Genetic analysis of rooting ability of transplanted rice (*Oryza sativa* L.) under different water conditions

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Abstract

In order to assess the benefits of superior rooting ability of rice (*Oryza sativa* L.) for growth after transplanting under water-limiting conditions, genetic differences in the rooting ability of rice seedlings 30 d after sowing, with their visible roots either pruned or not pruned, were quantified by several root parameters 4 d after transplanting (DAT), under flooded or non-flooded paddy fields (four treatments in total), together with production traits at maturity. Ninety-eight recombinant inbred lines from the two *japonica* ecotypes, a lowland variety Otomemochi, and an upland variety Yumenohatamochi, were genotyped with 107 simple sequence repeat (SSR) markers. Otomemochi in general produced more adventitious roots, partitioned a greater proportion of biomass to roots, and had a greater increment of root dry weight (ΔRW) at 4 DAT than Yumenohatamochi, but these variety differences were less clear under non-flooded conditions without root pruning. Several quantitative trait loci (QTLs) associated with rooting ability were identified mainly in chromosomes 1, 4, and 6 across the four treatments or in combined analysis. On the other hand, QTLs for ΔRW around RM2357 in chromosome 5 and for maximum new root length in RM215–RM205 in chromosome 9 were found only under root pruning treatments and under non-flooded conditions without root pruning, respectively. Greater ΔRW was associated with higher head dry weight per hill at maturity only in the non-flooded and root-pruning treatments. This study suggests the importance of rooting ability after transplanting and, possibly, other mechanisms for adaptation to non-flooded conditions.

Key words: Non-flooded paddy, rice (*Oryza sativa* L.), root pruning, transplanting, water scarcity.

Introduction

Transplanting has been the most widespread planting technique for paddy rice production in monsoon Asia. It is estimated at >80% in the region, particularly East and Southeast Asia (Jahn *et al.*, 1996; IRRI, 2002; Pandy and Velasco, 2002), although direct seeding is an alternative option where transplanting labourers are in short supply. Damage to rice seedlings is inevitable in the process of pulling and transplanting of seedlings, and it leads to growth stagnation for several days or a week after transplanting, being known as ‘transplanting shock’ (Matsuo *et al.*, 1995).

Transplanting shock might be reduced by good land preparation and by manufacturing very sophisticated transplanting machines, which is attainable only in irrigated paddies in developed countries, but not in most of the rice fields in developing countries. Transplanting shock can be worsened in rainfed lowlands if the amount of rainfall is limited before or after transplanting (Fukai and Cooper,
1995). Delayed timing of puddling and transplanting leads to ageing of seedlings in the nursery, which are then less vigorous, and it would thus take a longer time for recovery growth without the presence of standing water.

Irrigated lowland rice could also suffer from water shortage during transplanting in some places in drought years (e.g. 1994 and 2005 in Western Japan) due to the vulnerability of fresh water resources. In addition, water-saving irrigation with shallow or little standing water management during transplanting is desirable nowadays, since a large water supply during puddling and after transplanting could increase the loss of fertilizers through percolation, and lead to greater environmental pollution (Lu et al., 2000; Won et al., 2003).

Quantification of rooting ability and subsequent crop establishment in water-saving or water-limiting paddy fields therefore becomes important. Although a number of studies have been conducted to assess land and water productivity under non-flooded, water-saving lowland conditions (Kamoshita, 2003; Hayashi et al., 2006; Kamoshita et al., 2007), so far no study has focused on rooting ability, particularly on genotypic variation after transplanting. The objectives of this study are first to investigate rooting ability and dry matter production of rice under non-flooded conditions, secondly to examine the effects of root pruning on rooting ability and subsequent growth, and thirdly to identify putative quantitative trait loci (QTL) associated with the rooting ability.

### Materials and methods

#### Plant population

A population of 98 recombinant inbred lines (RILs) of the $F_8$ generation was derived from a cross between Otomemochi, a japonica lowland variety, and Yumenohatamochi, a japonica upland variety, at the Plant Biotechnology Institute, Ibaraki Agricultural Center. Yumenohatamochi is known to have a deep root system for adapting to upland fields (Hirasawa et al., 1988; Kato et al., 2006).

