Growth Characteristics of Bahiagrass Roots Treated with Micronutrients, Rare Earth Elements, and Plant Hormones

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SUMMARY. Bahiagrass (Paspalum notatum) is widely used for slope protection and water and soil conservation in southern China. The plants develop an extensive root system that plays a crucial role in the protection of both soil and water. However, little is currently known about the factors that influence early root growth in bahiagrass. Here, the effects of boron (B), calcium (Ca), iron (Fe), lanthanum (La), cerium (Ce), salicylic acid (SA), and melatonin (MLT) on root growth characteristics were examined. Bahiagrass seedlings were grown in 1/25 strength modified Hoagland nutrient solution supplemented with boric acid, calcium chloride, ferric ethylenediaminetetraacetic acid (Fe-EDTA), lanthanum chloride, cerium chloride, SA, or MLT. Root lengths, root surface areas, and the number of root tips were analyzed using a root scanning system after 2, 4, and 6 days of treatment. We found significant effects on root growth after some treatments. Thus, 0.270 or 0.360 mM B for 2 days enhanced root tip number, whereas 0.15 mM Fe for 6 days increased root surface area. Although 3 or 5 mM Ca caused an increase in root tip numbers, the root length was reduced. The addition of La to the nutrient solution significantly increased root length and surface area, and addition of Ce increased root surface area and root tip numbers. Root growth characteristics were optimal after 0.3 μM La for 6 days or 1.0 μM La for 4 days. For Ce treatment, optimal root characteristics were observed at 0.5 μM Ce for 6 days. Root tip numbers increased after 0.1 or 1.0 μM MLT for 6 days, whereas SA treatment reduced the root length, surface area, and root tip numbers. Overall, the analyses indicate that treatment with B, Fe, La, Ce, and MLT benefited root growth in bahiagrass seedlings.

Bahiagrass is a grass species that was introduced into China from the United States. It is now widely used in southern China for slope protection and water and soil conservation. Bahiagrass has excellent resistance to environmental stresses such as drought, heat, and heavy metals (Cathey et al., 2013; Schuerger et al., 2003; Tischler and Burson, 1995). One of the important characteristics of bahiagrass is its development of a strong root system that enhances adaptation and tolerance to abiotic stresses. In general, deep root systems are critical for turfgrasses to maintain cellular hydration by avoiding water deficit; furthermore, cultivars that show reduced changes in root characteristics can have an advantage in conditions where salt tolerance is required (Huang, 2008; Rimi et al., 2012; Wu et al., 2013). Plant root systems can be evaluated through analysis of various characteristics such as root length, root surface area, average root diameter, root volume, and the number of root tips (Lv et al., 2013; Neumann and Matzner, 2013).

The effects of plant nutrients and hormones on the development and growth of plant root systems have been widely studied in recent years (Christin et al., 2009; Liu et al., 2013; Tanimoto, 2012). Such studies have shown that primary and lateral root development and growth depend on the availability of macro- and micro-nutrients. The elements B, Ca, and Fe are essential to plant growth and development. Boron is involved in various biochemical and physiological processes, such as cell wall and membrane synthesis and function, nucleic acid and carbohydrate metabolism, root elongation, pollen germination, and pollen tube growth (Camacho-Cristóbal et al., 2008; Goldbach et al., 1991; Goldbach and Wimmer, 2007; O’Neill et al., 2004; Tomas et al., 2009). The role of calcium ions (Ca2+) as a ubiquitous cellular messenger is well established in plant root cells (Berridge et al., 2000; Li et al., 2011; Rincon-Zachary et al., 2010). In addition, Wu and Hendershot (2010) found that root elongation was highly sensitive to root Ca2+ content. Fe is a constituent of chlorophyll and plays an important role in photosynthesis and root growth (Barton and Abadia, 2006; Christin et al., 2009; Giechl et al., 2012a).

