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**K. Nemoto · Y. Ukai · D.-Q. Tang · Y. Kasai ·
M. Morita**

Inheritance of early elongation ability in floating rice revealed by diallel and QTL analyses

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Abstract In floating rice, stem elongation begins much earlier than in non-floating rice, which is the major survival mechanism for flooding. Inheritance of this early elongation ability was studied using diallel and quantitative trait locus (QTL) analyses. The diallel analysis was undertaken using a set of 6×6 half-diallel crosses involving four floating (‘Goai’, ‘Habiganj Aman VIII’, ‘Badal 106’, and *Oryza rufipogon* strain W120) and two non-floating (‘Latisail’ and ‘Patnai 23’) parents. The additive gene effects were higher than the dominant effects. The dominant alleles were concentrated in the cultivated floating parents (‘Goai’, ‘Habiganj ‘Aman VIII’, and ‘Badal 106’), whereas the recessive alleles were in the wild floating parent (W120). A QTL analysis using a ‘Patnai 23’ × ‘Goai’ F_2 population detected two putative QTLs. Of these QTLs, the one on chromosome 12 behaved as a partially dominant major gene that explained more than half of the total genetic variation.

Introduction

In the basins of the great rivers in South and Southeast Asia, water may rise to a height of more than 1 m during the monsoon season. Floating rice (*Oryza sativa* L.) has been the only crop that can be grown there. It exhibits marked elongation growth in rapidly rising water, which has allowed rice culture even in deepwater conditions in these regions. This capacity of elongation growth has long attracted the attention of physiologists and geneticists, as well as breeders (see Catling 1992 for a review).

The manner in which the growing stem responds to water by elongation is essentially the same in floating and non-floating rice cultivars. First, rice-stem elongation is caused by cell division and cell elongation in the intercalary meristem tissue, which is positioned at the bottom of individual internodes (Metraux and Kende 1984). The intercalary meristem is formed in a definite stage of plant development (usually, 2 months or more after planting) and is absent from seedlings (Takahashi 1988). Second, the formation of the intercalary meristem is only slightly affected by water (Inoue 1983), whereas deepwater conditions dramatically stimulate cell division and cell elongation in the preexisting intercalary meristem (see Kende et al. 1998 for a review). Thus, the intercalary meristem acts as a prerequisite for the elongation response of the plant to deepwater; young plants before the stage of intercalary meristem formation lack the capacity to respond to water, even in floating cultivars (Takahashi 1988). A major difference between floating and non-floating cultivars lies in the timing of intercalary meristem formation. In floating rice, the intercalary meristem is formed much earlier (a month or more) than in non-floating rice, and this precocious intercalary meristem formation allows floating rice to respond to deepwater by vigorous elongation, even in the earlier stage of plant development (Catling 1992; Inoue 1983; Takahashi 1988). This ability to form intercalary meristem in early growth stages is called “early elongation ability” (Mazaredo and Vergara 1979).

Inheritance of early elongation ability has been studied by several researchers using diverse floating rice accessions. Results of earlier studies are often inconsistent. Tripathi and Rao (1985) hypothesized a single dominant gene for early elongation. Using a cross between a floating cultivar and a non-floating dwarf cultivar carrying the gibberellin synthesis deficient *d35* mutation, Suge (1988) demonstrated that two complementary genes may be involved in the early elongation ability. These are a

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K. Nemoto (✉) · D.-Q. Tang · Y. Kasai · M. Morita
Asian Natural Environmental Science Center,
The University of Tokyo,
Yayoi, Bunkyo-ku, 113-8657 Tokyo, Japan
e-mail: unemoto@mail.ecc.u-tokyo.ac.jp
Tel.: +81-358417561
Fax: +81-3-58415070

Y. Ukai
Graduate School of Agricultural and Life Sciences,
The University of Tokyo,
Yayoi, Bunkyo-ku, 113-8657 Tokyo, Japan

completely dominant gene encoding a step in the gibberellin synthesis pathway and a partially dominant one with an unknown function. Because the former is considered the wild allele of the *d35* gene, his results virtually imply that a partially dominant major gene might control early elongation ability (Suge 1988). On the other hand, Sano and his colleagues (Eiguchi et al. 1993a, 1993b) identified a recessive major gene, *dw3*, for the early elongation ability of a floating *Oryza rufipogon* accession, strain W120.