#### Experimental condition

Ninety-eight RILs and two parents were grown in paddy fields at The University of Tokyo, Nishitokyo, Japan (latitude 35°43' N, longitude 139°32' E) under two water regimes and with two root pruning methods in 2004: flooded conditions with constant standing water (~5 cm) and roots of seedlings in the nursery not pruned (F-C); flooded conditions and all the visible roots of seedlings pruned at transplanting (F-RP); moist but non-flooded conditions without standing water and roots of seedlings not pruned (NF-C); and non-flooded conditions and roots pruned (NF-RP). Three seedlings 30 d after sowing in a greenhouse were transplanted in each hill of 15×15 cm, and at 4 days after transplanting (DAT) when the plants in some

### Table 1. Shoot dry weight, root dry weight, plant length, plant age in leaf number, ΔRW, number of new roots, maximum new root length, and root-to-shoot ratio at 4 DAT

| Treatment   | Shoot dry weight (g) | Root dry weight (g) | Plant length (cm) | Plant age in leaf number | ΔRW (g) | No. of new roots | Maximum new root length (cm) | Root-to-shoot ratio |
|-------------|----------------------|---------------------|-------------------|--------------------------|---------|-----------------|-----------------------------|-------------------|
| F-C         | Otomemochi           | 0.219               | 0.240             | 31.4**                   | 6.9**   | 0.065           | 9.3**                       | 7.4**             | 1.07*                  |
|             | Yumenohatamochi      | 0.252               | 0.224             | 34.6                     | 6.6     | 0.034           | 7.3                         | 8.1               | 0.88                   |
|             | 98 lines             | 0.289               | 0.269             | 31.1                      | 6.5     | 0.121           | 8.6                         | 8.4               | 1.00                   |
|             | Range                | 0.119–0.498         | 0.125–0.499       | 22.4–38.3                 | 5.7–7.2 | –0.038 to 0.345 | 4.7–13.7                    | 4.1–13.0          | 0.48–2.49              |
|             | Heritability         | 0.87                | 0.61              | 0.76                      | 0.80    | 0.62            | 0.67                        | 0.68              | 0.74                   |
| F-RP        | Otomemochi           | 0.253               | 0.142**           | 30.5**                    | 6.7**   | 0.142           | 12.4                        | 7.7               | 0.5**                  |
|             | Yumenohatamochi      | 0.259               | 0.088             | 35.3                      | 6.3     | 0.088           | 7.9                         | 7.9               | 0.34                   |
|             | 98 lines             | 0.260               | 0.104             | 28.6                      | 6.3     | 0.104           | 10.1                        | 7.8               | 0.41                   |
|             | Range                | 0.099–0.369         | 0.037–0.238       | 20.0–38.9                 | 5.3–7.6 | 0.037–0.238     | 4.7–17.3                    | 4.8–10.5          | 0.14–0.95              |
|             | Heritability         | 0.73                | 0.68              | 0.78                      | 0.88    | 0.68            | 0.77                        | 0.51              | 0.62                   |
| NF-C        | Otomemochi           | 0.235               | 0.236             | 29.1**                    | 7.0**   | 0.061           | 11.1                        | 7.0               | 0.97                   |
|             | Yumenohatamochi      | 0.272               | 0.260             | 34.1                      | 6.7     | 0.070           | 8.9                         | 8.5               | 0.90                   |
|             | 98 lines             | 0.281               | 0.249             | 30.7                      | 6.6     | 0.110           | 7.8                         | 7.1               | 0.89                   |
|             | Range                | 0.144–0.448         | 0.122–0.518       | 22.8–37.7                 | 5.6–7.4 | 0.015–0.353     | 4.0–14.0                    | 4.3–12.4          | 0.47–1.74              |
|             | Heritability         | 0.84                | 0.73              | 0.72                      | 0.87    | 0.72            | 0.72                        | 0.68              | 0.59                   |
| NF-RP       | Otomemochi           | 0.166**             | 0.080**           | 25.7**                    | 6.4*    | 0.080           | 10.1                        | 5.9               | 0.45**                 |
|             | Yumenohatamochi      | 0.192               | 0.047             | 31.3                      | 6.2     | 0.073           | 6.8                         | 6.0               | 0.20                   |
|             | 98 lines             | 0.223               | 0.111             | 27.5                      | 6.3     | 0.111           | 7.1                         | 6.0               | 0.42                   |
|             | Range                | 0.101–0.397         | 0.023–0.306       | 20.4–36.9                 | 5.3–7.3 | 0.023–0.306     | 3.0–12.3                    | 3.2–9.4           | 0.05–1.11              |
|             | Heritability         | 0.82                | 0.92              | 0.76                      | 0.85    | 0.92            | 0.75                        | 0.67              | 0.87                   |
| Average     | Otomemochi           | 0.204*              | –                 | 29.3**                    | 6.8**   | 0.079**         | 10.5**                      | 7.0               | –                      |
|             | Yumenohatamochi      | 0.237               | –                 | 33.4                      | 6.5     | 0.048           | 7.2                         | 7.3               | –                      |
|             | 98 lines             | 0.268               | –                 | 29.4                      | 6.4     | 0.115           | 8.6                         | 7.4               | –                      |
|             | Range                | 0.166–0.409         | –                 | 22.1–37.5                 | 5.5–7.1 | 0.039–0.226     | 5.1–13.8                    | 5.0–10.6          | –                      |
|             | Heritability         | 0.93                | –                 | 0.90                      | 0.94    | 0.85           | 0.90                        | 0.72              | –                      |

