Specific Variation in Shoot Growth and Root Traits under Waterlogging Conditions of the Seedlings of Tribe Triticeae Including Mizutakamoji (*Agropyron humidum*)

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Abstract: Waterlogging stress is an important limiting factor for wheat and barley production. Waterlogging tolerance was evaluated in the seedlings of seven species from the tribe Triticeae, including wheat, barley, durum wheat, rye (diploid and tetraploid), triticale, einkorn wheat, and Mizutakamoji (*Agropyron humidum*), to acquire basic information about their variation in waterlogging tolerance and to elucidate opportunities for genetic improvement of waterlogging tolerance in cultivated wheat and barley. The seedlings at the one leaf stage were subjected to waterlogging for 0 (Control: CT) or 12 days (Waterlogging: WT) in plastic cups (12 cm tall, 8 cm in diameter), and the morphological traits of shoots and roots were measured. Shoot dry weights (DW) of wheat (cv. Norin 61) and barley (cv. Benkemugi) were lower under WT by 73% and 59%, respectively, than those in CT. Of all the evaluated genotypes, only *A. humidum* showed no reduction in shoot DW under WT. The relative shoot DW (W/C in shoot DW; proportion of shoot DW in WT to that in CT) was significantly correlated with relative root DW (W/C in root DW). The W/C in root DW correlated significantly with W/C in the number and length of adventitious roots, and with W/C in frequency of branching roots on the seminal root, suggesting that development of adventitious roots and branching roots under WT might be related to waterlogging tolerance in tribe Triticeae. The results of this study indicated that wild species of tribe Triticeae, such as *A. humidum*, might be useful resources to analyze waterlogging tolerance in cultivated wheat and barley.


Waterlogging drastically reduces the yields of wheat and barley throughout the world (Setter and Waters, 2003). It is estimated that waterlogging adversely affects 10–15 million ha of wheat annually. Large-scale waterlogging in wheat occurs in irrigated rice-wheat rotation systems in south and east Asia because wheat is cultivated in the fields that have subsoil compaction for rice cultivation in flooding conditions (Samad et al., 2001). Furthermore, recently in Japan, wheat and barley, in spite of their poor adaptability to waterlogging, are cultivated in drained rice paddy field to reduce production of rice. This was similar to the report on maize by Mano et al. (2005a). Increasing waterlogging tolerance of wheat and barley is an important target to increase and stabilize cereal production in Asia.

Many researchers have described genotypic differences in the waterlogging tolerance of wheat and barley (Hamachi et al., 1988; Thomson et al., 1992; Musgrave and Ding, 1998; Pang et al., 2004), but it is reported that the growth or yield of tolerant wheat cultivars is reduced by 70–80% by waterlogging (Thomson et al., 1992). Development of wheat cultivars with waterlogging tolerance is at a standstill because of the absence of outstanding genetic resources for waterlogging tolerance in Japan. In maize, Mano et al. (2005b) showed that relative species of maize, teosinte, could adapt to waterlogging conditions better than maize. They also showed a potential for transferring waterlogging tolerance to maize from teosinte. Utilization of broad genetic resources might be necessary for further analyses and breeding for waterlogging tolerance of Asian wheat and barley.

The tribe Triticeae includes both domesticated and undomesticated species. These species can serve as a source of genes for improvement of stress tolerance in cultivated species (Fedak, 1985). *Agropyron humidum* Ohwi et Sakamoto (*Elymus humidus* Osada), called “Mizutakamoji” in the Japanese vernacular, is a species in the tribe Triticeae; it is indigenous to Japan (Fig. 1). This species reportedly adapts to moist areas because it is commonly found near paddy fields (Sasanuma et al., 2002). The present study is intended to analyze mechanisms of adapting to waterlogging condition in the species of tribe Triticeae and to identify genetic resources for improving the...
waterlogging tolerance of wheat and barley. Eight genotypes in the tribe Triticeae, including *A. humidum*, were evaluated for tolerance in shoot growth in waterlogged conditions and for the relationship between waterlogging tolerance and the development of seminal, adventitious and branching roots.