There is increasing evidence that floating rice has a varied phylogenetic background (Glaszmann 1987; Hakoda and Inoue 1988). This suggests that the genes differentiating early elongator (floating rice) from late elongator (non-floating rice) might vary, depending on the cross examined. To understand the genetic variation of the early elongation ability, we made a diallel analysis on six rice accessions, including W120. For the full genetic analysis of the diallel approach, there are several assumptions to be satisfied (no multiple alleles, uncorrelated gene distributions, etc.), which may be difficult to meet in most cases (Baker 1978). Despite such difficulty, one could effectively use a part of this approach (especially, the V_r-W_r graph analysis) as a preliminary survey to get an idea of the differences in genetic control between parents. This may be helpful to select parents for more detailed studies such as quantitative trait loci (QTLs) analysis. In this study, we verified the actual number and action of individual genes involved using QTL analysis on such a cross: 'Patnai 23' (a non-floating parent) × 'Goai' (a floating parent).

Materials and methods

Diallel analysis

Six parents, 'Patnai 23' (International Rice Research Institute accession no. IRGC 46531), 'Latisail' (IRGC 6176), 'Goai' (IRGC 49189), 'Habiganj Aman VIII', 'Badal 106', and W120, and their 15 F_1 hybrids constituting a 6×6 half-diallel set were used. 'Patnai 23' and 'Latisail' are non-floating, traditional tall *indica* cultivars from India. The cultivated floating parents ('Goai', 'Habiganj Aman VIII', and 'Badal 106') originate from Bangladesh. Bangladesh floating rice is highly diverse phylogenetically and contains all the known floating rice groups defined by isozyme polymorphism (Glaszmann 1987). 'Goai' is a member of group 3 (an intermediate group between *indica* and *japonica*) of the isozymatic classification by Glaszmann (1987). 'Badal 106' and 'Habiganj Aman VIII' show close affinity to group 1 (*indica*) and group 4 (an intermediate group between *indica* and *japonica*), respectively, according to our data on marker isozyme polymorphism (data not shown). All of these parents are strongly photoperiod sensitive and are grown as long-duration rainy season crops in the Ganges-Brahmaputra Basin. W120 is a strongly photosensitive, floating strain of wild rice (*O. rufipogon* Griff.) from Orissa, India, whose floating ability has been studied genetically (Eiguchi et al. 1993a, 1993b; Morishima et al. 1962).

Early elongation ability was evaluated for the 21 entries (the six parents and 15 F_1 hybrids) in a greenhouse at the University of Tokyo (35°43′N, 139°46′E) during the summer of 2000 (June–September). The seeds were pregerminated (30°C, 3 days), and sown in plastic pots (10 cm diameter, 12 cm height) filled with 0.5 l clay soil containing 0.1 g each of N, P_2O_5, and K_2O, with one plant per pot. When the seedlings were 2 weeks old, the pots were transferred to a water pool and water was added to increase depth by 3 cm every other day. This began from the soil level in the pots to a final depth of 20 cm, which was maintained. Five plants were grown for each entry, with two replications.

We evaluated the early elongation ability using the lowest elongated internode (LEI) concept (Inoue et al. 1985). Development of successive internodes, including intercalary meristem formation (or stem elongation), is sequential in rice (Nemoto et al. 1995), resulting in a parallel relationship between the position of the lowermost internode that exhibits elongation and the growth stage of the plant in which the intercalary meristem is formed in the stem. This relationship enables the timing of intercalary meristem formation to be measured using the position of the lowest elongated internode (Inoue et al. 1985). The lowest internode longer than 5 mm has been defined as the LEI (Inoue et al. 1985). Data for LEI with two replications were analyzed following Hayman (1954a, 1954b), using the computer program DIALL (Ukai 1989).

