Differences in Vegetative Growth Response to Soil Flooding between Common and Tartary Buckwheat

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Abstract: Common buckwheat (Fagopyrum esculentum Moench cv. Shinano No.1) and Tartary buckwheat (F. tataricum (L.) Gaertn. cv. Nepal) were grown in pots to examine their responses to soil flooding. Flooding treatment was carried out during the early growth stage by completely submerging the pots in a nutrient solution from 12 to 36 days after sowing. The plant growth rate, relative growth rate and mean leaf area under the flooding treatment were reduced to 72, 90 and 83% of the control, respectively, in Shinano No.1, and to 29, 71 and 45% of the control, respectively, in Nepal. The excess moisture stress had no effect on the net assimilation rate (NAR) in Shinano No.1, but lowered the NAR to 68% of that in the control in Nepal. Excess moisture stress decreased the total leaf area to 76 and 34% of the control in Shinano No.1 and Nepal, respectively. Leaf growth rate, number of leaves and leaf area per leaf, which influenced the total leaf area, were reduced by the excess soil moisture. The relative water content of leaves was unchanged in Shinano No.1, but was decreased in Nepal. Reduction in bleeding from the cut end of stem due to flooding was greater in Nepal than in Shinano No.1. Excess moisture stress reduced the K⁺ concentration of the stem and increased the Na⁺ concentration of leaves, stem and roots more strongly in Nepal than in Shinano No.1. Development of adventitious roots in the surface layer of the nutrient solution was better in Shinano No.1 than in Nepal. In conclusion, Shinano No.1 (common buckwheat) had a stronger tolerance to excess soil moisture than Nepal (Tartary buckwheat). In Shinano No. 1, leaf growth and photosynthetic rate were not markedly affected and the capacity of absorbing water and nutrients was retained by developing adventitious roots in the solution above the surface of the soil keeping proper physiological activity under excess moisture conditions.

Key words: Adventitious root, Common buckwheat, Flooding, Interspecific difference, Tartary buckwheat, Vegetative growth.

The demand for buckwheat is increasing in Japan owing to its health-promoting values such as low calorie, high rutin and mineral contents. Tartary buckwheat has a high yield stability (Adachi, 1986) and higher rutin content [1110-1950 mg 100g⁻¹ DW in seed (Kitabayashi et al., 1995b)] than common buckwheat [12.6-35.9 mg 100g⁻¹ DW in seed (Kitabayashi et al., 1995a)]. However, Tartary buckwheat is not popular in Japan because of its bitter taste. Tartary buckwheat has been used as a parent material for interspecific hybridization to improve seed productivity (Samimy, 1991). The consumption of common buckwheat continues to grow, with 133,000 tons supplied in 2002—an increase of more than three times the 40,000 tons in 1965. However, the degree of self-sufficiency for common buckwheat was only 20 percent in Japan in 2001. Interest in growing field crops has been encouraged by the decision of the Japanese government to boost self-sufficiency in field crops, which led to the conversion of paddy fields to upland crop fields. Common buckwheat is cultivated in approximately 70% of the converted paddy fields. However, most of the upland field crops are damaged by excess water, or suffer wet injury due to poor drainage. Common buckwheat is susceptible to excess water in the soil, especially at the early growth stage (Nishimaki, 1983; Takemae, 1986). A recent report indicated that the earlier the developmental stage of common buckwheat, the severer the reduction in seed yield due to flooding, which is caused by the low number of seeds resulting from a reduction in the number of flowers per branch (Sugimoto and Satou, 2000).

The average grain yield of common buckwheat in the three prefectures Kumamoto, Miyazaki and Kagoshima in 2001 was 117kg 10a⁻¹ (MAFF, 2001). This
was double the average of 65kg 10a⁻¹ for all prefectures in Japan. Common buckwheat is potentially suited for cultivation in Kyushu area, but the yield is unstable and the harvest area has been reduced due to several causes including wet injury. Increasing lodging resistance and seed setting as well as reduction in seed shattering are desirable to improve the low yield of common buckwheat (Nishimaki, 1983). Nishimaki (1983) also pointed out that cultivation techniques for reducing excess water injury and a variety with tolerance to moisture are required for the establishment of a stable high yield of common buckwheat. The mechanisms of tolerance to moisture in buckwheat need to be determined to achieve these targets.