*a, *Significantly different between parents at the 0.05% level. ** Significantly different between parents at the 0.01% level.
of the hills were sampled, plants in some other hills were thinned so that the hill spacing of each plot became 15×30 cm. Dry weights of shoot and roots, plant length, and plant age in leaf number were measured at transplanting and at 4 DAT. The number of new roots, maximum length of new roots, and the root-to-shoot ratio (dry weights of roots divided by those of shoots) were also recorded at 4 DAT. Heading dates were recorded in all plots, and dry weights of above-ground biomass and heads per hill, head number per hill, and dry weight of a single head were determined at maturity. All the dry weights were determined after drying in an oven at 80 °C for 3 d.

Because rooting is recovery and regrowth of roots from the transplanting shock (Hoshikawa, 1975), the dry weight increments of roots during 4 DAT (ΔRW) were calculated with the following formula:

\[ \Delta RW = RW4 - RWS \]

\[ \Delta RW = RW4 \]

where RW4 is the dry weight of roots at 4 DAT and RWS is the dry weight of roots of seedlings. Equation (1) was applied to F-C and NF-C plots, and equation (2) was applied to F-RP and NF-RP plots.

Molecular maker analysis

The genetic map was established at the Plant Biotechnology Institute, Ibaraki Agricultural Center using 98 lines of the population. The parents were analysed for their polymorphisms with 107 simple sequence repeat (SSR) markers (Manabe et al., 2005).

QTL analysis

Analysis of variance was done to analyse differences in phenotypic values among the four treatments and between parents and among 98 lines. Broad sense heritability was calculated. The QTL analysis was done with Windows QTL Cartographer version 2.0 (Wang et al., 2004) using composite interval mapping. The analysis was conducted both within each individual treatment and for the combined average of all the four treatments. Putative QTLs which showed LOD scores ≥2.5 were denoted in the tables and figures.

Results

Soil water potential

Soil water potential at 10 cm and 20 cm depth below the soil surface in the non-flooded field was between −3 and −15 kPa for 1 week after transplanting. Soil water potential was on average −13 and −10 kPa at 10 cm and 20 cm depth, respectively, during the whole growth period.

Phenotypic data at 4 DAT

Prior to transplanting, seedlings of Yumenohatamochi had significantly higher plant length than those of Otomemochi.
(37.2 cm versus 30.3 cm). There were no significant genotype differences in shoot and root dry weights and plant age.

