and flooded lowland conditions with an adequate and sufficiently frequent supply of water. Similar results have been reported in other studies conducted in Japan (Hasegawa, 1962; Wada et al., 2002). However, TDM of aerobic rice or under upland conditions was reported to be smaller than in flooded lowlands in the Philippines (Bouman et al., 2005) and Louisiana (Westcott and Vines, 1986), despite the supplementary irrigation to keep the soil matric potential above – 0.03 MPa at a depth of 15 cm. Temporary drying of the surface soil may occur more frequently in uplands in tropical or arid regions than is the case in temperate regions. In order to develop upland rice production as a water-saving alternative to flooded lowland rice, careful examination of the environmental conditions in the target regions (e.g., temperature, solar radiation, humidity, the soil’s water-holding capacity, amount of rainfall, and available irrigation water) is necessary to permit the production in upland comparable to that in the lowland ecosystems. As well, judicious use of mulches to retain water in near-surface soil layers should be investigated (Kato et al., 2006c). This approach (using straw, gravel and plastic film mulches) has proved to be strikingly effective in China (Wang et al., 2002; Fan et al., 2005).

2. Cultivar differences

The responses to upland conditions with different water regimes and to lowland conditions clearly varied with the cultivar (Fig. 2). In FL, TDM at maturity was the largest for NPB in both 2002 and 2003 (Table 5). This was associated with the vigorous vegetative growth of NPB in the earlier stages (as measured by plant height, tillering, and LAI) and with larger amount of N uptake and interception of cumulative radiation,
which resulted from the longer growth duration compared with the other cultivars (e.g., the number of days to heading was 10 to 14 days longer in NPB than in YHM).

Under upland conditions, NPB had the largest TDM under the most favorable conditions with adequate water supply (i.e., IU and RU in 2003; Fig. 2), but had the least TDM under suboptimal conditions with less water and N supply (i.e., IU and RU in 2002), and hence the difference in TDM between those two environmental conditions was largest in NPB among three cultivars. The reasons for the small TDM of NPB in 2002 may be (1) poor vegetative growth, such as poor tillering and small LAI, which resulted in the lowest radiation interception (Fig. 1) among the three cultivars; (2) the relatively small amount of N uptake, which may be related to the relatively shallow root system (Table 7; Yoshida and Hasegawa, 1982); and (3) stomatal closure and reduced photosynthesis in response to surface soil drying (Lafl itte and Bennett, 2002). Compared with NPB, YHM took up more N and maintained larger TDM under suboptimal conditions (i.e., IU and RU in 2002 (Table 5), and during the water deficit period in WD in 2003 (Table 6)). YHM had a deeper root system (Table 7) and a larger rate of tillering than NPB (Table 4) under upland conditions. Thus, a deep root system may play an important role not only for continuous water uptake under drought conditions (Lilley and Fukai, 1994; Kohata et al., 1996), but also for nutrient uptake under upland conditions with suboptimal water availability, where only surface soil layers become dry, thereby reducing nutrient availability in these layers. The positive roles of deeper roots for nutrient uptake under the conditions of surface soil drying was shown in sorghum, where the injection of 4 g m⁻² of nitrogen fertilizer as a solution into 70-cm soil depth during prolonged dryness of surface soil increased yield by 30 % (Foale et al., 1992).

In our study, it is difficult to estimate the amount of nitrogen uptake by the roots at each depth. Further detailed physiological studies are needed to assess the roles of deeper roots and their genotypic variation in water and nutrient uptake under the different degrees of soil dryness.

In two companion papers, we discuss grain yield and yield components in upland rice (Kato et al., 2006a), and relationships among deep root development, water uptake, and plant water status under drought conditions (Kato et al., 2006b).

Conclusions

When the water supply was adequate and frequent, it was possible to achieve similarly large amount of TDM in rice under upland conditions with flooded lowland conditions under the temperate climate on Andosols in Japan. However, the amount of N uptake and TDM of rice decreased as the water supply decreased under upland conditions. This study also showed contrasting patterns of plant growth (e.g., tillering and plant height) and dry matter production in lowland and upland rice cultivars under upland and lowland conditions. A current elite lowland cultivar could achieve TDM values comparable to those of a recently developed Japanese improved upland cultivar under well-watered upland conditions, but would experience greater reductions in TDM with decreasing water supply. Plant characteristics such as a deep root system and the ability to maintain larger amount of N uptake are advantageous for developing new elite cultivars in upland ecosystems for water-saving agriculture.

Acknowledgments

We thank N. Washizu, K. Ichikawa, C. Sasaki, C. Yamazaki, S. Nakata, and H. Kimura of the Field Production Science Center, the University of Tokyo for their technical assistance in carrying out these experiments. We also thank 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 by the MAFF Genebank, National Institute of Agrobiological Sciences, Japan. This study was financially supported in part by the Moritani Foundation Scholarship and Inter-departmental Research Funds from the Graduate School of Agricultural and Life Sciences, The University of Tokyo.

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