Rare earth elements comprise a group of 17 elements with similar chemical properties (Liu et al., 2013), and range in relative atomic mass from 139 (La) to 175 (lutetium) (Zheng et al., 2000). The availability of La and Ce has been shown to influence root elongation, plant defense systems, floral initiation, reproductive growth, chlorophyll content, and photosynthetic rate (He and Loh, 2000; Hong et al., 2002; Liu et al., 2012). La promotes the stabilization of the cytoskeleton and affects lipid peroxidation and Ca2+-ATPase activities at the plasma membranes (Liu and Hasenstein, 2005; Zheng et al., 2000). However, an excess of rare earth elements can inhibit the development of strong root systems.
growth of plants (Liu et al., 2013; Ma et al., 2010).

Recently, there has been considerable interest in the behavior of plant hormones in promoting root growth in plants (Arite et al., 2012; Gonzalez-Perez et al., 2012; Wang et al., 2013). For example, SA acts as an endogenous signal and regulates oxidant levels in response to biotic stresses (Guo et al., 2007); it can also induce plant resistance to various abiotic stresses (Borsani et al., 2001; Drazic and Mihailovic, 2005; Kang et al., 2003). One of the adaptive strategies of plants to compensate for stress is altering root architecture. Song et al. (2011) reported that relative root elongation in seedlings grown in nutrient solutions supplemented with SA was greater than in seedlings without SA treatment at 24 h after treatment with aluminum (Al) stress. The hormone MLT, which was initially thought to be restricted to animals, has now been identified in plants and shown to influence root growth (Sarropoulou et al., 2012a, 2012b). MLT also enhances plant resistance to stresses, such as chilling (Szafranska et al., 2013), drought (Zhang et al., 2013), and chemicals (Arnao and Hernandez-Ruiz, 2009) through stimulating the growth of roots.

The present study was initiated to investigate the effects of micronutrients (B, Ca, and Fe), rare earth elements (La and Ce), and hormones (SA and MLT) on root growth in bahiagrass with the aim of identifying root growth promoters and their effective concentrations. To carry out this investigation, we examined and compared the morphological responses of bahiagrass roots to various treatments.

**Materials and methods**

**Plant materials and germination.** Bahiagrass seeds were obtained from Clover Group Corporation, Beijing, China. Healthy seeds were surface sterilized with 0.5% (v/v) sodium hypochlorite solution and then repeatedly washed with double-distilled water (DDW). The seeds were dried for 4 h at 40 °C and then germinated on filter paper soaked in DDW for 1 d in the dark and for 6 d with illumination at a temperature of 28 °C.

Table 1. Concentration levels of boron, calcium, iron, lanthanum, cerium, SA, and MLT. The concentration level (1–4) of each chemical was tested to determine its effect on bahiagrass root growth.

| Treatment* | Control | Level 1 | Level 2 | Level 3 | Level 4 |
|------------|---------|---------|---------|---------|---------|
| H3BO3 (mM) | 0       | 0.135   | 0.225   | 0.270   | 0.360   |
| CaCl2 (mM) | 0       | 3       | 5       | 6       | 8       |
| Fe-EDTA (mM)| 0     | 0.15    | 0.25    | 0.30    | 0.40    |
| LaCl3 (μM) | 0       | 0.1     | 0.3     | 0.5     | 1.0     |
| CeCl3 (μM) | 0       | 0.1     | 0.3     | 0.5     | 1.0     |
| SA (mM)    | 0       | 0.15    | 0.3     | 0.6     | 0.9     |
| MLT (μM)   | 0       | 0.1     | 1.0     | 10.0    | 100.0   |

*H3BO3 = boric acid; CaCl2 = calcium chloride; Fe-EDTA = ferric ethylenediaminetetraacetic acid; LaCl3 = lanthanum chloride; CeCl3 = cerium chloride; MLT = melatonin; SA = salicylic acid.

**Fig. 1.** Root lengths in bahiagrass treated with boron (B), calcium (Ca), or iron (Fe) for 2, 4, or 6 d. A shows the results of B, B shows the results of Ca, and C shows the results of Fe. Bahiagrass seedlings were 7-d old at the start of the treatment. The treatment concentrations are listed in Table 1. Control plants were grown in 1/25 Hoagland solution. The reported data are the means of 27 seedlings. Differences between treatment means were assessed using a one-way analysis of variance. Bars within the same treatment time and with the same letter are not significantly different at the \( P = 0.05 \) level; 1 cm = 0.3937 inch.