QTL analysis

From the cross 'Patnai 23' × 'Goai', an F_2 population of 186 plants was generated. Phenotypic evaluation of the F_2 plants along with the parents (30 plants each) for early elongation ability was undertaken in a greenhouse at the University of Tokyo during the summer of 2001 (June–September). The growth conditions and phenotyping procedure were as in the diallel analysis experiment.

For genotyping, the DNA of F_2 plants was extracted from 3 g of fresh leaf tissue using the benzyl chloride method (Zhu et al. 1993). For the RFLP analysis, DNA was digested with five restriction enzymes: *Bgl*II, *Dra*I, *Eco*RI, *Eco*RV, and *Hin*dIII. Southern blotting, hybridization, and detection using the ECL Direct Nucleic Acid Labeling and Detection Kit (Amersham Pharmacia Biotech, UK) were conducted as described by Kurata et al. (1994). The 192 RFLP land-markers set (Rice Genome Research Program, RGP, http://rgp.dna.affrc.go.jp) derived from the published RFLP linkage map (Kurata et al. 1994) was surveyed on the parents, and the selected probes were mapped. Some sequence-tagged site (STS) markers (RGP, http://rgp.dna.affrc.go.jp) and simple-sequence repeat (SSR) markers (Chen et al. 1997; McCouch et al. 2002) were also mapped. Polymerase chain reaction (PCR) amplifications were undertaken as described in the RGP home page (http://rgp.dna.affrc.go.jp) and in Chen et al. (1997). The amplified products of the mapping population were separated on 4% agarose gel in 1× TAE buffer. The patterns were visualized using ethidium bromide.

The program MAPMAKER/EXP, version 3.0 (Lander et al. 1987) was used to construct a linkage map. MAPMAKER/QTL, version 1.1 (Lincoln et al. 1992) was used to identify QTLs for early elongation ability via simple interval mapping. A QTL was declared when the LOD score exceeded the threshold of 3.0.

Results and discussion

Diallel analysis on the early elongation ability

All parents and F_1 hybrids started stem elongation by the early September. During this period, all entries remained vegetative, which eliminated any possibility that stem elongation (intercalary meristem formation) was induced by floral initiation. Table 1 shows the LEI position in the six parents and 15 F_1 hybrids. In the floating parents ('Goai', 'Badal 106', 'Habiganj Aman VIII', and W120), the LEI position was 7–8 (i.e., the lower six or seven internodes, which were established in the seedling stages, were compressed without intercalary meristem). The LEI position was 10–11 (i.e., the lower nine or ten internodes

Table 1 Diallel table for lowest elongated internode position (average of two replications)

	Female					
	Non-floating rice		Floating rice			
Male	‘Patnai 23’	‘Latisail’	‘Goai’	‘Habiganj Aman VIII’	‘Badal 106’	*Oryza rufipogon* strain W120
Non-floating rice						
’Patnai 23’	11.00[a]	10.77	9.00	8.88	9.20	9.60
’Latisail’	-	10.80[a]	9.00	8.80	9.00	10.00
Floating rice						
’Goai’	-	-	7.70[a]	7.00	8.00	8.00
’Habiganj Aman VIII’	-	-	-	7.00[a]	7.70	7.50
’Badal 106’	-	-	-	-	8.00[a]	8.00
Oryza rufipogon strain W120	-	-	-	-	-	8.00[a]

[a] LSD 0.05=0.27

were compressed without intercalary meristem) in the non-floating parents, ‘Patnai 23’ and ‘Latisail’. These results are very similar to those of Islam and Inoue (1988), who examined early elongation ability in 211 long-duration, traditional rice cultivars from deepwater areas of Bangladesh. In their study, cultivars from highly flooded areas (considered as true floating cultivars) predominantly had internode seven or eight as the LEI, whereas those from more shallow flooded areas predominantly had internode 10 or 11 as the LEI. The F_1 hybrids showed intermediate values between the parental values in their LEI positions.