At 4 DAT, shoot dry weight and plant length were significantly lower in NF-RP compared with the other treatments. Yumenohatamochi had higher shoot dry weight and plant length, and a lower number of leaves in all the plots than Otomemochi (Table 1). Otomemochi had, in general, more ΔRW, number of new roots, and higher root-to-shoot ratio than Yumenohatamochi, but these variety differences were less clear under NF-C. Yumenohatamochi had a longer maximum new root length than Otomemochi in F-C. The lines had more new roots and maximum new root length in flooded treatments and least in NF-RP, but the differences in ΔRW were not great among the treatments (Table 1). The interactions between lines and treatments were significant for all the traits, and the rankings of lines differed among the treatments. Figure 1 shows the frequency distribution for ΔRW, number of new roots, maximum new root length, and average root-to-shoot ratio of all the treatments among 98 RILs.

The correlation coefficients between ΔRW and shoot dry weight, number of new roots, and root to shoot ratio in NF-RP were highest among the four treatments (Table 2).

### Maturity

Total above-ground dry weight, head dry weight per hill, and head number per hill of both parents were suppressed under non-flooded conditions (NF-C and NF-RP) compared with flooded conditions, but the reduction in Yumenohatamochi was smaller than that of Otomemochi. Yumenohatamochi had, in general, a greater dry weight of a single head than Otomemochi (Table 3). The total above-ground dry weight and head dry weight per hill at maturity were more reduced by the non-flooded water management than by the root-pruning treatment at transplanting. The correlation coefficient between ΔRW at 4 DAT and total

### Table 2. Correlation coefficient between ΔRW and shoot dry weight, number of new roots, and root-to-shoot ratio at 4 DAT

| Treatment | Shoot dry weight<sup>a</sup> | No. of new roots<sup>a</sup> | Root-to-shoot ratio<sup>a</sup> |
|-----------|-----------------------------|----------------------------|-------------------------------|
| F-C       | 0.462**                     | 0.283**                    | 0.411**                       |
| F-RP      | 0.617**                     | 0.319**                    | 0.760**                       |
| NF-C      | 0.602**                     | 0.086                      | 0.596**                       |
| NF-RP     | 0.692**                     | 0.596**                    | 0.900**                       |

<sup>a</sup>,<sup>**</sup>Significant at the 0.01% level.

### Table 3. Total above-ground dry weight, head dry weight per hill, head number per hill, and dry weight of a head at maturity

| Treatment | Total above-ground dry weight (g per hill)<sup>a</sup> | Head dry weight per hill (g per hill)<sup>a</sup> | Head no. per hill<sup>a</sup> | Dry weight of a head (g)<sup>a</sup> |
|-----------|--------------------------------------------------------|-------------------------------------------------|----------------------------|-----------------------------------|
| F-C       |                                                        |                                                 |                             |                                   |
| Otomemochi| 37.1                                                   | 20.4                                            | 12.6                        | 1.62                              |
| Yumenohatamochi| 36.9                                                  | 20.0                                            | 10.8                        | 1.85                              |
| 98 lines  | 30.3                                                   | 15.2                                            | 10.0                        | 1.55                              |
| Range     | 16.6–44.8                                             | 8.0–21.1                                        | 6.3–15.5                    | 0.91–2.33                         |
| Heritability| 0.54                                                  | 0.56                                            | 0.69                        | 0.88                              |
| F-RP      |                                                        |                                                 |                             |                                   |
| Otomemochi| 27.1                                                   | 15.2                                            | 9.8                         | 1.54                              |
| Yumenohatamochi| 30.4                                                  | 16.5                                            | 8.6                         | 1.90                              |
| 98 lines  | 25.8                                                   | 13.1                                            | 8.1                         | 1.65                              |
| Range     | 16.5–41.6                                             | 6.8–22.6                                        | 5.0–12.5                    | 0.90–2.65                         |
| Heritability| 0.63                                                  | 0.69                                            | 0.50                        | 0.87                              |
| NF-C      |                                                        |                                                 |                             |                                   |
| Otomemochi| 17.6**                                                 | 9.3**                                           | 8.1                         | 1.14                              |
| Yumenohatamochi| 27.0                                                  | 13.9                                            | 9.2                         | 1.50                              |
| 98 lines  | 18.6                                                   | 9.2                                             | 7.8                         | 1.22                              |
| Range     | 10.2–29.8                                             | 4.9–14.6                                        | 3.3–15.3                    | 0.57–2.10                         |
| Heritability| 0.77                                                  | 0.78                                            | 0.81                        | 0.9                                |
| NF-RP     |                                                        |                                                 |                             |                                   |
| Otomemochi| 14.3**                                                 | 8.1                                             | 6.4**                       | 1.27                              |
| Yumenohatamochi| 20.8                                                  | 8.8                                             | 8.7                         | 1.02                              |
| 98 lines  | 18.6                                                   | 9.3                                             | 7.4                         | 1.28                              |
| Range     | 8.3–36.4                                              | 3.4–20.8                                        | 3.3–13.0                    | 0.50–2.56                         |
| Heritability| 0.83                                                  | 0.85                                            | 0.79                        | 0.92                              |
| Average   |                                                        |                                                 |                             |                                   |
| Otomemochi| 24.0**                                                 | 13.2*                                           | 9.2                         | 1.39**                            |
| Yumenohatamochi| 28.8                                                  | 14.8                                            | 9.3                         | 1.57                              |
| 98 lines  | 23.4                                                   | 11.7                                            | 8.4                         | 1.43                              |
| Range     | 17.0–35.7                                             | 6.8–19.6                                        | 5.5–12.6                    | 0.85–2.21                         |
| Heritability| 0.84                                                  | 0.86                                            | 0.88                        | 0.96                              |