**Materials and Methods**

In this study, we used the genotypes of Triticeae species listed in Table 1. A pot experiment was conducted in October 2005 in a glass house (20°C, natural day length) located at the National...
Table 1. Genotypes used in this study.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Cultivar/Accession</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Triticum aestivum</td>
<td>Norin 61</td>
<td>1</td>
</tr>
<tr>
<td>Hordeum vulgare</td>
<td>Benkeimugi</td>
<td>1</td>
</tr>
<tr>
<td>Agropyron humidum</td>
<td>Collected at Uji, Kyoto, Japan</td>
<td>2</td>
</tr>
<tr>
<td>Triticum turgidum</td>
<td>Cham 1</td>
<td>3</td>
</tr>
<tr>
<td>Triticum boeoticum</td>
<td>KU101-1</td>
<td>4</td>
</tr>
<tr>
<td>× Triticosecale</td>
<td>Presto</td>
<td>5</td>
</tr>
<tr>
<td>Secale cereale</td>
<td>4R507 (tetraploid)</td>
<td>5</td>
</tr>
<tr>
<td>Secale cereale</td>
<td>Warko (diploid)</td>
<td>5</td>
</tr>
</tbody>
</table>

Sources of seeds: (1) National Agricultural Research Center for Tohoku Region; Courtesy of (2) Dr. R. Miura, Kyoto University, Kyoto, Japan; (3) Dr. M.M. Nachit, International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria; (4) Dr. T. Kawahara, Kyoto University, Kyoto, Japan; (5) Mr. T. Yoshihira, Rakuno Gakuen University, Hokkaido, Japan.

Table 2. Soil water content and soil bulk density in each treatment.

<table>
<thead>
<tr>
<th>Soil water content (g ml⁻¹)</th>
<th>Soil bulk density (g ml⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CT 0.51 ± 0.03 (n=3)</td>
<td>0.64 ± 0.02</td>
</tr>
<tr>
<td>WT 0.75 ± 0.08</td>
<td>0.71 ± 0.04</td>
</tr>
</tbody>
</table>

1) Control.  
2) Mean ± standard error (n=3).  
3) Waterlogging.

Table 3. Effect of waterlogging on shoot DW (mg plant⁻¹).

<table>
<thead>
<tr>
<th>Genotype</th>
<th>CT (g)</th>
<th>WT (g)</th>
<th>W/C (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. humidum</td>
<td>20.2 ± 1.2</td>
<td>31.2 ± 2.8</td>
<td>1.55</td>
</tr>
<tr>
<td>× Triticosecale</td>
<td>102.2 ± 7.4</td>
<td>82.6 ± 3.6</td>
<td>0.81</td>
</tr>
<tr>
<td>T. boeoticum</td>
<td>59.4 ± 8.4</td>
<td>46.2 ± 6.7</td>
<td>0.78</td>
</tr>
<tr>
<td>T. aestivum</td>
<td>119.1 ± 1.4</td>
<td>86.5 ± 10.9</td>
<td>0.73</td>
</tr>
<tr>
<td>S. cereale (tetraploid)</td>
<td>158.0 ± 9.0</td>
<td>103.6 ± 6.4</td>
<td>0.66</td>
</tr>
<tr>
<td>T. turgidum</td>
<td>99.1 ± 5.3</td>
<td>61.0 ± 7.6</td>
<td>0.62</td>
</tr>
<tr>
<td>H. vulgare</td>
<td>106.0 ± 7.8</td>
<td>62.2 ± 11.4</td>
<td>0.59</td>
</tr>
<tr>
<td>S. cereale (diploid)</td>
<td>110.8 ± 9.4</td>
<td>32.2 ± 3.0</td>
<td>0.29</td>
</tr>
<tr>
<td>Average</td>
<td>96.8 ± 7.2</td>
<td>63.2 ± 5.0</td>
<td>0.65</td>
</tr>
</tbody>
</table>

ANOVA:  
Treatment (T) **
Genotype (G) **
T × G **

1) Control.  
2) Waterlogging.  
3) Mean ± standard error (n=4).  
4) Mean ± standard error (n=32).  
5) Significant at 1.0% level.

Genotypes in the table are listed in the order of W/C.

