The wheat plastochron mutant, *fushi-darake*, produced by heavy-ion beam mutagenesis†

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Grasses such as wheat (*Triticum aestivum*) are the major source of carbohydrates for humans, and the yield of grain from these crops is largely dependent on inflorescence architecture. A detailed understanding of development in wheat plants is of value not only to wheat breeding but also for basic scientific research. From the large scale mutant panel of diploid einkorn wheat (*Triticum monococcum*) developed by heavy-ion beam irradiation[1], we identified a mutation that had an abnormally large number of nodes; we termed this mutation *fushi-darake* (*fdk*), which means too many nodes in Japanese.

The *fdk* showed drastic changes to their structural organization compared to wild type (WT) plants in the field (Fig. 1). Contrary to WT, *fdk* plants had 1/2 alternate phyllotaxy with rapid leaf emergence. Consequently, the *fdk* plants had a larger number of nodes and leaves compared to the WT plants. In the *fdk* plants, vegetative shoot branches emerged from the nodes in the upper part of the culm of most tillers (Fig. 1). In these ectopic shoots, normal leaves were produced with 1/2 alternate phyllotaxy. The culms of *fdk* plants were unable to support the heavy upper vegetative shoots, with the result that the plants collapsed onto the ground (Fig. 1).

We examined the timing of leaf unfolding in WT and *fdk* seedlings grown in a growth chamber. The rate of leaf emergence was more rapid in *fdk* compared to WT after the 3-leaf stage. This indicates that rapid leaf emergence in *fdk* resulted from a rapid rate of leaf initiation: the plastochron of *fdk* plants was estimated to be half of that in WT.

fdk WT

Fig. 1. *fushi-darake* (*fdk*) mutant plant grown in the field and green house. WT: wild-type wheat strain KU104-1

To investigate further the morphological differences between WT and *fdk* plants, we carried out an SEM (scanning electron microscope) analysis of shoot apical meristem (SAM) development. SAM development in *fdk* plants was very different to that of WT plants. The SAM elongated but its branch meristems (BMs) resembled leaf primordia rather than spikelet meristems (SMs). Ectopic flat dome-like BMs that were similar to leaf primordia were initiated with a1/2 alternate pattern. These observations, together with those on the morphology of the *fdk*, suggest that the flat dome-like BMs develop into vegetative shoots.

The inflorescence of grass species is composed of a unique unit called the spikelet. When the wheat plant transits from the vegetative to reproductive growth phase (flowering), the SAMs are elongated and spikelet meristems (SMs) initiate as lateral branches. Our SEM analysis of the *fdk* mutant indicated that differentiation of SMs was delayed and the leaf primordia were initiated from branch meristems (BMs) with 1/2 alternate phyllotaxy. These observations suggest that 1/2 alternate phyllotaxy with rapid leaf emergence produced the shortened plastochron in the *fdk* mutant. The SAMs further elongated and produced flat dome-like BMs at the position of the original SMs. We also found that *fdk* plants had vegetative shoot branches emerging from the nodes of upper part of culm of almost all tillers. Thus, our results suggest that these vegetative shoots are likely to be developed from the BMs of elongated SAMs. In conclusion, our findings indicate that the abnormal phenotype of the *fdk* mutant resulted from transformation of SMs into vegetative shoots.

Three plastochron mutants, *plastochron 1* (*pla1*)[2], *pla2*[3] and *pla3*[4], have been identified in rice (*Oryza sativa*). Among them, we found that wheat *fdk* and rice *pla1* mutants show similar phenotypes. These facts indicate that some common genetic cascades are involved in the phenotype of wheat *fdk* and rice *pla1*. The WT gene, *PLASTOCHRON 1* (*PLA1*), encodes a member of a plant-specific subfamily of cytochrome P450, CYP78A11, which potentially catalyzes substances controlling plant development[5]. The similar phenotypes of the *fdk* with *pla1*, suggest that *PLA1* or related genes may be candidates for the *fdk* mutation in wheat.

† Condensed from the article in American J. Plant. Sci. **4**, 28 (2013)

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