<sup>a</sup>,<sup>**</sup>Significantly different between parents at the 0.05% level. ** Significantly different between parents at the 0.01% level.
above-ground dry weight, head dry weight per hill, head number per hill, and dry weight of a head at maturity were significant only in NF-RP (Table 4).

**QTLs at 4 DAT**

A total of 12 chromosome regions with putative QTLs within each treatment or across four treatments were detected for traits at 4 DAT (Table 5; Fig. 2). Three regions with QTLs for the number of new roots were observed on chromosomes 4 and 9, explaining 7.0–31.2% of the variation, and the QTLs around RM3335 on chromosome 4 were detected in all the treatments. Among the two chromosome regions with QTLs for ARW, the QTL in chromosome 6 was found in the combined analysis and its positive allele came from Yumenohatamochi, while RM3476–RM1054 in chromosome 5 showed the presence of a QTL for ARW only in the root-pruning treatments (F-RP and NF-RP), accounting for 12.2–23.8% of the phenotypic variation and with the positive allele derived from Otomemochi. The latter region also had a QTL for shoot dry weight with a phenotypic variation of 13.0–17.1% and with all of their positive alleles from Otomemochi. Three regions with QTLs for plant age in leaf number were observed on chromosomes 3, 4 and 10, explaining 12.4–20.9% of the variation, and all of their positive alleles were also carried by Otomemochi. Among the six QTLs for maximum new root length, two QTLs in chromosome 4 in combined analysis derived their positive allelic effects from Yumenohatamochi, while one QTL in RM215–RM205 in chromosome 9 was found only under NF-C, with the phenotypic variation 13.4% and with its positive effect from Otomemochi. Two QTLs for root-to-shoot ratio were observed on chromosomes 1 and 6, and explained 17.5% and 15.2% of the variation, respectively.

### Table 4. Correlation coefficient between ARW at 4 DAT and total aboveground dry weight, head dry weight per hill, head number per hill, and dry weight of a head at maturity

| Treatment | Total aboveground dry weight | Head dry weight per hill | Head no. per hill | Dry weight of a head |
|-----------|-----------------------------|-------------------------|------------------|---------------------|
| F-C       | 0.142                       | 0.185                   | 0.055            | 0.151               |
| F-RP      | 0.127                       | 0.176                   | 0.255            | −0.032              |
| NF-C      | −0.100                      | −0.096                  | 0.042            | −0.133              |
| NF-RP     | 0.569**                     | 0.596**                 | 0.343**          | 0.385**             |