Much research has been done on the metabolic and morphological responses of plants to flooding; energy metabolism, fermentation pathway and toxicity of end products, transportation of photosynthate, linking hormones, water and nutrient uptake, root development, aerenchyma formation, signal transduction from root to shoot, and modified gene expression (For reviews; Drew, 1983; Armstrong et al., 1994; Vartapetian and Jackson, 1997; Jackson and Ricard, 2003; Setter and Waters, 2003; Subbaiah and Sachs, 2003). Before research at the cellular level, the function of roots should be investigated since energy is required for uptake and exclude ions (Thomson et al., 1989). Maintenance of root growth is considered to be an important adaptive response to excess water in several crops (Erdmann and Wiedenroth, 1986; Daugherty and Musgrave, 1994; Huang et al., 1994b; Huang et al., 1997). Unfortunately, there is a dearth of current research information on the wet endurance of common and Tartary buckwheat during the early growth stage. Our objective was therefore to investigate the growth responses of Tartary buckwheat in comparison with those in common buckwheat under excess soil moisture based on dry matter production and root function.

**Materials and Methods**

1. **Plant materials and culture**

Common buckwheat (F. esculentum Moench cv. Shinano No.1) and Tartary buckwheat (F. tataricum (L.) Gaertn. cv. Nepal) were grown in pots as reported for other crops (Leyshon and Sheard, 1974; Trought and Drew, 1980; Daugherty and Musgrave, 1994; Huang et al., 1994a; Malik et al., 2002; Singh and Singh, 2003), because it is much easier to control water conditions compared with field experiments. Seeds of both species were sown in soil of Andosol (kurobokudo) in plastic pots (7.5 cm in inner diameter and 20 cm in height) during autumn in a greenhouse at Kyushu Tokai University, Japan. Treatment was initiated by completely submerging the pots below 3cm of the surface of half strength of a Hoagland and Arnon’s nutrient solution (KNO₃: 1057 mg l⁻¹, NH₄H₂PO₄: 115 mg l⁻¹, MgSO₄·7H₂O: 493 mg l⁻¹, Ga(NO₃)₃·4H₂O: 945 mg l⁻¹, EDTA-Fe: 22.6 mg l⁻¹, MnCl₂·4H₂O: 1.801 mg l⁻¹, H₃BO₃: 2.860 mg l⁻¹, ZnSO₄·7H₂O: 0.220 mg l⁻¹, CuSO₄·5H₂O: 0.079 mg l⁻¹ and (NH₄)₆Mo₇O₂₄·4H₂O: 0.037 mg l⁻¹) at 12 days after sowing (Fig. 1). As a control, pots were placed into small containers to prevent influx of nutrient solution and watered with the nutrient solution every three days. Moreover, 3 cm of soil layer was placed under pots to promote root growth in the control. Plants were grown for 24 days in both treatments.

2. **Growth analysis**

Leaf area and leaf number were measured one day before and 24 days after the start of treatment. Shoot and root samples were cured at 110°C for 30 minutes,
followed by drying at 65°C for 48 hours to weigh. Plant growth rate (PGR), net assimilation rate (NAR), mean leaf area (MLA) and relative growth rate (RGR) were calculated by the following equations:

\[
PGR (\text{mg day}^{-1}) = \frac{W_2 - W_1}{T_2 - T_1} \quad \text{(1)}
\]

\[
NAR (\text{g m}^{-2} \text{day}^{-1}) = PGR \times \frac{\log L_2 - \log L_1}{L_2 - L_1} \times 10^4 \quad \text{(2)}
\]

\[
MLA (\text{cm}^2) = \frac{L_2 - L_1}{\log L_2 - \log L_1} \quad \text{(3)}
\]

\[
RGR (\text{g g}^{-1} \text{day}^{-1}) = \frac{\log W_2 - \log W_1}{T_2 - T_1} \quad \text{(4)}
\]

Where \( W_1 \) and \( W_2 \) were the dry weight of whole plant at one day (\( T_1 \)) before and 24 days (\( T_2 \)) after the start of treatment, respectively; \( L_1 \) and \( L_2 \) were the total leaf area per plant one day (\( T_1 \)) before and 24 days (\( T_2 \)) after the start of treatment, respectively.