Analysis of variance showed that both additive and dominance effects were significant (F=622.34 and 6.02, respectively). The genetic parameters for the LEI position were as follow. The environmental variance was very small (E=0.009); hence, the broad-sense (h^2_B) and narrow-sense (h^2_N) heritabilities were very high (0.994 and 0.962, respectively). The additive variance (D=2.901) was much larger than the dominance variances (H_1=0.209, H_2=0.178), with an average degree of dominance [SQR (H_1/D)]=0.269. The average direction of dominance (h=–0.089) was negative but close to 0, indicating that some dominant alleles conferred early elongation (i.e., the lower LEI position) and others conferred late elongation (i.e., the higher LEI position).

Figure 1A shows the relationship between array variance (V_r) and array parent-offspring covariance (W_r) for LEI position. The regression coefficient of W_r on V_r was close to unity (0.988), suggesting that non-allelic interactions were absent. The regression line cut the W_r axis above the origin, indicating that the early elongation was partially dominant. Interestingly, the floating parents were clustered into two separate groups on the regression line. One group, comprising the cultivated floating parents (‘Badal 106’, ‘Goai’, and ‘Habiganj Aman VIII’), occupied a position near the origin, indicating that the dominant alleles for LEI position were predominant in this group. The other group, represented by the wild floating parent W120, was located farthest from the origin, indicating that it possesses most of the recessive alleles. The non-floating parents, ‘Patnai 23’ and ‘Latisail’, occupied an intermediate position between the two floating groups. These results explain well the discrepancy in the earlier reports on the inheritance of early elongation: the dominant alleles were predominant in the cultivated floating parents, as supported by Tripathi and Rao (1985) and Suge (1988), whereas the recessive alleles accumulated in the wild floating parent, W120, which is in agreement with Eiguchi et al. (1993a, 1993b).

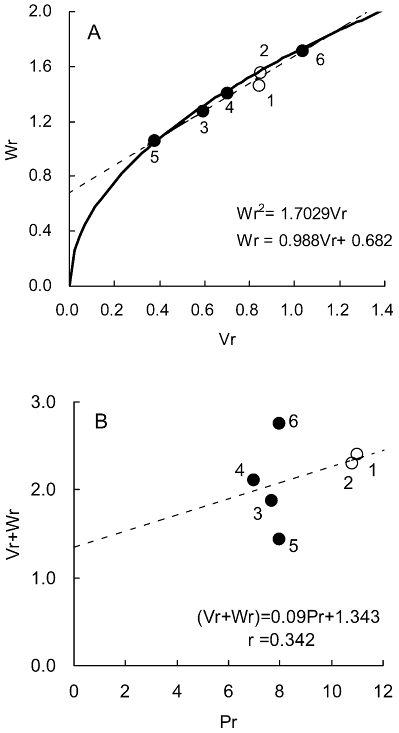

Fig. 1A, B W_r-V_r graph for lowest elongated internode (LEI) position (**A**) and P_r,-W_r+V_r graph for LEI position (**B**) in a 6×6 diallel cross. *1* ‘Latisail’, *2* ‘Patnai 23’, *3* ‘Goai’, *4* ‘Habiganj Aman VIII’, *5* ‘Badal 106’, *6 Oryza rufipogon* strain W120, *black circles* floating parent, *white circles* non-floating parent

In Fig. 1B, the six parents were projected onto P_r (LEI position of the parents) and W_r+V_r (parental order of dominance) coordinates. P_r and W_r+V_r showed a positive