**Treatment and plant growth conditions.** Seven days after germination, seedlings with root lengths of \( 2.0 \pm 0.1 \) cm were selected, wrapped in sponge, and inserted into a foam sheet with 1-cm holes. Each foam sheet contained 10 holes: one was used for aeration and the other nine
contained a single seedling each. The foam sheet was placed in a plastic pot with a diameter of 11 cm and height of 16 cm; each pot of nine seedlings provided nine replicates for each experimental condition. The pots were filled with 1/25 strength modified Hoagland nutrient solution. This strength of solution was selected after a preliminary experiment showed best root growth among solutions of different strengths (1/5, 1/10, 1/20, and 1/40). The selected solution contained 0.2 mM calcium nitrate \([\text{Ca(NO}_3\text{)]}_2\], 0.2 mM potassium nitrate \([\text{KNO}_3\text{]}\), 0.08 mM magnesium sulfate \([\text{MgSO}_4\text{]}\), 0.04 mM monopotassium phosphate \([\text{KH}_2\text{PO}_4\text{]}\), 9 µM B, 0.06 µM copper \([\text{Cu}\text{]}\), 0.02 µM molybdenum \([\text{Mo}\text{]}\), 1.84 µM manganese \([\text{Mn}\text{]}\), 0.16 µM zinc \([\text{Zn}\text{]}\), and 10 µM Fe. The nutrient solution was aerated continuously and replaced every 2 d. The B, Ca, Fe, La, Ce, SA, and MLT treatments were produced by adding boric acid \([\text{H}_3\text{BO}_3\text{]}\), calcium chloride \([\text{CaCl}_2\text{]}\), Fe-EDTA, lanthanum chloride \([\text{LaCl}_3\text{]}\), cerium chloride \([\text{CeCl}_3\text{]}\), SA, and MLT at the required concentrations to the nutrient solution. Four concentrations of B, Ca, Fe, La, Ce, SA, and MLT were used (Table 1). Including the control, five concentrations were tested for each of the seven treatments. Thus, the complete experiment comprised a two-way factorial study of \(7 \times 5 = 35\) treatments. Seedlings were grown in a controlled-environment growth chamber with day/night temperatures of \(30 \pm 1 \degree\text{C}/25 \pm 1 \degree\text{C}\), a daylength of 16 h, light intensity of 50 klux, and relative humidity of 80% ± 5%.

**Root morphology analysis.** Seedlings were harvested and washed with distilled water after being treated for 2, 4, and 6 d; all roots were then excised. Root lengths, root surface areas, and the number of root tips of each seedling were determined using a WinRHIZO Pro image analysis system (version 2004a; Regent Instruments, Quebec City, QC, Canada). Each treatment had nine replicate plants per pot, and the experiment was run in triplicate. Therefore, there were \(9 \times 3 = 27\) seedlings in each treatment group.

![Fig. 2. Root lengths in bahiagrass treated with lanthanum (La) or cerium (Ce) for 2, 4, or 6 d. A shows the results of La and B shows the results of Ce. Bahiagrass seedlings were 7-d old at the start of the treatment. The treatment concentrations are listed in Table 1. Control plants were grown in 1/25 Hoagland solution. The reported data are the means of 27 seedlings. Differences between treatment means were assessed using a one-way analysis of variance. Bars within the same treatment time and with the same letter are not significantly different at the \(P = 0.05\) level; 1 cm = 0.3937 inch.](image)

![Fig. 3. Root lengths in bahiagrass treated with salicylic acid (SA) or melatonin (MLT) for 2, 4, or 6 d. A shows the results of SA and B shows the results of MLT. Bahiagrass seedlings were 7-d old at the start of the treatment. The treatment concentrations are listed in Table 1. Control plants were grown in 1/25 Hoagland solution. The reported data are the means of 27 seedlings. Differences between treatment means were assessed using a one-way analysis of variance. Bars within the same treatment time and with the same letter are not significantly different at the \(P = 0.05\) level; 1 cm = 0.3937 inch.](image)
**Statistical Analysis.** Variance and correlation analyses were performed using SPSS (version 13.0; IBM Corp., Armonk, NY). Differences between means of the treatments were assessed by one-way analysis of variance, with significance set as \( P < 0.05 \).

