Aerenchyma Formation in the Seminal Roots of Japanese Wheat Cultivars in Relation to Growth under Waterlogged Conditions

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Abstract: Morphological adaptation of roots is critical for plants to survive under waterlogging. In this study, we evaluated the capacity of wheat to form aerenchyma in seminal roots in combination with the growth angle of the roots. We used five Japanese cultivars from the waterlogging-prone Kanto-Kyushu region in Japan, and a non-Japanese cultivar, Bobwhite for comparison. Seedlings in pot culture were waterlogged at a 3-cm depth for 7 days. The first adverse effect of waterlogging on plant growth was a significant reduction of root dry mass. The reduction rate varied with the cultivar, and it was 19.2% in cv. Shiroganekomugi and 40.0% in cv. Norin 61. Root aerenchyma was initially observed on the 2nd day of waterlogging and developed until the 7th day, in all 6 cultivars. Quantitative analysis of the aerenchyma development revealed no significant difference in radial distribution among the cultivars, whereas a slight difference was found in the axial distribution. As a consequence, the heavier root weight of Shiroganekomugi was not related to either the radial or axial developing capacity of aerenchyma but might be due to the effect of its shallow root angle in the soil. These results suggest that the capacity to form aerenchyma in the seminal root is not sufficient for expression of waterlogging tolerance in the Japanese wheat cultivars.

Key words: Aerenchyma, Bobwhite, Root growth angle, Seminal root, Shiroganekomugi, Waterlogging.

Wheat (Triticum aestivum L.), a crop important for human nutrition, is mainly grown in dryland areas (precipitation, 600–700 mm yr⁻¹) of the world. In Japan, annual rainfall in the wheat-producing areas of Kanto-Kyushu region is greater than 1,000 mm. Moreover, wheat is often cultivated in drained rice paddy fields, where the soil moisture is relatively high. Because there is a surplus of rice grain in Japan, the current agricultural strategy to mitigate the problem of rice overproduction is to cultivate wheat in upland fields that have been converted from paddy fields. More than 20% of the wheat producing area in Japan is affected by wet conditions (Oyanagi, 2008). It is a great challenge to harvest wheat in such an environment, because wheat plants (particularly during the early stage) in the converted paddy fields suffer from waterlogging stress.

The approximate distribution of the wheat production area in Japan is categorized into 3 major zones: Hokkaido region, 56% (almost upland cultivation; winter-type wheat in winter and spring-type wheat in spring); Tohoku region, 4% (winter-type wheat in winter), and Kanto-Kyushu region, 40% (spring- or intermediate-type wheat in winter) (MAFF, 2011). Although the Kanto-Kyushu region is one of the main production areas, bread wheat cultivated in this area is known to suffer from severe waterlogging stress. There are more than 30 wheat cultivars commercially grown in the Kanto-Kyushu region (MAFF, 2008). However, none of them can tolerate waterlogging on the farm. Therefore, there is an urgent need to establish wheat lines that are tolerant to waterlogging in order to increase bread wheat production in Japan.

Knowledge of adaptation strategies of plants to waterlogging is important for establishing wheat lines with waterlogging tolerance. Two morphological characters of roots related to waterlogging tolerance are well known: aerenchyma (an internal trait) and architecture of root system (an external trait). Aerenchyma is a specialized plant tissue containing enlarged gas spaces and functions in aeration in plants (Armstrong, 1979). Root aerenchyma enhances gas exchange and supply oxygen to the root tips from aerial part of plant tissues under hypoxic condition of waterlogged soils. In general, aerenchyma is classified into 2 types according to the developmental process: lysigeny and schizogeny (Haque et al., 2010; Evans, 2003). Lysigenous aerenchyma formation is widespread among both wetland and non-wetland species (Justin and Armstrong, 1987) and further divided into 2 types. One is environmentally induced...
in the roots of non-wetland species when exposed to low oxygen concentrations, for example in wheat (Trought and Drew, 1980), barley (Benjamin and Greenway, 1979), or maize (Drew et al., 1979). Another is constitutively formed in the roots of many wetland species such as rice, and the aerenchyma volume increases with low oxygen concentrations in the root environment (Armstrong, 1971; Colmer et al., 1998). Root distribution in soil varies with the crop species (Yu et al., 1969) and wheat lines (Oyanagi et al., 2004). In addition, soil qualities, such as water content, oxygen and nutrient availability, and redox potential, etc. (FAO, 2011) vary with the position in soil (Boggie, 1977). For example, the upper-layer soil, which is closer to the atmosphere, tends to contain higher concentrations of oxygen than the lower-layer soil. Therefore, the root architecture has some effect on the plant growth under waterlogged conditions. The aerenchyma and root architecture are considered to independently contribute to waterlogging tolerance.