The dry weight of adventitious roots emerging from the aboveground part of the plant and those in soil were also measured. Dry weights of other roots within the pots were also measured. Leaf growth rate (\( GR_L \)), dry-matter partitioning ratio to leaf (\( DPL \)), leaf area per leaf (\( LA_L \)) and specific leaf area (\( SLA \)) were calculated by the following equations:

\[
GR_L (\text{g day}^{-1}) = \frac{WL_2 - WL_1}{T_2 - T_1} \quad \text{(5)}
\]

\[
DPL (\%) = \frac{WL_2 - WL_1}{W_2 - W_1} \times 100 \quad \text{(6)}
\]

\[
LA_L (\text{cm}^2) = \frac{L_2}{LN} \quad \text{(7)}
\]

\[
SLA (\text{cm}^2 \text{g}^{-1}) = \frac{L_2}{WL_2} \quad \text{(8)}
\]

Where \( WL_1 \) and \( WL_2 \) were the total dry weight of leaf per plant one day before (\( T_1 \)) and 24 days after (\( T_2 \)) the start of treatment, respectively. LN was the number of leaves per plant 24 days (\( T_2 \)) after the start of treatment.

3. Measurement of relative water content of leaves

The fresh weight (FW) of the third leaf was weighed immediately after being detached from the stem at midday, and put into sealed plastic bags containing a small amount of distilled water. The turgid weight (TW) was measured five hours later at 20°C. The dry weight (DW) of the leaves was measured after oven-drying as described previously and the relative water content (RWC) was calculated by the following equation:

\[
RWC (\%) = \frac{FW - DW}{TW - DW} \times 100 \quad \text{(9)}
\]

4. Measurement of bleeding sap (Root pressure)

Plant shoots were removed with a sharp razor at the height of 5cm above the surface of the nutrient solution at 24 days after the start of the treatment. A polyethylene bag containing weighed cotton was attached to the cut surface of the stem and shaded with aluminum foil and styrene foam boards. Then, after two hours, the polyethylene bags containing weighed cotton were weighed to calculate the xylem sap rate.

5. Ion (Na⁺ and K⁺) content

About 0.5g of the oven-dried leaf, stem (including petiole) and root harvested 24 days after the start of the treatment was digested with sulfuric acid and hydrogen peroxide (Mizuno and Minami, 1980) to determine the concentration of Na⁺ and K⁺ by atomic absorption spectrophotometry.

6. Statistical analysis

Growth measurements were conducted for three samples in each treatment. All measurements, except for growth measurements, were conducted in triplicate each with two samples. All the data were analyzed using
the t-test. A regression analysis was also carried out to explore the correlation of PGR with NAR and MLA.

Results and Discussion

1. Plant growth

Excess soil moisture, even for a short period, can cause considerable damage in the growth and yield of field crops (Leyshon and Sheard, 1974; Mochizuki and Matsumoto, 1991; Sugimoto and Satou, 2000; Malik et al., 2002; Lee et al., 2003). The reductions in PGR and MLA were reduced by excess soil moisture to 72 and 83% of the control for Shinano No.1 and 29 and 45% for Nepal (Table 1). The RGR of Shinano No.1 and Nepal also fell to 90 and 71% respectively. The growth reduction was thought to be caused by injury of excess soil moisture as shown in other pot experiments (Leyshon and Sheard, 1974; Trought and Drew, 1980; Daugherty and Musgrave, 1994; Huang et al., 1994a; Malik et al., 2002; Lee et al., 2003; Singh and Singh, 2003).