**Results**

**Root Lengths.** Seedlings grown in nutrient medium supplemented with various concentrations of B did not show any difference in root lengths compared with controls at any of the three treatment times (2, 4, and 6 d; Fig. 1A). However, the addition of Ca to the medium resulted in shorter root lengths compared with the controls at all three intervals, except the highest Ca concentration (Fig. 1B). Root lengths in seedlings grown in medium supplemented with Fe were equal to the controls at the lowest concentration but were shorter at higher concentrations (Fig. 1C).

For the two rare earth elements, addition of La significantly increased root length at 4 and 6 d, although not in a consistent, concentration related fashion (Fig. 2A). The addition of Ce had no effect on root lengths at any interval or concentration (Fig. 2B). The plant hormone SA significantly inhibited root elongation at all tested concentrations (Fig. 3A). The lower concentration of MLT had no effect on root lengths, but the two highest tested concentrations (10 and 100 \( \mu M \)) resulted in shorter root lengths compared with the control at day 4 (Fig. 3B).

**Root Surface Area.** Seedlings cultured in medium supplemented with B, Ca, or Fe showed no consistent changes in root surface area at any concentration of the supplement or at any sampling interval (Fig. 4). Supplementation with 0.25 mM Fe significantly increased root surface area at the 6-d interval; however, no other significant effect was observed in other Fe treatments (Fig. 4C). B and Ca treatments had no significant effects on the bahiagrass root surface area (Fig. 4A and B). In contrast to the effects of micronutrients, seedlings cultured in medium supplemented with 0.3 or 0.5 \( \mu M \) La showed significant increases in root surface area on day 6; a significant effect was also found for 1.0 \( \mu M \) La but only on day 4 (Fig. 5A). Seedlings treated with 0.5 or 1.0 \( \mu M \) Ce showed significant increases in root surface area at the 6-d sampling interval (Fig. 5B). SA treatment resulted in a reduced root surface area compared with controls (Fig. 6A). There were no differences in root surface areas of control and MLT-treated seedlings (Fig. 6B).

**Number of Root Tips.** Seedlings grown in B-supplemented medium had a significantly larger number of root tips at 2 d in medium supplemented with 0.27 or 0.36 mM B and at 6 d with 0.36 mM B (Fig. 7A). Ca (3 and 5 \( \mu M \)) increased root tip numbers at 2 d, but not at longer intervals (Fig. 7B). Fe treatment had no significant effect on root tip numbers at any concentration or at any sampling interval (Fig. 7C). The only significant effect of La supplementation was found with 0.5 \( \mu M \) La at the 4-d interval (Fig. 7A). Somewhat similarly, Ce treatment increased root tip numbers with 1.0 \( \mu M \) Ce at the 2-d interval and 0.5 \( \mu M \) Ce at the 6-d interval; no other treatments had a significant effect (Fig. 8B).