The relationship between capacity of aerenchyma formation and waterlogging tolerance in wheat has been studied using non-Japanese cultivars (Thomson et al., 1992; Huang et al., 1994; Setter and Waters, 2003). Plants with a higher capacity of aerenchyma formation showed higher waterlogging tolerance (i.e. heavier shoot and root weights) under waterlogging and/or low oxygen conditions. However, the aerenchyma formation capacity in Japanese wheat cultivars may be different from that in non-Japanese cultivars, because no Japanese cultivars have been found to tolerate waterlogging on the farm. Japanese cultivars have been bred independently of cultivars in other countries. Therefore, we studied the process of aerenchyma formation under waterlogged conditions, including the time elapsed before formation of aerenchyma and axial distribution of aerenchyma along the seminal root, using spring-type wheat cv. Bobwhite as a representative hexaploid wheat (Haque et al., 2010). However, information about variation in aerenchyma formation in Japanese wheat cultivars is limited. Therefore, we need to know whether the commercial cultivars in Kanto-Kyushu region vary in aerenchyma formation. The capacity of aerenchyma formation of Japanese cultivars needs to be studied to develop waterlogging tolerant cultivars through the improvement of root capacity.

In this study, 5 Japanese wheat cultivars from the Kanto-Kyushu region of Japan were grown under waterlogged pot condition for 7 days (d), and possible contributions of root aerenchyma to the wheat seedling growth under waterlogging stress were investigated. Bobwhite, a non-Japanese cultivar, was also used as a standard hexaploid wheat.

Materials and Methods

1. Plant materials

Japanese cultivars of wheat (Triticum aestivum L.) (spring- or intermediate-type wheat; Norin 61, Shiroganekomugi, Chikugoizumi, Minaminokomugi, and Kinuhime) and a non-Japanese Bobwhite (spring-type wheat) for comparison were used in this experiment. Norin 61, Shiroganekomugi, and Chikugoizumi were chosen because they are major cultivars in the Kanto-Kyushu area (MAFF, 2011), and Shiroganekomugi, Minaminokomugi, and Kinuhime were selected because they showed different root growth angles (Oyanagi et al., 1991, 1993, 2001).

2. Growth conditions and water treatments

Growth conditions and water treatments were based on the methods described by Haque et al. (2010). Seeds were germinated on moist filter paper placed in petri dishes in a dark growth cabinet at 23ºC. Three healthy germinated seeds were sown at a depth of 3 cm in 54 tall pots (height 30 cm ×diameter 15.9 cm; Fujiwara Scientific, Tokyo, Japan) containing the soil described below. Each control pot had eight 0.6-cm diameter holes drilled in the bottom. The bottom of each pot was filled with a 3-cm layer of coarse perlite, and above the perlite, 2.6 kg of fertilized granular soil (pH 6.5, 1.0 g N, 2.6 g P2O5, 1.6 g K2O; Kureha Corporation, Tokyo, Japan), and then 2.4 kg of volcanic soil (pH 6.1; Green Tech, Tochigi, Japan) were added. Thus, the soil distribution in the 30-cm tall pot from the bottom was as follows: 3 cm of perlite, 11 cm of granular soil and 13 cm of volcanic soil. Wheat seeds were sown on 19th October, 1st November and 29th November, 2010 and the wheat plants were grown in a greenhouse kept at 17–23ºC under natural light in Tsukuba city, Ibaraki prefecture. Pots were watered daily by immersing in water to a depth of 14 cm from the bottom. Pots were rotated in the greenhouse every second day to minimize the effect of different positions on growing conditions.

Waterlogging (WL) treatment was initiated when seedlings were 5 d old. For WL treatment, the water level was maintained at 3 cm above the soil surface, and in the control, the pots were watered daily to a depth of 14 cm from the bottom, then allowed to drain. In our previous study, we examined 3 levels of WL, including the water level of 15 cm below the soil surface (Haque et al., 2010). Our data showed that the effect of WL with the water level of 15 cm below the soil surface was slight, and the effect of WL was significant only when the water level was 3 cm above the soil surface. Therefore, we maintained the water level at 3 cm above the soil surface in WL in this study.