** Significant at the 0.01% level.

### Table 5. Putative QTLs for shoot and root traits at 4 DAT under the four treatments and the average

| Traits                        | Treatment | Chromosome | Marker interval | Position (cM) | LOD | Variation (%) | Additive value |
|-------------------------------|-----------|------------|-----------------|---------------|-----|---------------|----------------|
| Shoot dry weight              | F-RP      | 5          | RM2357–RM1054   | 0             | 4.7 | 17.1         | 0.03           |
|                               | NF-RP     | 5          | RM2357–RM1054   | 0             | 3.5 | 15.1         | 0.02           |
|                               | Average   | 5          | RM2357–RM1054   | 0             | 3.3 | 13.0         | 0.02           |
| Plant age in leaf number      | F-C       | 3          | RM1338–RM6080   | 39            | 3.5 | 15.8         | 0.14           |
|                               | F-RP      | 4          | RM3785–RM1388   | 5             | 4.3 | 16.5         | 0.14           |
|                               | NF-C      | 10         | RM467–RM184     | 0             | 3.8 | 12.4         | 0.16           |
|                               | NF-RP     | 4          | RM3785–RM1388   | 0             | 4.9 | 20.9         | 0.19           |
| ARW                           | F-C       | 6          | RM5814–RM3509   | 6             | 5.2 | 22.4         | −0.04          |
|                               | F-RP      | 5          | RM2357–RM1054   | 0             | 6.8 | 23.8         | 0.02           |
|                               | NF-RP     | 5          | RM3476–RM2357   | 16            | 2.6 | 12.2         | 0.03           |
|                               | Average   | 6          | RM5814–RM3509   | 2             | 2.8 | 10.6         | −0.01          |
| No. of new roots              | F-C       | 4          | RM3335–RM1153   | 0             | 6.5 | 20.0         | 0.95           |
|                               |           | 9          | RM160–RM3808    | 1             | 2.6 | 7.0          | −0.61          |
|                               | F-RP      | 4          | RM3335–RM1153   | 0             | 6.9 | 21.4         | 1.33           |
|                               | NF-C      | 4          | RM3335–RM1153   | 0             | 7.3 | 26.9         | 0.98           |
|                               | NF-RP     | 4          | RM3335–RM1153   | 0             | 5.4 | 18.3         | 0.92           |
|                               | Average   | 4          | RM5953–RM3643   | 0             | 3.3 | 7.3          | −0.57          |
|                               |           | 4          | RM3276–RM3335   | 10            | 11.4| 31.2         | 1.1            |
|                               |           | 4          | RM3288–RM5503   | 1             | 4.4 | 16.1         | −0.39          |
| Maximum new root length       | F-RP      | 1          | RM1387–RM1067   | 2             | 2.7 | 12.4         | 0.44           |
|                               |           | 6          | RM7023–RM3183   | 3             | 2.5 | 11.6         | −0.43          |
|                               | NF-C      | 9          | RM215–RM205     | 0             | 2.7 | 13.4         | 0.76           |
|                               | NF-RP     | 6          | RM5814–RM3509   | 4             | 2.7 | 13.8         | −0.52          |
|                               | Average   | 4          | RM5953–RM3643   | 0             | 5.4 | 18.5         | −0.47          |
|                               |           | 4          | RM3288–RM5503   | 1             | 4.4 | 16.1         | −0.39          |
| Root-to-shoot ratio           | F-RP      | 6          | RM4447–RM5509   | 0             | 3.3 | 15.2         | −0.04          |
|                               | Average   | 1          | RM3475–RM3494   | 2             | 4.8 | 17.5         | 0.13           |

*a* Distance from the first marker to the QTL.  
*b* Phenotypic variation explained by the QTL.  
*c* Effects of substituting a single allele from one parent to another. Positive values show that the allelic contribution is from Otomemochi and negative values from Yumenohatamochi.
QTLs at maturity

A total of seven chromosome regions with putative QTLs for production traits at maturity were detected (Table 6 and Fig. 3). Two QTLs for head dry weight per hill were observed in RM2811–RM5953 on chromosome 4 (only under NF-RP) and in RM5509–RM5814 in chromosome 6 (under the other three treatments), explaining 12.9–24.4% of the variation. One QTL for total aboveground dry weight was observed on chromosome 4 close to the QTL for head dry weight per hill in the NF-RP treatment which is mentioned above, explaining 18.6% of the variation. QTLs for dry weight of a single head were observed in RM5509–RM5814 on chromosome 6, close to the QTL for head dry weight per hill. Four regions with QTLs for head number per hill were observed on chromosomes 4 and 9, explaining 7.8–34.1% of the variation; the QTLs around RM3276 on chromosome 4 were detected in all the treatments while the QTLs in RM5953–RM3643 in chromosome 4 were detected only under NF-C. QTLs for heading date around RM4853 and RM5924 on chromosome 3 were observed in all the four treatments, explaining 10.5–39.9% of the variation.