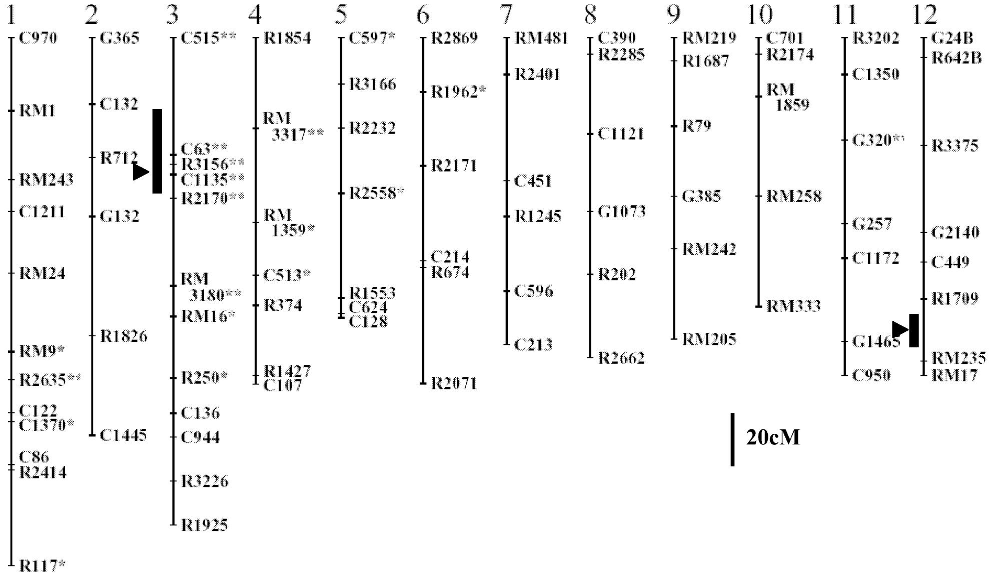

Fig. 2 Chromosomal location of quantitative trait loci (QTLs) for early elongation ability (LEI position). QTLs with an LOD greater than 2.4 are shown. *Bars to the left* of the chromosomes indicate 1-LOD likelihood intervals, and *arrowheads* indicate the position of the peak LOD in the interval. *One asterisk* and *two asterisks* indicate segregation distortion significant at 0.05 and 0.01, respectively

correlation (r=0.342), suggesting that genes for early elongation (i.e., the lower LEI position) were generally dominant. However, within the cultivated floating parents (‘Badal 106’, ‘Goai’, and ‘Habiganj Aman VIII’), the lower LEI position of the parents is associated with a higher (W_r+V_r) value, suggesting that some recessive allele(s) might confer the lower LEI position in such early elongators as ‘Habiganj Aman VIII’. This agrees with the fact that a floating cultivar, ‘Habiganj Deepwater 8’ (presumably synonymous with ‘Habiganj Aman VIII’), carries *dw3* (Y. Sano, personal communication).

QTL analysis on early elongation ability

We determined the number and action of genes involved in the early elongation ability of cultivated floating rice using QTL analysis. For this purpose, we chose the cross ‘Patnai 23’ × ‘Goai’ because (1) the remaining two floating cultivars (‘Habiganj Aman VIII’ and ‘Badal 106’) occupied a position close to the non-floating parents in the V_r-W_r graph in Fig. 1 (‘Habiganj Aman VIII’) or had a weak phenotype for the early elongation ability (‘Badal 106’), and (2) ‘Patnai 23’ showed normal fertility in the hybrid with ‘Goai’ (data not shown). All plants started stem elongation by the end of summer, and during this period they all remained vegetative. The LEI position for ‘Goai’ and ‘Patnai 23’ averaged 7.7 and 10.9, respectively. The frequency distribution of the LEI position of the F_2 population was approximately normal and almost within the range of the parental values. The numbers of individuals in each class (LEI=8, 9, 10 and 11) were 17, 93, 70, and 6, respectively. The heritability in a broad sense was 0.64.