No effect of moisture stress was observed on the NAR in Shinano No.1, but the NAR in Nepal was reduced to 68% of the control (Table 1). It appeared that common buckwheat (Shinano No.1) had a stronger wet tolerance than Tartary buckwheat (Nepal). There were significant positive correlations between MLA and PGR (Shinano No.1; r = 0.887, Nepal; r = 0.996) and between NAR and PGR (Nepal; r = 0.932) as shown in Fig. 2. The maintenance of NAR and smaller reduction of MLA under excess moisture in Shinano No.1 may be caused by a higher PGR. In a similar study on soybean, the reduction in crop growth rate was also attributed to that in both leaf area ratio (LAR) and NAR when excess moisture stress was applied after floral differentiation (Sugimoto et al., 1988a). In our experiment, MLA was calculated instead of LAR because LAR is too abstract. Inanaga et al. (1996) already used MLA to analyze growth of individual plants for interspecific difference in drought tolerance.

2. Leaf expansion

Soil flooding reduced the leaf area to approximately 40-70% of that in the non-flooded soybean plants in pot experiments (Bacanamwo and Purcell, 1999). Leaf area was reduced by flooding to 63% of the control for tolerant genotype of wheat to 52% of the control in the sensitive genotype (Huang et al., 1994a). A similar reduction was reported by Malik et al. (2002), and was also seen in our experiment. The total leaf area was decreased to 76 and 34% of the control in Shinano No.1 and Nepal (Table 2). Leaf area per leaf (LAL) showed interspecific differences similar to that in the total leaf area. Unlike Shinano No.1, the number of leaves (LN) in Nepal was significantly reduced by excess moisture stress to 60% of the control. The specific leaf area (SLA) in both buckwheat species was increased by moisture stress but no interspecific differences were observed. Leaf growth rate (GR_L) was reduced to 65% in Shinano No.1 and to 30% in Nepal (Table 2). Dry-matter partitioning ratio to leaf (DPL) was not much influenced by excess moisture in Nepal, but was decreased significantly in Shinano No.1. These results suggest that the leaf growth rate, number of leaves per plant and leaf area per plant influenced the total leaf area and MLA under excess moisture stress. A delay and reduction of growth was observed in Nepal but only growth reduction occurred in Shinano No.1 under excess soil moisture. Mechanisms of the response to flood and injury by flood in non-submerged leaves differ fundamentally from those in roots because the tissues are not directly subjected to oxygen shortage. The relative water content (RWC) of leaf was unchanged by flooding in Shinano No.1, but was decreased significantly in Nepal (Table 2). The reduction of root growth and function in the flooded soil may lead either to an insufficient supply of water, phytohormones and nutrients to the shoots or to the abnormal supply of substances, including toxins,
Differences in Vegetative Growth Response to Soil Flooding between Common and Tartary Buckwheat originating from the roots in anaerobic soil (Drew, 1983). The physiological activity and/or amount of roots seem to affect shoot growth including leaf expansion in the two buckwheat species.

3. Bleeding rate of xylem sap

Water absorption is divided into passive and active absorption. Active water absorption is one of the indicators of the physiological activity of a root system because it requires respiratory energy (Kramer and Boyer, 1995; Yamaguchi et al., 1995; Ma et al., 2004). The amount of active water absorption can be estimated from the amount of bleeding sap from the cut end of the stem. The rate of bleeding per plant and per cross sectional area was reduced by excess moisture stress to around 42 and 40% of the control in Shinano No.1 and to 11 and 40% of the control in Nepal (Table 3). The bleeding rate per plant reflects the amount and activity of the root. The bleeding rate per root dry weight was increased 2.6 times by the stress in Shinano No.1 but decreased to 74 % of the control in Nepal. The root dry weight of Shinano No.1 fell to 19% and that of Nepal to 12% of the control (Table 3). The increase in bleeding rate per root dry weight under excess moisture stress in Shinano No.1, might be attributed to much more absorption of water by the smaller roots than in the control. This result suggests that the physiological activity of the root could be increased by the stress. Previous investigators suggested that the bleeding sap rate per leaf area was increased by excess moisture stress because new roots emerged around the soil surface in soybean (Sugimoto et al., 1988b).