Discussion

Phenotypic responses and variation

Otomemochi, the lowland parent, showed higher rooting ability than Yumenohatamochi, the upland parent, as is evident from the former’s larger values for ARW, number of new roots, and root-to-shoot ratio at 4 DAT on average of the four treatments. However, under the non-flooded treatment without root pruning, the varietal differences for those root traits at 4 DAT were not clear. Other studies also
showed evidence that seedlings of rice genotypes differ in root and shoot growth in response to changing water availability such as drought and rewatering (Banoc et al., 2000; Wade et al., 2000; Kamoshita et al., 2004). This study for the first time clearly showed such genotypic variation under transplanted lowland fields with different water regimes, although only two lowland and upland varieties, but with similar seedling size, were compared. At maturity, Otomemochi showed lower total above-ground dry weight, head dry weight per hill, and dry weight of a single head under non-flooded conditions than flooded conditions; under similar conditions, Yumenohatamochi showed a smaller reduction. Yumenohatamochi was developed for improving drought resistance in upland fields in Japan (Hirasawa et al., 1998), but this study suggested that Yumenohatamochi was also better adapted to water-limiting non-flooded lowland conditions than Otomemochi.

**QTLs for rooting ability under different water regimes**

QTLs for root-related traits have been extensively studied using different mapping populations, mostly from the cross of *japonica* and *indica* parents; previously, 498 QTLs for root-related traits (cf. mostly measured during the seedling stage) were reported in rice according to the Gramene QTL Database (Jaiswal et al., 2006; http://www.gramene.org/qtl/), such as total and deep root dry weight, maximum rooting length, root number, and root thickness (Kamoshita et al., 2002; Price et al., 2002; Fukai and Kamoshita, 2005). Our study is unique in that the population is from the cross of Table 6. Putative QTLs for production traits at heading and maturity under the four treatments, and the average

| Traits                      | Treatment | Chromosome | Maker interval      | Position (cM) | LOD  | Variation (%) | Additive value |
|-----------------------------|-----------|------------|---------------------|---------------|------|---------------|----------------|
| Above-ground dry weight per hill | NF-RP     | 4          | RM2811–RM5953       | 4             | 3.6  | 18.6          | −2.4           |
| Head dry weight per hill    | F-C       | 6          | RM5509–RM5814       | 6             | 4.7  | 21.7          | −1.3           |
|                             | F-RP      | 6          | RM5509–RM5814       | 2             | 4.3  | 18.5          | −1.5           |
|                             | NF-C      | 6          | RM5509–RM5814       | 8             | 2.6  | 12.9          | −0.84          |
|                             | NF-RP     | 4          | RM2811–RM5953       | 4             | 3.7  | 18.0          | −1.5           |
|                             | Average   | 6          | RM5509–RM5814       | 4             | 5.2  | 24.4          | −1.0           |
| Head number per hill        | F-C       | 4          | RM3337–RM3785       | 26            | 3.7  | 13.5          | 0.66           |
|                             | F-RP      | 4          | RM5503–RM3276       | 0             | 3.3  | 10.6          | −0.6           |
|                             | NF-C      | 4          | RM3276–RM3335       | 2             | 4.1  | 16.6          | −0.6           |
|                             | NF-RP     | 4          | RM3276–RM3335       | 2             | 3.0  | 13.6          | −0.77          |
|                             | Average   | 9          | RM553–RM160         | 0             | 3.1  | 9.4           | −0.62          |
| Dry weight of a head        | F-C       | 4          | RM3276–RM3335       | 0             | 9    | 25.6          | 0.16           |
|                             | F-RP      | 4          | RM3276–RM3335       | 2             | 6.3  | 23            | 0.19           |
|                             | NF-C      | 4          | RM3276–RM3335       | 0             | 3    | 9.3           | 0.09           |
|                             | NF-RP     | 4          | RM3276–RM3335       | 8             | 5.1  | 20.3          | −0.14          |
|                             | Average   | 4          | RM3276–RM3335       | 3             | 6.7  | 28.2          | −1.0           |
| Heading day                 | F-C       | 3          | RM4853–RM1332       | 0             | 12.9 | 34.3          | 2.95           |
|                             | F-RP      | 3          | RM4853–RM1332       | 0             | 7.1  | 18.8          | −2.20          |
|                             | NF-C      | 3          | RM4853–RM1332       | 10            | 10   | 26.3          | 2.72           |
|                             | NF-RP     | 3          | RM4853–RM1332       | 0             | 7.7  | 20.4          | −2.4           |
|                             | Average   | 3          | RM4853–RM1332       | 0             | 13.2 | 34.6          | 3.26           |