3. Measurement of seedling growth parameters

The chlorophyll concentration was measured at 0, 2, and 7 d after the start of WL treatment (d0, d2 and d7) in the same 4 plants (from 2 pots). Measurements were made at 4.5 cm from the base of the first emerged leaves by using a SPAD 502 chlorophyll meter (Konica Minolta, Osaka, Japan). For each treatment and cultivar, 3 plants in 1 pot.
were harvested at d 0 of WL, 6 plants in 2 pots at d 2, and 6 plants in 2 pots at d 7. At d 0, the plants in 1 pot from each of the 6 cultivars (6 pots) were harvested to determine plant height, primary seminal root length, total length of seminal root, total shoot dry mass, and total root dry mass. At d 2 and d 7 of WL, 3 plants of each cultivar were randomly selected from 2 pots in WL and control and harvested to determine the above 5 characters as at d 0. Root length was measured only for root axes, i.e., not including branch roots. Roots were oven dried for 2 d at 80ºC, and the dry weight was measured. The other 3 plants from the 2 pots of each cultivar were used to analyze root anatomy. Plants that showed no injury during root preparation were selected and used for tissue sections. Experiments were replicated 3 times. Data were summarized by calculating means and standard errors, and analyzed by two-way analysis of variance (ANOVA).

4. Seminal root anatomy

In each treatment, 3 primary seminal roots (the first-emerged seminal root is regarded as the primary seminal root among the total of 5 seminal roots in wheat) from 3 plants at each sampling day were evaluated for aerenchyma formation. After gentle washing, we segmented the roots at 0, 3, and 5 cm from the root base (the root-shoot junction) and at 2, 5, 10, and 15 cm from the root tip. The root segments were then embedded in 5% agar. Transverse cross-sections of each root segment (4–6 sections per segment, each section 100–400 µm thick) were obtained using a microslicer (DTK-1000; Dosaka EM, Kyoto, Japan). The sections were observed and photographed with a light microscope equipped with a camera (BX51 microscope and DP72 camera; Olympus, Tokyo, Japan) at ×10.

5. Measurement of aerenchyma

The percentage of aerenchyma area in the cortex was measured in cross sections taken at 2, 5, 10 and 15 cm behind the root tip, and at 0, 3, and 5 cm from the root-shoot junction, by randomly taking 1 primary seminal roots from 1 individual plant at each sampling site. Sections were photographed with a digital camera, and the percentage of aerenchyma area in the cortex was measured using an image-analysis program (BX51 microscope and DP72 camera; Olympus, Tokyo, Japan), and then calculated with the following equation:

\[
\% \text{ aerenchyma area} = \frac{Ae}{\text{Contex total}} \times 100
\]

\[Ae = \text{Tortal area of aerenchyma}\]
\[T = \text{Total area of root}\]
\[S = \text{Total area of stele}\]

6. Measurement of growth angle of roots

The experiment was conducted according to Oyanagi et al. (2001) in the same greenhouse as described above. A plastic meshwork basket (open top diameter: 16 cm, flat bottom diameter: 8.5 cm, height: 6 cm, mesh size: 4 mm²) was filled with volcanic soil and placed in the top part of the pot (diameter: 16 cm, height: 20 cm). Three germinated seedlings, each with 0.5–1.0 mm primary seminal roots, were transplanted into the basket at a depth of 1 cm. The sites on the basket mesh from which the roots appeared were observed for 7–10 d after transplantation. Relative air humidity in the pots was maintained at approximately 100%. The growth angle of the seminal roots was determined by measuring the angle from the horizontal. The mean growth angle of 4–5 seminal roots per plant was calculated. Five pots in each cultivar were used as replicates.

Results

1. Shoot growth

Overall, shoot growth was reduced by WL treatment. At d 2 of WL, no significant effect of WL was observed in the shoot traits among the cultivars (Table 1, Figs. 1 and 2). However, the plant height of several Japanese cultivars was slightly increased by WL treatment. In Shiroganekomugi, it was increased 3.0% at d 2 and 5.9% at d 7, and in Minaminokomugi it was increased by 1.3% at d 2 and 4.0% at d 7 (Table 1). At d 7, shoot dry mass accumulation was reduced by 13.2–18.0% (Fig. 2), but the difference among cultivars was not significant.