4. Accumulation of K⁺ and Na⁺ in leaves, stems and roots

Selectivity of K⁺ and Na⁺ is considered to be a good indicator of root impairment since energy is required for uptake and extrusion of ions and this selectivity in wheat seedlings was particularly sensitive to O₂ deficiency (Thomson et al., 1989). Excess moisture stress decreased the K⁺ concentration of the stem in both buckwheat species (Fig.3). In both species, the K⁺ concentration of the leaves was not affected, but that of the roots was significantly increased by the stress. The Na⁺ concentrations of the leaves and stem were greatly increased under the stress in both species, but more strikingly in Nepal than in Shinano No.1. In the roots, the Na⁺ concentration increased under the stress in Nepal but not in Shinano No.1. In both plants, Na⁺ accumulation in the plant did not reach a seriously toxic level since in a previous study (Matsuura et al., 2005) only 16 and 48% reduction of growth in Tartary and common buckwheat, respectively, was observed.

| Table 2. Influence of excess soil moisture on total leaf area (L₂), leaf area per leaf (Lₐ), number of leaves (LN), specific leaf area (SLA), leaf growth rate (GRₗ), dry-matter partitioning rate to leaf (DPL), and relative water content (RWC). |
|--------------------------------------------------|
| L₂ (cm²) | Lₐ (cm²) | LN | SLA (cm².g⁻¹) | GRₗ (mg day⁻¹) | DPL (%) | RWC (%) |
|----------|----------|----|---------------|----------------|---------|---------|
| Shinano No.1 C 340 (100) | 23.2 (100) | 15 | 407 (100) | 24.5 (100) | 36 | 85 |
| T 260* (76) | 16.9**(73) | 15NS | 472*(117) | 15.9***(65) | 30* | 85** |
| Nepal C 327 (100) | 16.1 (100) | 20 | 400 (100) | 24.4 (100) | 44 | 84 |
| T 112**(34) | 9.1**(56) | 12** | 447**(112) | 7.3**(30) | 41** | 78* |
| C : Control, T : Treatment, ** and * indicate significance at p <0.01 and 0.05, and NS not significant. Figures in parentheses show percentage of treatment to control. |

| Table 3. Flow rate of bleeding sap from the cut end of stem (per plant, sectional area and root dry weight) and root dry weight of the two buckwheat species under excess soil moisture. |
|--------------------------------------------------|
| Xylem sap rate | Per plant (mg plant⁻¹ h⁻¹) | Per cross sectional area (mg cm⁻² h⁻¹) | Per root dry weight (mg g⁻¹ h⁻¹) | Root dry weight (g) |
|--------------------------------------------------|
| Shinano No.1 C 216 (100) | 3.77 (100) | 0.8 (100) | 0.257 (100) |
| T 91**(42) | 1.50**(40) | 2.0**(250) | 0.044**(19) |
| Nepal C 108 (100) | 2.47 (100) | 0.4 (100) | 0.275 (100) |
| T 10**(11) | 0.25**(40) | 0.3** (74) | 0.035**(12) |
| C : Control, T : Treatment, ** and * indicate significance at p <0.01 and 0.05, and NS not significant. Figures in parentheses show percentage of treatment to control. |
in the plants accumulating much more Na⁺. Sharma and Swarup (1988) reported that short-term flooding in the field increased the Na⁺ concentration in the shoots and roots of wheat but the concentration did not reach toxic levels. They therefore concluded that the reduced growth and yield under excess moisture conditions was not due to ion toxicity but to the reduced uptake of nutrients. In our experiment, the Na⁺ accumulation in the leaves and stem was increased, but the K⁺ accumulation in the stem was decreased by the stress in the two buckwheat species. There are some differences from other experiments (Buwalda et al., 1988; Thomson et al., 1989). Drew and Lauchli (1985) reported that the increase of Na⁺ transport to shoots was first detected when the O₂ was decreased to 15% of ambient (21%), whereas K⁺ transport was not inhibited until O₂ was decreased to less than 5% in maize. This may be one of the reasons for the effect of excess water on the Na⁺ and K⁺ accumulation in two buckwheat species. Hypoxic treatment reduced the K⁺ concentration in the shoot more than that in the roots and increased the Na⁺ concentration more greatly in the seminal roots than in the crown roots in wheat and this suggested that the seminal roots may be affected by O₂ deficiency adversely to that in the shoots and crown roots (Buwalda et al., 1988). Leakage of K⁺, free amino acids and soluble sugars from the roots of intact wheat seedlings was observed at a low O₂ concentration in nutrient solution (Greenway et al., 1992). Short-term flooding reduced the concentrations of N, P and K by 51, 60 and 58%, respectively, in the young plants and reduction of grain yield was 55% in barley (Leyshon and Sheard, 1974). The decrease of K⁺ in the stem and increase of Na⁺ in leaves, stem and roots under the stress were greater in Nepal than in Shinano No.1. The larger reduction in the growth of the two buckwheat species might not have been caused by higher accumulation of Na⁺, but by reduced uptake and/or lose of nutrients due to excess soil moisture.