Agricultural Research Center for Tohoku Region (Fukushima, Japan, 37°N, 140°E). The day length in this season is suitable for wheat and barley in this region. The pots used for testing were 400-ml plastic cups (12.0 cm tall, 8.0 cm in diameter), and those for the control treatment (CT), had 10 holes (2-mm in diameter) drilled in the bottom and sides. All pots for CT were filled with volcanic ash soil (Shibanomet-suchi; GREEN TEK Co. Ltd., Tochigi, Japan) to which adequate water and chemical fertilizer N, P and K at 0.7, 3.3, 0.7 g pot⁻¹, respectively, were added. For the waterlogging treatment (WT), the same amount of fertilizer as in CT was added to volcanic ash soil. The soil was ground with adequate water, then filled into the pots with no holes to simulate potted layer of paddy soil. Seeds were germinated in a cell tray (2.5 cm tall, 1.5 cm in diameter cell⁻¹) containing humus (Serubaido-120; KUREHA Corp., Tokyo, Japan) in a glass house. The experimental design was split-plot with four replications (main-plot, treatment; sub-plot, genotype). Three seedlings at the one-leaf stage were transplanted to a pot at 1.0 cm below the soil surface. Transplanting was for using the uniform seedlings in the experiment. Length of seminal roots ranged from 2.5 to 7.0 cm in each species, and branching roots started to develop at the transplanting. Transplanting did not give any injuries to root systems. During the experiment, both CT and WT were fully irrigated every morning. Water levels of the WT pots were maintained at 1.0 cm above the soil surface from the transplanting to measurement. At 12 days after transplanting, the plant length, leaf number on the main stem, and the number of stems were measured. After washing away the soil, the number of adventitious roots, total length of adventitious roots, frequency of root branching on a seminal root, and maximum length of seminal roots were recorded. The frequency of root branching was calculated by counting the number of branching roots on the 10 cm length from the base of randomly selected seminal root for seminal root of greater than 10 cm length, and by counting all branching roots for the seminal root under 10 cm. The withered roots were not counted. Shoots and roots were sampled separately, and the dry weight (DW) were measured after oven-drying at 80°C for 48 h. The soil water content and soil bulk density of each treatment were also evaluated from other pots in which T. aestivum seedlings were grown. Statistical analyses were conducted using computer software (SPSS Ver. 13.0 J for Windows; SPSS Japan Inc., Tokyo, Japan).

Results

1. Soil conditions

Table 2 shows the soil water content and soil bulk density of each treatment. The soil water content and soil bulk density values in WT were about 1.5 times and 1.1 times, respectively, higher than those in CT.
Table 4. Effect of waterlogging on root DW (mg plant⁻¹).

<table>
<thead>
<tr>
<th>Genotype</th>
<th>CT</th>
<th>WT</th>
<th>W/C</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. humidum</td>
<td>7.1</td>
<td>6.9</td>
<td>0.97</td>
</tr>
<tr>
<td>× Triticosecale</td>
<td>27.1</td>
<td>18.2</td>
<td>0.67</td>
</tr>
<tr>
<td>T. boeticicum</td>
<td>18.7</td>
<td>8.3</td>
<td>0.44</td>
</tr>
<tr>
<td>T. aestivum</td>
<td>35.2</td>
<td>19.4</td>
<td>0.55</td>
</tr>
<tr>
<td>S. cereale (tetraploid)</td>
<td>34.3</td>
<td>16.6</td>
<td>0.48</td>
</tr>
<tr>
<td>T. turgidum</td>
<td>33.0</td>
<td>9.7</td>
<td>0.29</td>
</tr>
<tr>
<td>H. vulgare</td>
<td>25.8</td>
<td>8.2</td>
<td>0.32</td>
</tr>
<tr>
<td>S. cereale (diploid)</td>
<td>24.2</td>
<td>4.2</td>
<td>0.17</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td>25.6</td>
<td>11.4</td>
<td>0.45</td>
</tr>
</tbody>
</table>

ANOVA
- Treatment (T) ***
- Genotype (G) **
- T × G **

1) Control.
2) Waterlogging.
3) Mean ± standard error (n=4).
4) Mean ± standard error (n=32).
5) Significant at 1.0% level.

Genotypes in the table are listed in order of W/C in shoot DW.

2. Shoot growth

Significant differences in shoot DW were found between treatments and among genotypes (Table 3). When these genotypes were grown in WT, shoot DW was 0.65 times lighter than that in CT on the average. Shoot DW of the genotypes used in CT and WT were 20.2–158.0 and 31.2–103.6 mg, respectively. In both treatments, shoot DW was the lightest in A. humidum; and the heaviest in S. cereale (tetraploid). The relative shoot DW (W/C in shoot DW; proportion of shoot DW in WT to that in CT) showed significant difference among genotypes: the value of W/C in shoot DW ranged from 0.29 in S. cereale (diploid) to 1.55 in A. humidum. The W/C values in shoot DW of major cultivated species, T. aestivum and H. vulgare, were 0.73 and 0.59, respectively. Significant differences were also found between treatments and among genotypes in plant length, leaf number on the main stem and stem number (data not shown). The average W/C values of plant length, leaf number on the main stem and stem number were 0.81, 0.94 and 0.60, respectively for the eight genotypes. Treatment × genotype interactions in these traits were also significant.