**Fig. 4. Root surface areas in bahiagrass treated with boron (B), calcium (Ca), or iron (Fe) for 2, 4, or 6 d. A shows the results of B, B shows the results of Ca, and C shows the results of Fe.** Bahiagrass seedlings were 7-d old at the start of the treatment. The treatment concentrations are listed in Table 1. Control plants were grown in 1/25 Hoagland solution. The reported data are the means of 27 seedlings. Differences between treatment means were assessed using a one-way analysis of variance. Bars within the same treatment time and with the same superscript letter are not significantly different at the \( P = 0.05 \) level; 1 cm\(^2\) = 0.1550 inch\(^2\).
BAHIAGRASS ROOT GROWTH AFTER SUPPLEMENTATION WITH ESSENTIAL ELEMENTS. Our examination of the effects of supplementing culture medium with B, Ca, and Fe showed that B and Fe at corresponding concentrations significantly affected root growth characteristics. El-Sharkawi et al. (1999) reported that B treatment stimulated branching in seminal roots and the development of hairs on roots of wheat (*Triticum aestivum*) through an increase in the uniform lignification of vascular tissue. Li et al. (2011) also indicated that the effects of B on plants primarily occurred in the lateral roots. The mechanism for these effects may be related to indoleacetic acid (IAA) content and to IAA oxidase enzyme (Bohnsack and Albert, 1977). Although some researchers have reported that B treatments can induce plant root elongation (Brdar-Jokanovic et al., 2010; Martin-Rejano et al., 2011), this was not the case here for bahiagrass, as we found no significant effects on root lengths or surface areas. Our results are consistent with those of Favaretto et al. (2007) on arrowleaf clover (*Trifolium vesiculosum*) and Correa et al. (2006) on rice (*Oryza sativa*).

Culture of bahiagrass seedlings in medium supplemented with a low Fe concentration (0.15 mM) slightly increased root lengths and the numbers of root tips at 6 d; however, root surface areas increased significantly. The promotion of plant root growth by Fe has been suggested as being related to auxin accumulation in the roots; (Giehl et al., 2012a, 2012b; Qi et al., 2012). However, in the present experiments, the positive effect on root lengths was blocked at higher Fe concentrations. One possible explanation is that high concentrations of Fe are toxic to bahiagrass.

We found here that supplementation with a low Ca concentration increased the number of root tips at the first sampling interval. One possible explanation for this effect is that Ca may influence cell division alignment during
mitosis at the cell initials and procambium (Pitchay, 2002). In the present study, a positive effect was only present at low Ca concentrations and higher levels had a negative effect on root tip numbers. The Ca supplementation also caused a reduced root length in treated bahiagrass seedlings compared with controls. This effect might be due to Ca toxicity. Since no Ca concentration consistently had a positive or no effect on all root growth characteristics, we conclude that supplementation with Ca is not suitable for promoting bahiagrass root growth.

**Effects of rare earth elements on bahiagrass root growth.** Growth of seedlings in medium supplemented with 0.3 μM La for 6 d or 1.0 μM La for 4 d increased root lengths and surface areas, but had no effect on the number of root tips. The study by Liu et al. (2013) is consistent with our results. They demonstrated that 0.05 mM La increased the total noble root length and root fresh weights in rice seedlings because of the increased nutritional status of the roots; however, this treatment had no effect on nodal or lateral root numbers of the seminal root. This study suggested that exogenous La affects root growth mainly through increasing root elongation. It has also been shown that La improves root growth in other species, such as Chinese silk vine [Periploca sepium (Zhang et al., 2011)], snow lotus [Saussurea involucrata (Guo et al., 2012)], and maize [Zea mays (Liu and Hasenstein, 2005)]. In contrast to the effects of La, we found that Ce did not affect bahiagrass root characteristics except for root surface area and root tip number after treatment with a high concentration (0.5 μM) for 6 d. Liu et al. (2012) reported similar results in rice, in which Ce treatment caused shorter seminal root lengths than controls but an increased lateral root number. None of the La and Ce treatments had a negative effect on bahiagrass root growth. Therefore, La and Ce could be regarded as good promoters of bahiagrass root growth.