* a Distance from the first marker to the QTL.
* b Phenotypic variation explained by the QTL.
* c Effects of substituting a single allele from one parent to another. Positive values show that the allelic contribution is from Otomemochi and negative values from Yumenohatamochi.
two temperate glutinous japonica ecotypes, and that QTLs for rooting ability after transplanting (i.e. ARW, number of new roots, maximum new root length, and root-to-shoot ratio) were identified. Almost 40% of the QTLs for rooting ability and for production traits at maturity (e.g. head number, single head dry weight, and head dry weight per hill) were detected in combined analysis, which were mainly in chromosomes 1, 4 and 6, with their positive allelic contribution coming from both lowland and upland parents (e.g. QTLs for ARW and heads dry weight per hill in RM5814–RM3509 in chromosome 6, QTLs for number of new roots, head number per hill, and dry weight of a single head in RM5953–RM3643 and in RM3276–RM3335 in chromosome 4, QTLs for maximum new root length in RM5953–RM3643 and in RM3288–RM5503 in chromosome 4, and QTLs for root-to-shoot ratio in RM3475–RM3494 in chromosome 1).

We found that at least some of the QTLs in this study were closely located with the reported QTLs for root-related traits; the QTLs for ARW and maximum new root length after transplanting around RM5814 in chromosome 6 in this study were co-located with a QTL for deep root weight at heading stage in the same population by Manabe et al. (2005). This chromosome region also had QTLs for root dry weight at the vegetative stage (Yadav et al., 1997; Liang et al., 2005), root-to-shoot ratio (Xu et al., 2001), root penetration index, penetrated root number (Ray et al., 1996), and maximum root length (Zheng et al., 2003) in five different populations from the crosses between japonica and indica parents. The QTL for maximum new root length around RM3288 in chromosome 4 in this study was co-located with QTLs for root dry weight and root thickness in an Azucena×Bala population (Price et al., 2002). The QTLs for the number of new roots around RM3335 in chromosome 4 in this study were co-located with QTLs for various root traits (e.g. root thickness, root-to-shoot ratio, root pulling force, and deep root weight) in two mapping populations (Zheng et al., 2000; Zhang et al., 2001; Kamoshita et al., 2002; Price et al., 2002). On the other hand, the QTL for root-to-shoot ratio around RM3475 in chromosome 1 and the QTL for the number of new roots around RM5953 in chromosome 4 were not co-located with the previously reported root QTLs. These chromosome regions may be associated with unique genetic regulation of rooting ability only after transplanting, but not affecting gross root morphology in other plant growth stages. Alternatively, these chromosome regions may be unique only for our population (i.e. japonica×japonica). In marker-assisted selection for deep rooting character in the Azucena×IR64 population (Shen et al., 2001), four key chromosome regions were identified, but only one in chromosome 9 (i.e. RZ228–RM242–RZ12–RM201–RG667) was co-located with the QTLs in this study (i.e. the number of new roots and maximum new root length).

Fewer QTLs were detected specifically under non-flooded conditions: a QTL for maximum new root length in the RM215–RM205 interval on chromosome 9 and a QTL for head number in the RM5953–RM3643 interval on chromosome 4. This may be due to smaller phenotypic differences between the two parents in root-related parameters under non-flooded conditions, or larger error variation in
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