Before linkage map construction, the 192 RFLP landmarkers set (RGP, http://rgp.dna.affrc.go.jp) was surveyed among the parents. As a result, 45% of the markers detected polymorphism and monomorphic regions mainly on chromosomes 1, 3, 4, 7, 9, 10, and 12 were observed, for which region polymorphism of PCR markers (SSR and STS markers) was surveyed. Eventually, we mapped 88 selected markers (17 SSR, 1 STS, and 70 RFLP markers), which constituted 12 linkage groups. The linkage map spanned 1,497 cM, with an average marker distance of 19.4 cM (Fig. 2). Of the 88 markers, 20 (23%), grouped into eight or nine regions, showed significant deviations (0.05) from expected segregation ratios based on the chi-square test. Among the 20 markers, 15 showed an excess of the ‘Patnai 23’ homozygote. The most severe distortion was found for the marker C1135 on chromosome 3, which was strongly skewed in favor of ‘Patnai 23’ alleles (‘Patnai 23’ homozygote:heterozygote: ’Goai’ homozygote = 49:49:2). The marker C1135 is very close to the locus where similar distortion was observed in the ‘Nipponbare’ (*japonica*) × ‘Kasalath’ (*indica*) F_2 linkage map (Harushima et al. 1996).

The analysis with MAPMAKER detected one QTL for the LEI position located on chromosome 12 (R1709-RM235), where the allele of the floating parent, ‘Goai’, conferred early elongation (i.e., a lower LEI position) (Fig. 2). This QTL had a large effect (LOD=18.6, additive effect of the ‘Patnai 23’ allele = 0.638, dominance effect = −0.091), explaining 48% of the total phenotypic variance. Since heritability in a broad sense was 0.64, 75% of the total genetic variation in LEI position might be explained by this QTL. In addition, one QTL below the threshold of significance (LOD=2.4) was detected on chromosome 3 (R3156-C1135), where the allele of ‘Goai’ conferred early elongation. This putative QTL had a much smaller effect (additive effect of the ‘Patnai 23’ allele = 0.256, dominance effect = −0.065), explaining only 5.9% of the total variance. However, the contribution of this QTL may be somewhat underestimated due to the severe genetic distortion in this chromosomal region as mentioned above. The ratios of dominance effect/additive effect were −0.25 (chromosome 3) and −0.14 (chromosome 12). This agreed with the results of the diallel analysis, in that early elongation was partially dominant over late elongation. These results also agree with the view of Suge (1988), in that early elongation ability is regulated practically by a single major, partially dominant gene. In the QTL region on chromosome 3, Sripongpangkul et al. (2000) identified an epistatic QTL for stem-elongation growth in deepwater condition (franked by the marker P2M10-2) using a cross between a semidwarf elite line and an Indian floating rice.

At present, no candidate genes can be proposed for these QTLs. Takahashi (1988) showed that the combined application of gibberellins (GAs), abscisic acid (ABA), and ethylene is most effective for the induction of early elongation in non-floating rice, although the role of ethylene is considered to enhance the action of GA and ABA. Hamamura and Saengpetch (1977) suggested that the accumulation of ABA and GAs in floating rice seedlings might be responsible for their early elongation. Nevertheless, the early-elongation QTLs do not coincide with the QTLs for ABA accumulation under drought (Quarrie et al. 1997), nor the known loci of GA synthesis and GA-signaling genes. Although many dwarfing mutations have been mapped in rice (Huang et al. 1996), our QTLs failed to hit any of these loci. On the other hand, the mutations that prolong the juvenile phase (*Teopod 1*, *Teopod 2* and *Corngrass*) also delay the onset of stem elongation in maize. This suggested that intercalary meristem formation in grasses is, at least in part, under the control of the phase change from juvenile to adult. It would be an attractive hypothesis that the early intercalary meristem formation in floating rice is caused by an altered timing of the phase change, but neither of the two QTLs seemed to be syntenous to these maize heterochronic genes.

Although the results of our QTL analysis are consistent with those of previous studies, other genes might also be involved in early elongation. As mentioned above, 'Habiganj Aman VIII' might have (an) additional QTL(s) for early elongation (Fig. 1). Furthermore, previous reports demonstrated that a Thai floating rice, 'Leb Mue Nahng III', when crossed with Bangladesh floating cultivars, gave rise to transgressive segregation in elongation ability (Hamamura and Kupkanchanakul 1979; Thakur and HilleRisLambers 1988), suggesting that Thai floating cultivars have a gene system for early elongation ability that is different from Bangladesh cultivars. An understanding of the diversity of genes for early elongation ability requires an examination of these cultivars.

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