**Effects of supplementation with plant hormones on bahiagrass root growth.** Although the effects of various plant hormone treatments on root growth have been investigated (Tanimoto, 2012; Yoshimitsu et al., 2011; Yun et al., 2009), relatively little data are available to date for MLT and SA. The present study showed that treatment with low concentrations of MLT (0.1 or 1.0 μM for 6 d) significantly increased the number of root tips in bahiagrass seedlings, although there was no effect on root lengths and surface areas. These findings were consistent with those of Park and Back (2012) in transgenic rice seedlings. Zhang et al. (2014) indicated that MLT treatment enhances lateral root formation through effects on cell wall formation, carbohydrate metabolic processes, oxidation/reduction processes, and catalytic activity. However, we found that high concentrations of MLT (10 or 100 μM) inhibited root elongation in bahiagrass. This outcome might be due to hormonal feedback regulation. In contrast, almost all SA treatments significantly reduced root length, surface area, and number of root tips in bahiagrass seedlings. Similar results were reported by Lv et al. (2013) in rice seedlings.
In summary, our analyses indicate that B, Fe, La, Ce, and MLT at particular concentrations for a given time can benefit root growth in bahiagrass seedlings.

Literature cited
Arite, T., H. Kameoka, and J. Kyozuka. 2012. Strigolactone positively controls crown root elongation in rice. J. Plant Growth Regul. 31:165–172.

Arnao, M.B. and J. Hernandez-Ruiz. 2009. Chemical stress by different agents affects the melatonin content of barley roots. J. Pineal Res. 46:295–299.

Barton, L. and J. Abadia. 2006. Iron nutrition in plants and rhizospheric microorganisms. Springer, Dordrecht, The Netherlands.

Berridge, M.J., P. Lipp, and M.D. Bootman. 2000. The versatility and universality of calcium signalling. Nat. Rev. Mol. Cell Biol. 1:11–21.

Bohnsack, C.W. and L.S. Albert. 1977. Early effects of boron deficiency on indoleacetic acid oxidase levels of squash root tips. Plant Physiol. 59:1047–1050.

Borsani, O., V. Valpuesta, and M.A. Botella. 2001. Evidence for a role of salicylic acid in the oxidative damage generated by NaCl and osmotic stress in Arabidopsis seedlings. Plant Physiol. 126:1024–1030.

Brdar-Jokanovic, M., I. Maksimovic, E. Nikolic-Doric, M. Kraljevic-Balalic, and B. Kobiljski. 2010. Selection criterion to assess wheat boron tolerance at seedling stage: Primary vs. total root length. Pak. J. Bot. 42:3939–3947.

Camacho-Cristobal, J.J., J. Rexach, and A. Gonzalez-Fontes. 2008. Boron in plants: Deficiency and toxicity. J. Integr. Plant Biol. 50:1247–1255.

Cathey, S.E., J.K. Kruse, T.R. Sinclair, and M.D. Dukes. 2013. Transpiration and visual appearance of warm season turfgrasses during soil drying. Environ. Exp. Bot. 89:36–43.

Christin, H., P. Petty, K. Ouerhani, S. Burgado, C. Lawrence, and M.A. Kassem. 2009. Influence of iron, potassium, magnesium, and nitrogen deficiencies on the growth and development of sorghum (Sorghum bicolor L.) and sunflower (Helianthus annuus L.) seedlings. J. Biotech Res. 1:64–71.

Correa, J.C., A.D.M. Costa, C.A. Costa Crucioli, and M. Mauad. 2006. Influence of boron addition on growth of roots and shoot of upland rice crops. Rev. Bras. Cienc. Solo 30:1077–1082.

Fig. 8. The number of root tips in bahiagrass treated with lanthanum (La) or cerium (Ce) for 2, 4, or 6 d. A shows the results of La and B shows the results of Ce. Bahiagrass seedlings were 7-d old at the start of the treatment. The treatment concentrations are listed in Table 1. Control plants were grown in 1/25 Hoagland solution. The reported data are the means of 27 seedlings. Differences between treatment means were assessed using a one-way analysis of variance. Bars within the same treatment time and with the same letter are not significantly different at the \( P = 0.05 \) level.

Fig. 9. The number of root tips in bahiagrass treated with salicylic acid (SA) or melatonin (MLT) for 2, 4, or 6 d. A shows the results of SA and B shows the results of MLT. Bahiagrass seedlings were 7-d old at the start of the treatment. The treatment concentrations are listed in Table 1. Control plants were grown in 1/25 Hoagland solution. The reported data are the means of 27 seedlings. Differences between treatment means were assessed using a one-way analysis of variance. Bars within the same treatment time and with the same letter are not significantly different at the \( P = 0.05 \) level.
Drazic, G. and N. Mihailovic. 2005. Modification of cadmium toxicity in soybean seedlings by salicylic acid. Plant Sci. 168:511–517.