3. Root traits

Root DW differed significantly between treatments and among genotypes (Table 4). Root DW in WT was 0.45 times less than that in CT. Root DW in CT and WT ranged from 7.1 mg in A. humidum to 35.2 mg in T. aestivum and from 4.2 mg in S. cereale (diploid) to 19.4 mg in T. aestivum. Root DW in WT compared to CT (W/C in root DW) significantly differed with the genotype, showing significant treatment × genotype interactions. It ranged from 0.17 in S. cereale (diploid) to 0.97 in A. humidum. The W/C values in root DW in T. aestivum and H. vulgare were 0.55 and 0.32, respectively.

Significant differences were also apparent between treatments and among genotypes in the number of adventitious roots (Table 5), the frequency of branching roots on the seminal root (Table 6), and the maximum length of seminal root (Table 7). In these genotypes, adventitious roots were 1.65 times larger in number and 1.79 times longer in WT than those in CT. However, the frequency of branching roots on the

Table 5. Effect of waterlogging on the number and length of adventitious roots.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>CT</th>
<th>WT</th>
<th>W/C</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. humidum</td>
<td>0.5</td>
<td>6.0</td>
<td>12.0</td>
</tr>
<tr>
<td>× Triticosecale</td>
<td>2.3</td>
<td>6.3</td>
<td>2.78</td>
</tr>
<tr>
<td>T. boeticicum</td>
<td>1.5</td>
<td>2.5</td>
<td>1.67</td>
</tr>
<tr>
<td>T. aestivum</td>
<td>3.3</td>
<td>5.5</td>
<td>1.69</td>
</tr>
<tr>
<td>S. cereale (tetraploid)</td>
<td>4.3</td>
<td>7.0</td>
<td>1.65</td>
</tr>
<tr>
<td>T. turgidum</td>
<td>1.5</td>
<td>2.0</td>
<td>1.33</td>
</tr>
<tr>
<td>H. vulgare</td>
<td>2.5</td>
<td>3.3</td>
<td>1.30</td>
</tr>
<tr>
<td>S. cereale (diploid)</td>
<td>5.0</td>
<td>1.5</td>
<td>0.30</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td>2.6</td>
<td>4.3</td>
<td>1.65</td>
</tr>
</tbody>
</table>

ANOVA
- Treatment (T) ***
- Genotype (G) **
- T × G **

1) Control.
2) Waterlogging.
3) Mean ± standard error (n=4).
4) Mean ± standard error (n=32).
5) Significant at 1.0% level.

Genotypes in the table are listed in order of W/C in shoot DW.
The seminal root was 0.21 times less and the maximum length of seminal root was 0.44 times less in WT than in CT. Significant treatment × genotype interactions were observed for all root traits. For example, S. cereale (diploid) had the most abundant adventitious roots in CT, but the fewest adventitious roots in WT. The value of W/C for the number of adventitious roots ranged from 0.30 in S. cereale (diploid) to 12.00 in A. humidum. The genotype rank of the total length of adventitious roots roughly reflected that of the number of adventitious roots in both treatments: the W/C ranged from 0.17 in S. cereale (diploid) to 29.83 in A. humidum. Frequency of branching roots in S. cereale (diploid) seminal root was the largest in CT, but the smallest in WT, and W/C ranged from 0.00 in S. cereale (diploid) to 0.63 in A. humidum. The maximum length of the seminal root of T. aestivum was the longest in CT, but the shortest in WT, and W/C ranged from 0.21 in T. aestivum to 0.70 in × Triticeae. The W/C in the main cultivated species, T. aestivum and H. vulgare, were 1.69 and 1.30 for the number of adventitious roots, 2.88 and 1.24 for the total length of adventitious roots, 0.43 and 0.10 for the frequency of branching roots on the seminal root and 0.21 and 0.44 for the maximum length of the seminal root.

4. Relationships between traits

The W/C in shoot DW, as an indicator of waterlogging tolerance, showed a significant correlation with W/C in root DW in these genotypes (Fig. 2). The W/C in root DW showed a significant correlation with W/C in the number and length of adventitious roots (Fig. 3), and the frequency of branching roots on the seminal root (Fig. 4). An outstanding genotype, as illustrated in Fig. 3, was A. humidum. Although data are not shown, W/C in root DW showed a significant correlation with W/C in the stem number. The W/C in the length of seminal roots showed no significant correlation with W/C in root DW.
Discussion

Waterlogging treatment (WT) used in this study had higher soil water content and soil bulk density than CT. In paddy fields, repeated puddling over the years breaks capillary pores, reduces void ratio, destroys soil aggregates, and disperses fine clay particles (Sharma and De Datta, 1986). It was considered that the WT could represent the soil structure of paddy fields where wheat and barley was susceptible to waterlogging stress.

