During improvement of cereal grasses, the increase in yield potential often results from a decrease in tiller number (via an increase in tiller bud dormancy) and the compensating increase in sink size (i.e., panicle or ear size) (Khush, 2000). Mutants that exhibit an altered tiller number are a rich source of information for understanding the genetic factors that regulate tiller number in cereal grasses. In rice, several tillering mutants have been identified, but most of them have been only poorly characterized. In this paper, we describe the tillering behavior of one such rice mutant, \textit{fine culm 1 (fc1)}.

The \textit{fc1} mutant is characterized by thin culms and many tillers. It has been utilized as a morphological marker gene in the rice linkage map project undertaken at Kyushu University. This mutant is particularly interesting for the following reason. Seeking for the genetic basis of morphological evolution of maize from its bushy progenitor, teosinte, Doebley et al. (1995) revealed that the major quantitative trait locus (QTL) for tillering was allelic to the classical morphological mutation \textit{teosinte branched 1 (tb1)}. Later, the \textit{tb1} was cloned and appeared to encode a putative transcriptional factor (Doebley et al., 1997). Nemoto et al. (2001) pointed out that there exists circumstantial evidence that suggests that \textit{fc1} is a loss-of-function mutant of the \textit{tb1} ortholog in rice. First, the \textit{fc1} mutant exhibits profuse tillering like the maize \textit{tb1} mutant (Iwata et al., 1977) and, second, the \textit{fc1} mutation is located on the chromosomal region syntenic with the maize \textit{tb1} region (Ahn et al., 1993; Yoshimura et al., 1997). The rice ortholog of \textit{tb1} was cloned by Lukens et al. (2001). Using transgenic rice, Takeda et al. (2003) confirmed that this gene controls tiller bud dormancy in the same way as maize \textit{tb1}. They also showed that the \textit{fc1} mutant has a loss-of-function allele of this gene (Takeda et al., 2003). Despite such an importance, the mutant phenotype of \textit{fc1} has not been fully described yet. In this paper, we describe in detail the tillering behavior of the \textit{fc1} mutant.

\textbf{Materials and Methods}

Phenotypic characterization of the mutant ‘M56’ (the \textit{fc1} mutant, which was induced from Norin 8 by gamma-ray irradiation) and the wild type (Norin 8) plants was undertaken at Tohoku University during the summer of 2002 (July–September). The seeds were sown in plastic pots (15.8-cm diameter, 19.5-cm high) filled with 3.2 l clay soil, with one plant per pot. The pots were watered and fertilized (160 mg of N, 40 mg of P2O5 and 60 mg of K2O) regularly, every 10 d. Water was maintained at approximately 3 cm above the soil level throughout the growth period.

\textbf{Results and Discussion}

The \textit{fc1} mutant is a profusely tillering plant with a thin culm (Fig. 1). The mutation does not affect the timing of floral initiation (data not shown). We analyzed the developmental morphology of the \textit{fc1} mutant and the background line, Norin 8. Figure 2 shows the increase of tiller number in the wild type and \textit{fc1} mutant plants. In the \textit{fc1} mutants, the rate of tiller increase was much higher and resulted in a final tiller number that was roughly twice that of the wild type plants. In general, a rice plant potentially generates hundreds of tillers, but the actual number is strongly down-regulated by tiller bud dormancy (see Nemoto et al., 1995 for a review). This dormancy occurs predominantly in tiller buds on (1) the lowest node of individual tillers to which a scale-like leaf called "prophyll" is attached, and (2) the uppermost several nodes of individual tillers, often associated with elongated internodes. Interestingly, extra-tillering in \textit{fc1} mutant plants was mainly due to the reduced...
frequency of tiller bud dormancy at the prophyll nodes (84.6% and 20.7% for wild type and \textit{fe}1 plants, respectively), whereas the \textit{fe}1 mutation had little effect on dormancy in the upper nodes (88.0% and 84.3% for wild type and \textit{fe}1 plants, respectively) (Table 1). These facts suggest that (1) the main target site of \textit{fe}1 function is the lowermost node of each tillers, and (2) dormancy in the upper nodes is regulated by factors other than \textit{fe}1. From these results, we suggest that, unlike the maize counterpart, \textit{tb}1 (Hubbard et al., 2002), the role of \textit{fe}1 as a regulator of tiller number might be rather subsidiary in rice (i.e., it affects only a specific node). This view is consistent with the fact that rice has numerous tiller number QTLs.

Rice shows an array of genetic variation in tillering ability and it would be interesting to determine if the rice \textit{tb}1 (=\textit{fe}1) locus is involved in it. Many investigators have identified tiller number QTLs from diverse crosses of rice including cultivated rice (\textit{Oryza sativa}) × wild rice (\textit{O. rufipogon}) cross (e.g., Xiao et al., 1998). Until recently, however, no QTLs had been mapped in the vicinity of \textit{fe}1. Recently, advances in computer software have facilitated the detection of QTLs that have only a negligible main-effect, but a significant epistatic effect when they interact with one another (Wang et al., 1999). Using this new approach, Luo et al. (2001) identified the marker intervals C746-CDO337 on chromosome 3 (approximately equivalent to the \textit{fe}1 locus) as an epistatic QTL that are involved in the tiller number expressed in hybrid rice. This fact suggests that \textit{fe}1 might, at least in part, be involved in the heterosis of tiller number expressed in hybrid rice, which is consistent with the fact that tillers on prophyll nodes tend to grow out in both \textit{fe}1 mutants (Table 1) and hybrid rice (Kusuda et al., 1990).
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Table 1. Comparison of the rate of dormancy in the tiller buds of wild type and fc1 mutant plants. Frequency of dormant tiller buds on successive nodes of the axis of primary tillers (the tillers borne directly from the main tiller) is shown. Nodal positions are numbered acropetally, beginning from the prophyll node. Values are means ± SE (n=10).

| Nodal position | Frequency of tiller buds in dormancy (%) |
|---------------|------------------------------------------|
|               | Wild type plants | fc1 mutant plants |
| Prophyll node | 84.6 ± 4.6 | 20.7 ± 3.4 |
| 1st node      | 33.2 ± 4.8 | 31.7 ± 4.3 |
| 2nd node      | 48.6 ± 1.4 | 46.8 ± 4.8 |
| 3rd node      | 56.4 ± 2.8 | 59.8 ± 3.9 |
| >3rd node     | 88.0 ± 1.1 | 84.3 ± 1.8 |

a Significant at 0.1% level.
b Not significant.