El-Sharkawi, H.M., K.A. Farghali, and S.A. Sayed. 1999. Growth characteristics of Triticum aestivum. L. roots under different treatment combinations of boron, matric water potential and temperature. Seed Sci. Technol. 27:239–249.

Favaretto, N., A.C. Vargas Motta, C. Barcik, S.B. Campos Lustosa, and J.J. Comin. 2007. Shoot and root responses of Trifolium vesiculosum to boron fertilization in an acidic Brazilian soil. Braz. Arch. Biol. Technol. 50:597–604.

Giehl, R.F.H., J.E. Lima, and N. von Wiren. 2012a. Localized iron supply triggers lateral root elongation in Arabidopsis by altering the AUX1-mediated auxin distribution. Plant Cell 24:33–49.

Giehl, R.F.H., J.E. Lima, and N. von Wiren. 2012b. Regulatory components involved in altering lateral root development in response to localized iron: Evidence for natural genetic variation. Plant Signal. Behav. 7:711–713.

Goldbach, H.E., J. Blaser-Grill, N. Lindermann, M. Porzelt, C. Hornmann, B. Lupp, and B. Gesner. 1991. Influence of boron on net proton release and its relation to other metabolic processes, p.51–59. In: D.D. Randall, D.G. Blevins, W.H. Campbell, and J. Long (eds.). Current topics in plant biochemistry and physiology. Univ. Missouri, Columbia, MO.

Goldbach, H.E. and M.A. Wimmer. 2007. Boron in plants and animals: Is there a role beyond cell-wall structure? J. Plant Nutr. Soil Sci. 170:39–48.

Gonzalez-Perez, L., A. Vazquez-Glaria, L. Perrotta, A. Acosta, S.A. Scriven, R. Herbert, J.C. Cabrera, D. Francis, and H.J. Rogers. 2012. Oligosaccharins and Pectimorf stimulate root elongation and shorten the cell cycle in higher plants. Plant Growth Regulat. 62:211–221.

Guo, B., Y. Liang, Z. Li, and W. Guo. 2007. Role of salicylic acid in alleviating cadmium toxicity in rice roots. J. Plant Nutr. 30:427–439.

Guo, B., L. Xu, Z. Guan, and Y. Wei. 2012. Effect of lanthanum on rooting of in vitro regenerated shoots of Sauromatum involucrinia. Kar. et Kir. Biol. Trace Elem. Res. 147:334–340.

He, Y. and C. Loh. 2000. Cerium and lanthanum promote floral initiation and reproductive growth of Arabidopsis thaliana. Plant Sci. 159:117–124.

Hong, F.S., L. Wang, X.X. Meng, Z. Wei, and G.W. Zhao. 2002. The effect of cerium (III) on the chlorophyll formation in spinach. Biol. Trace Elem. Res. 89:263–276.

Huang, B. 2008. Mechanisms and strategies for improving drought resistance in turfgrass. Acta Hort. 783:221–227.

Kang, G.Z., C.H. Wang, G.C. Sun, and Z.X. Wang. 2003. Salicylic acid changes activities of H2O2-metabolizing enzymes and increases the chilling tolerance of banana seedlings. Environ. Exp. Bot. 50:9–15.

Li, M., S. Ou, S. Peng, G. Zhou, Q. Wei, and Q. Li. 2011. Growth, root morphology and boron uptake by citrus rootstock seedlings differing in boron-deficiency responses. Sci. Hortic. 129:426–432.

Liu, D., X. Wang, X. Zhang, and Z. Gao. 2013. Effects of lanthanum on growth and accumulation in roots of rice seedlings. Plant Soil Environ. 59:196–200.