2. Root growth

We measured root parameters such as primary seminal root length, total seminal root length, and total root dry mass. The primary seminal root length and total seminal root length were significantly reduced by WL treatments, but not with the cultivar (Table 1). The highest reduction in the primary seminal root length was observed in Norin 61 (20.9% at d 2 and 40.8% at d 7 of WL) and lowest in Shiroganekomugi (15.4% at d 2 and 33.1% at d 7 of WL) (Table 1). The total length of seminal roots was highly inhibited in Norin 61 (15.9% at d 2 and 28.9% at d 7 of WL) and least inhibited in Shiroganekomugi (7.6% at d 2 and 16.3% at d 7 of WL) (Table 1). The total root dry mass showed significant inhibition both between treatments and among cultivars. The highest reduction in root dry mass by WL treatment was found in Norin 61 (18.3% after 2 d and 40.0% at d 7 of WL) and the lowest in Shiroganekomugi (6.5% after 2 d and 19.2% at d 7 of WL) (Fig. 2). Treatment × cultivar interactions in the root dry mass was significant at d 7, which indicated that Shiroganekomugi was less affected by WL treatment in root weight among the 6 cultivars.

3. Root aerenchyma formation

None of the cultivars formed aerenchyma under control
Table 1. Effects of 2 d and 7 d of waterlogging (WL, 3 cm flooding) on plant height, primary seminal root length, and total length of seminal roots in Bobwhite and 5 Japanese wheat cultivars. Percentages indicate the reduced rates due to the waterlogging treatment. Nine plants were used in 3 replicates. Single and double asterisks indicate significant differences at the 5% and 1% level by analysis of variance, respectively. SK, Shiroganekomugi; CI, Chikugoizumi; MK, Minaminokomugi.

| Cultivar | Treatment | Plant height (cm) | Primary seminal root length (cm) | Total seminal root length (cm) |
|----------|-----------|-------------------|---------------------------------|------------------------------|
| Initial  | Control   | 10.1±0.1          | 12.8±0.3                        | 51.4±1.1                     |
| Bobwhite | Control   | 11.4±0.2          | 14.8±0.3                        | 49.7±1.2                     |
| SK       | Control   | 11.8±0.3          | 13.4±0.9                        | 54.4±1.1                     |
| CI       | Control   | 11.9±0.3          | 14.1±0.4                        | 56.7±1.9                     |
| MK       | Control   | 9.2±0.2           | 14.1±0.2                        | 52.6±1.9                     |
| Kinuhime | Control   | 11.9±0.2          | 15.0±0.3                        | 55.2±1.9                     |

| Cultivar | Treatment | Plant height (cm) | Primary seminal root length (cm) | Total seminal root length (cm) |
|----------|-----------|-------------------|---------------------------------|------------------------------|
| 2 d of waterlogging |          |                   |                                 |                              |
| Bobwhite | Control   | 15.9±0.4          | 20.3±0.7                        | 80.9±1.9                     |
| SK       | Control   | 16.7±0.3          | 21.1±1.3                        | 70±2.7                       |
| CI       | Control   | 17.5±0.4          | 19.7±0.8                        | 79.8±1.9                     |
| MK       | Control   | 15.6±0.3          | 16.6±0.8                        | 72.2±1.1                     |
| Kinuhime | Control   | 17.1±0.2          | 18.5±0.6                        | 79.4±1.4                     |

| Cultivar | Treatment | Plant height (cm) | Primary seminal root length (cm) | Total seminal root length (cm) |
|----------|-----------|-------------------|---------------------------------|------------------------------|
| 7 d of waterlogging |          |                   |                                 |                              |
| Bobwhite | Control   | 22.9±0.8          | 26.2±1.2                        | 109.7±4.2                    |
| SK       | Control   | 25.4±0.6          | 30.8±1.1                        | 111.6±3.2                    |
| CI       | Control   | 27.1±0.9          | 30.8±1.1                        | 111.6±3.2                    |
| MK       | Control   | 26.1±0.6 (−0.4%)  | 16.5±0.2 (37.0%)                | 82.1±3.7 (25.2%)             |
| Kinuhime | Control   | 28.3±0.6          | 25.9±1.7                        | 103.2±1.8                    |

ANOVA

| Treatment (T) | ns | * | * |
| Cultivar (CV) | ** | ** | ** |
| T×CV          | ns | ns | ns |


Fig. 1. Morphology of Bobwhite and 5 Japanese wheat cultivars grown for 7 d under a waterlogged condition (3 cm flooding). The photograph shows a representative of 3 replicates. C: control. WL: waterlogging.