This study showed a significant difference in W/C in shoot DW (waterlogging tolerance) among seedlings of Triticeae species. The W/C in shoot DW of A. humidum was much higher than that of other genotypes. A. humidum might be useful to increase the waterlogging tolerance of wheat and barley and to create new crops with high adaptability to waterlogging. Fatih (1983), Martin et al. (1999) and Soliman et al. (2001) reported fertile amphiploids between wheat and another species of genus Agropyron, such as A. cristatum and A. intermedium. Khan (2000) also reported the recombination of chromosomes between wheat and A. intermedium. Furthermore, chromosome addition lines of A. elongatum on the genetic background of wheat demonstrated the possibility of improving drought tolerance (Sutka et al., 1995; Farshadfar et al., 2004) and salt tolerance (Dvorak and Ross, 1986; Forster et al., 1987, 1988; Omielan et al., 1991; Mahmood and Quarrie, 1993; Suiyun et al., 2004) in wheat. Although fertile hybrids of A. humidum with wheat and barley have not been acquired, such lines might be useful in breeding programs to transfer waterlogging tolerance into wheat and barley genetic backgrounds.

Analyses of shoot growth showed that the stem number, an important component of growth, is strongly affected by waterlogging in tribe Triticeae, as reported by Taeb et al. (1993). Two genotypes that had high tolerance to waterlogging in this study, A. humidum and × Triticosecale, maintained their ability to produce tillers in waterlogged conditions. It is also said that wheat’s ‘uniculm’ genotype, which has few tillers, was sensitive to waterlogging (Yoshida et al., 2006). These results suggest that the high ability to produce tillers under waterlogged conditions might be related to waterlogging tolerance in seedlings of tribe Triticeae because more numerous stems can transport more O₂.
from shoots to roots.

The W/C in shoot DW correlated significantly with W/C in root DW. A study by Malik and co-workers (Malik et al., 2002) concluded that oxygen deficiency caused by waterlogging affects root growth and then reduces the shoot growth and yield. The results of that study suggested that the root system plays an important role in maintaining shoot growth in waterlogging conditions. Evaluation of several morphological components of roots showed that the W/C in root DW is related to development and/or survival of adventitious roots and branching roots in these genotypes. A genotype with waterlogging tolerance, *A. humidum*, showed markedly greater numbers and lengths of adventitious roots in waterlogged conditions than those in control. A significant correlation between the number of adventitious roots and waterlogging tolerance was also shown among cereal species (Yamauchi et al., 1988) and among wheat cultivars (Singh and Singh, 2003). High root porosity, attributable to the formation of aerenchyma, especially in adventitious roots, provides an internal pathway with low resistance for the movement of *O₂* between shoots and root tips of plants (Justin and Armstrong, 1987); it enables the root to penetrate into anaerobic soils. A similar mechanism has also been reported in wheat (Huang et al., 1994; Watkin et al., 1998; Malik et al., 2003), barley (Garthwaite et al., 2003), maize (Mano et al., 2006), rice (Colmer, 2003), soybean (Shimamura et al., 2003), and other wetland species (McDonald et al., 2002). Tolerance to waterlogging in *A. humidum* might be related to longitudinal movement of *O₂* within the root towards the apex because of the high porosity of adventitious roots and high productivity of tillers, although root porosity was not measured in this study.

Regarding waterlogging tolerance in other genotypes, *T. aestivum* showed a larger value for W/C in shoot DW than did *H. vulgare*. On the other hand, Yamauchi et al. (1988) reported that some genotypes in barley had higher waterlogging tolerance than wheat. These results may reflect the difference of cultivars and/or the experimental conditions. The wheat genotype used in this study, Norin 61, is evaluated to have relatively high tolerance to waterlogging (Yoshida et al., 2006). The barley genotype, Benkeimugi, has no data for waterlogging tolerance. More detailed evaluation will be needed with diverse materials within species and under diverse experimental conditions.

In conclusion, this study showed the difference in waterlogging tolerance among seedlings of tribe triticeae. Their tolerance was related to root growth under waterlogged conditions. It was considered that *A. humidum* could be a source of genetic/physiological analysis to increase the waterlogging tolerance in wheat and barley. *A. humidum* is indigenous to Japan, and is specified as an endangered species in Japan (Ministry of the Environment, 2006). The results of this study also indicate that maintenance of genetic diversity in wild species can be beneficial for analyses and genetic improvement of stress tolerance in crop cultivars.

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** In Japanese with English title.