5. Root growth
Flooding reduced root growth to less than 50% of the control in rape (Daugherty and Musgrave, 1994), soybean (Lee et al., 2003) and wheat (Malik et al., 2002). In our experiment, neither buckwheat species developed adventitious roots from the stem above the soil surface in the control. However, adventitious roots emerged in both cultivars under flooded conditions and Shinano No.1 had more roots than Nepal (Table 4). The dry weight of adventitious roots under excess moisture was 33 mg in Shinano No.1 and only 7 mg in Nepal (Table 4). Many new adventitious roots emerged from the stem of Shinano No.1 in the nutrient solution and some roots grew in the solution without penetrating the soil (see Fig. 1). The ratio of adventitious roots to total roots on a dry weight basis was 74% in Shinano No.1 and 25% in Nepal. The increased bleeding rate per root dry weight in Shinano No.1 may have resulted from the development of adventitious roots as reported previously (Sugimoto et al., 1988b). In wheat, the seminal root system stopped growing, when subjected to soil water logging even for a short period but the adventitious root continued growth (Malik et al., 2002). Soybean yield was increased by earthing up under excess soil moisture (Lee et al., 2003). Production of numerous adventitious roots may be a measure of strong tolerance to excess moisture in common and Tartary buckwheat. Therefore, maintenance of vegetative growth through the development of many adventitious roots would be very important for high and stable yields of field crops grown under excess soil moisture. Differences in root growth between the two buckwheat species may be caused by the difference in cell death that could be caused by acidosis rather than ATP deficiency and ethanol (Jackson and Ricard, 2003). Formation of aerenchyma in roots under soil flooding is thought to be an adaptive trait (Mustrough and Albrecht, 2003; Setter and Waters, 2003). There is a correlation between tolerance to flooding and aerenchyma formation in wheat (Huang et al., 1994a) but not in *Hordeum* (Garthwaite et al., 2003). Further
Table 4. Dry weight of adventitious roots (DWa) and ratio (% of adventitious root to total root weight (Pra) of the two buckwheat species under excess soil moisture.

| Species   | DWa (mg) | Prona (%) |
|-----------|----------|-----------|
| Shinano   | 33±3     | 74±4      |
| Nepal     | 7±1      | 25±4      |

Values indicate mean ± standard error.

1) Adventitious roots emerged from the stem, in the solution above the surface soil (see Fig. 1).

investigation will be needed on the biochemical and structural adaptation in roots to understand the flooding tolerance of common and Tartary buckwheat.

In conclusion, Shinano No.1 (common buckwheat) had a stronger tolerance to excess soil moisture than Nepal (Tartary buckwheat). In Shinano No.1, leaf growth and photosynthetic rate were not markedly affected and the capacity of absorbing water and nutrients was retained by developing adventitious roots in the solution above the surface of the soil keeping proper physiological activity under excess moisture conditions.