Fig. 2. Effects of 2 d and 7 d of waterlogging (WL) on the seedlings of Bobwhite and 5 Japanese wheat cultivars. (A) Chlorophyll content, (B) shoot dry mass, (C) root dry mass. Experiments were repeated 3 times. Four plants for chlorophyll measurements, and 3 plants for root and shoot measurements were used. Values represent the mean ±SE (n = 3). Percentages indicate the rate of reduction due to the waterlogging treatment. Single and double asterisks indicate significant differences at the 5% and 1% level by analysis of variance, respectively; BW, Bobwhite; N61, Norin 61; SK, Shiroganekomugi; CI, Chikugoizumi; MK, Minaminokomugi; KH, Kinuhime.
Fig. 3. Cross sections of the primary seminal roots showing the distribution of aerenchyma formation after exposure for 2 d (2dWL) or 7 d (7dWL). (A) Bobwhite, Norin 61, and Shiroganekomugi. (B) Chikugoizumi, Minaminokomugi, and Kinuhime. Sections were made at 2, 5, 10 and 15 cm from the tip, and at 0, 3 and 5 cm from the base (root-shoot junction). The roots of 9 plants were observed. Numerals in the figure show the distance from the base (root-shoot junction), and from the root tip. Numbers below the photographs represent the mean length of the seminal roots. 2dWL; root sections after 2 d of WL. 7dWL; root sections after 7 d of WL. Vertical solid lines indicate completely formed aerenchyma; broken lines indicate the initial stage of aerenchyma formation.
condition but they formed aerenchyma in the primary seminal root after 2 d WL. Then the aerenchyma continued to develop until d 7 (Fig. 3A and B). To quantify root aerenchyma formation, we calculated the percentage of aerenchyma in the cortex of root sections at d 7 of WL (Fig. 4). The results showed no significant difference among cultivars in the percentage of aerenchyma area at 2–10 cm behind root tip where aerenchyma was observed in all cultivars (Fig. 4). However, the distribution of aerenchyma along the root axis slightly varied with the
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Aerenchyma was observed at 3 cm from the root base, which was close to the root-shoot junction in Bobwhite. In Japanese cultivars, however, aerenchyma was not observed near the root base, though in Shiroganekomugi, Norin 61 and Chikugoizumi aerenchyma was observed at 5 cm from the root base. Aerenchyma in Minaminokomugi and Kinuhime was observed far from the base (Figs. 3B and 4).

4. **Growth angles of seminal roots**

We evaluated the growth angles of seminal roots in the 5 Japanese cultivars and Bobwhite. In the pot experiment, 4.1 seminal roots per plant, on the average, penetrated through the basket within 7 d. From the position of the penetration, we determined the root growth angle. The mean and standard deviations of the root growth angle in each cultivar are shown in Fig. 5. The root growth angle was smallest in Shiroganekomugi (37.1° from the horizontal), while it ranged from 53.9° to 54.7° in other cultivars. Variance analysis showed that the differences in growth angle between the Japanese cultivars and Bobwhite were not significant at the 1% level. Only in Shiroganekomugi, the angle was significantly smaller than in the other cultivars.

**Discussion**

1. **Difference in seedling growth among wheat cultivars under WL**

In this study, root growth was affected by WL earlier than shoot growth. Length and dry weight of root were reduced by WL for only 2 d, but those of shoot were not (Table 1 and Fig. 2). This phenomenon is consistent with our previous study with cv. Bobwhite (Haque et al., 2010, 2011) and with cv. Cascades (Malik et al., 2002). This suggests that roots are primarily affected by WL, while shoot growth is affected as a consequence of root inhibition. Cultivar variation in the response to WL stress was significant only in the root dry mass (RDM) at d 7 of WL (Fig. 2). A decline in RDM might be the first symptom of root affected by WL stress. The RDM was greatly decreased in Norin 61, but less in Shiroganekomugi, indicating that Shiroganekomugi is more tolerant to WL at the seedling stage compared with the other cultivars. The mechanism of variation in RDM among the cultivars is not clear; however, the differences in internal root morphology (aerenchyma formation capacity) and/or external root morphology (architecture of root system) might be involved.