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References

Adachi, T. 1986. Is it possible to overcome the low yield of buckwheat by means of biotechnology? Proc.3rd Int. Symp. on Buckwheat, Pulawy, Poland. 108-116.
Armstrong, W., Brandle, R. and Jackson, M.B. 1994. Mechanisms of flood tolerance in plants. Acta Bot. Neerl.43 : 307-358.
Bacanamwo, M. and Purcell, L.C. 1999. Soybean root morphological and anatomical traits associated with acclimation to flooding. Crop Sci. 39 : 143-149.
Buwalda, F., Barrett-Lennard, E.G., Greenway, H. and Davies, B.A. 1988. Effects of growing wheat in hypoxic nutrient solutions and of subsequent transfer to aerated solutions. II. Concentrations and uptake of nutrients and sodium in shoots and roots. Aust.J. Plant Physiol. 15 : 599-612.
Cannell, R.Q., Belford, R.K., Blackwell, P.S. Govi, G. and Thomson, R.J. 1985. Effects of waterlogging on soil aeration and on root and shoot growth and yield of winter oats (Avena sativa L.). Plant Soil 85 : 361-373.
Chang, H.T. and Loomis, W.E. 1945. Effect of carbon dioxide on absorption of water and nutrients by roots. Plant Physiol. 20 : 221-232.
Daugherty, C.J. and Musgrave, M.E. 1994. Characterization of populations of rapid-cycling Brassica rapa L. selected for differential waterlogging tolerance. J. Exp. Bot. 45 : 385-392.
Drew, M.C. 1983. Plant injury and adaptation to oxygen deficiency in the root environment: A review. Plant and Soil 75 : 179-199.
Drew, M.C. and Lauchli, A. 1985. Oxygen-dependent exclusion of sodium ions from shoots by roots of Zea mays (cv Pioneer 3906) in relation to salinity damage. Plant Physiol. 79 : 171-176.
Erdmann, B. and Wiedenroth, E.M. 1986. Changes in the root system of wheat seedlings following root anaerobiosis. II. Morphology and anatomy of evolution forms. Ann.Bot. 58 : 607-616.
Everard, J.D. and Drew, M.C. 1989. Mechanisms controlling changes in water movement through the roots of Helianthus annuus L. during conditions exposure to oxygen deficiency. J.Exp.Bot. 40 : 95-104.
Garthwaite, A.J., von Bothmer, R. and Colmer, T.D. 2003. Diversity in root aeration traits associated with waterlogging tolerance in the genus Hordeum. Functional Plant Biol. 30 : 875-889.
Grable, A.R. 1966. Soil aeration and plant growth. Adv. Agron. 18 : 57-106.
Greenway, H., Waters, I. and Newsome, J. 1992. Effects of anoxia on uptake and loss of solutes in roots of wheat. Aust. J. Plant Physiol. 19 : 233-247.
Huang, B., Johnson, J.W., NeSmith, D.S. and Bridges, D.C. 1994a. Growth, physiological and anatomical responses of two wheat genotypes to waterlogging and nutrient supply. J. Exp.Bot. 45 : 193-202.
Huang, B., Johnson, J.W., NeSmith, D.S. and Bridges, D.C. 1994b. Root and shoot growth of wheat genotypes in response to hypoxia and subsequent resumption of aeration. Crop Sci. 34 : 1538-1544.
Huang, B., Johnson, J.W., Box, J.E. and NeSmith, D.S. 1997. Root characteristics and hormone activity of wheat in response to hypoxia and ethylene. Crop Sci. 37 : 812-818.
Inanaga, S., Kitamura, H., Matsuura, A., Hirasawa, T. and Sugimoto, Y. 1996. Interspecific differences of drought tolerance among soybean, peanut and common millet during vegetative growth in Tottori sand dune. Sand Dune Res. 45 : 29-35.
Jackson, M.B. and Ricard, B. 2003. Physiology, biochemistry and molecular biology of plant root systems subjected to flooding of the soil. In H. de Kroon, and E.J.W. Visser eds., Root Ecology. Springer-Verlag, Berlin, 193-213.
Kitabayashi H., Ujihara, A., Hirose, T and Minami, M. 1995a. Varietal differences and heritability for rutin content in common buckwheat, Fagopyrum esculentum Moench. Breed. Sci. 45 : 75-79.
Kitabayashi H., Ujihara, A., Hirose, T and Minami, M. 1995b. On the genotypic for rutin content in Tartary buckwheat, Fagopyrum tataricum Gaertn. Breed. Sci. 45 : 189-194.
Kramer, P.J. 1951. Causes of injury to plants resulting from flooding of the soil. Plant Physiol. 26 : 722-736.