2. **Difference in capacity for aerenchyma formation among cultivars**

The percentage of aerenchyma area (mostly in adventitious roots) under WL stress has been found to vary with the genotype in non-Japanese wheat (Thomson et al., 1992; Huang et al., 1994; Setter and Waters, 2003). In contrast, in commercial cultivars from the Kanto-Kyushu region, neither the time elapsed before aerenchyma formation (all cultivars formed aerenchyma at the second d of WL) nor the radial development of aerenchyma (percentage area of aerenchyma area in cortex) varied with the genotype in this study (Figs. 3 and 4). To our knowledge, this is the first report describing the timing and percentage area of aerenchyma in the seminal roots of common Japanese wheat cultivars under waterlogged conditions. This study showed a lack of varietal difference in WL tolerance among Japanese wheat cultivars; however, further study is necessary to understand the physiological relationship between aerenchyma formation and root weight among Japanese and non-Japanese cultivars. Differences in experimental conditions and physiological characteristics, such as photo- and thermo-sensitivity, should be taken into consideration in the comparative study on various cultivars with diverse germplasm (Setter and Waters, 2003).

The longitudinal distribution of aerenchyma along the root axis, significantly varied with the cultivar (Bobwhite > Norin 61, Shiroganekomugi and Chikugoizumi > Minaminokomugi and Kinuhime) (Fig. 4). The extension of aerenchyma towards the root-shoot junction might be advantageous to oxygen diffusion from shoots to roots, which can support the survival of plant roots in oxygen-deficient environments (Armstrong, 1971). Elucidation of the function of axial distribution of aerenchyma would be important to understand the significance of root aerenchyma in WL tolerance of wheat.

3. **Relationship between root weight and root morphological responses**
In non-Japanese wheat cultivars, a larger percentage of aerenchyma in roots was related to less reduction of root growth under waterlogging stress (Thomson et al., 1992). Therefore, we assumed that the superior RDM of Shiroganekomugi compared with the other cultivars could be due to differences in the capacity to form aerenchyma. The present study showed that the timing of formation and percentage of aerenchyma area in the cortex did not significantly vary with the cultivar (Figs. 3 and 4), and only the axial distribution of aerenchyma varied (Fig. 4). These results do not explain why Shiroganekomugi showed minimum reduction of RDM. Thus, none of the aerenchyma-forming capacities, such as time elapsed before formation, percentage of aerenchyma area in the cortex, and axial distribution, were correlated with the larger RDM in Shiroganekomugi.

One factor in the superior RDM in Shiroganekomugi might be the shallowness of its seminal root system (Fig. 5). In the waterlogging experiment, we observed that the root system of Shiroganekomugi was distributed only in the volcanic soil (upper) layer (0–13 cm from the soil surface). Moreover, oxygen concentration in the upper layer was found to be relatively higher (about 6–8%; data not shown) than the lower layer in our pot condition (about 0.5%; Haque et al., 2011). These observations suggest that the shallow root system of Shiroganekomugi allowed the cultivar to survive because of the oxygen-rich volcanic soil layer, and thus evade the negative effect of the WL condition. However, the gradient of oxygen concentration in soil layers would disappear within the several days of WL. Soil quality in the pot would vary with the soil depth not only in oxygen concentration but also redox potential and nutrient availability etc. Therefore, further experiments on the soil environment are needed to clarify the reasons for the superior RDM in Shiroganekomugi.

In this study, two morphological traits of wheat related to waterlogging tolerance, aerenchyma formation and root distribution, in 5 Japanese cultivars were examined in comparison with a non-Japanese cultivar, Bobwhite. Cultivar differences were observed in axial distribution of aerenchyma and root angle, and these characters are possible key traits to breed waterlogging-tolerant varieties. Nevertheless, the capacity for aerenchyma formation did not correlate with wheat growth especially in root weight under a waterlogged condition. Wheat aerenchyma might be too immature or underdeveloped to show tolerance to WL. We have not yet found a good germplasm for aerenchyma formation in T. aestivum and its relatives. It may well be preferable to find the key gene(s) for aerenchyma formation in distant species with a high capacity to form well-developed aerenchyma (e.g., constitutive aerenchyma in rice) that can be introduced into a useful host wheat such as Bobwhite followed by gene introgression into elite Japanese cultivars by crossing.

Acknowledgments

Thanks are due to the International Maize and Wheat Improvement Center (CIMMYT), Mexico, for providing seeds of T. aestivum cv. Bobwhite (line SH 98 26) and the NARO Institute of Crop Science, Tsukuba, Japan, for providing seeds of Japanese cultivars. We also thank Dr. F. Abe and Dr. S. Oda (NARO Institute of Crop Science) for critical review of the manuscript.

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