Liu, D., X. Wang, Y. Lin, Z. Chen, H. Xu, and L. Wang. 2012. The effects of cerium on the growth and some antioxidant metabolisms in rice seedlings. Environ. Sci. Pollut. Res. 19:3282–3291.

Liu, M. and K.H. Hasenstein. 2005. La3+ uptake and its effect on the cytoskeleton in root protoplasts of Zea mays. L. Planta 220:658–666.

Lv, B., X. Li, H. Ma, Y. Sun, L. Wei, C. Jiang, and Z. Liang. 2013. Differences in growth and physiology of rice in response to different saline-alkaline stress factors. Agron. J. 105:1119–1128.

Ma, Y., L. Kuang, X. He, W. Bai, Y. Ding, Z. Zhang, Y. Zhao, and Z. Chai. 2010. Effects of rare earth oxide nanoparticles on root elongation of plants. Chemosphere 78:273–279.

Martin-Rejano, E.M., J.J. Camacho-Cristobal, M. Begona Herrera-Rodriguez, J. Rexach, M. Teresa Navarro-Gochicoa, and A. Gonzalez-Fontes. 2011. Auxin and ethylene are involved in the responses of root system architecture to low boron supply in Arabidopsis seedlings. Physiol. Plant. 142:170–178.

Neumann, J. and E. Matzner. 2013. Biomass of extramatrical ectomycorrhizal mycelium and fine roots in a young norway spruce stand: A study using ingrowth bags with different substrates. Plant Soil 371:435–446.

O’Neill, M.A., T. Ishii, P. Albersheim, and A.G. Darvil. 2004. Rhamnogalacturonan II: Structure and function of a borate cross-linked cell wall pectic polysaccharide. Annu. Rev. Plant Biol. 55:109–139.

Park, S. and K. Back. 2012. Melatonin promotes seminal root elongation and root growth in transgenic rice after germination. J. Pineal Res. 53:385–389.

Pitchay, D.S. 2002. Impact of 11 nutrient deficiencies on shoot and root growth, and foliar analysis standards of 13 ornamental taxa with emphasis on Ca and B control of root apical meristem development. PhD Diss., North Carolina State University, Raleigh, NC.

Qi, Y., S. Wang, C. Shen, S. Zhang, Y. Chen, Y. Xu, Y. Liu, Y. Wu, and D. Jiang. 2012. OsARF12, a transcription activator on auxin response gene, regulates root elongation and affects iron accumulation in rice (Oryza sativa). New Phytol. 193:109–120.

Rimi, F., S. Macolino, and U. Ziliotto. 2012. Rooting characteristics and turfgrass quality of three Bermuda grass cultivars and a zoysiagrass. Acta Agr. Scand. Sect. B-S P 62:24–31.

Rincon-Zachary, M., N.D. Teaster, J.A. Sparks, A.H. Valster, C.M. Motes, and E.B. Blancaflor. 2010. Fluorescence resonance energy transfer-sensitized emission of yellow cameleon 3.60 reveals root zone-specific calcium signatures in Arabidopsis in response to aluminum and other trivalent cations. Plant Physiol. 152:1442–1458.

Sarropoulou, V.N., I.N. Thrios, and K.N. Dimassi. 2012a. Melatonin promotes adventitious root regeneration in vitro shoot tip explants of the commercial sweet cherry rootstocks CAI-6P (Prunus cerasus L.), Gisela 6 (P. cerasus × P. canescens) and MxM 60 (P. avium × P. mahaleb). J. Pineal Res. 52:38–46.

Sarropoulou, V., K. Dimassi, I. Thrios, and M. Koukourikou-Petridou. 2012b. Melatonin enhances root regeneration, photosynthetic pigments, biomass, total carbohydrates and proline content in the cherry rootstock PHL-C (Prunus avium × Prunus cerasus). J. Pineal Res. 52:162–168.

Schuenger, A.C., G.A. Capelle, J.A.D. Benedetto, C. Mao, C.N. Thai, M.D. Evans, J.T. Richards, T.A. Blank, and E.C. Stryjewski. 2003. Comparison of two hyperspectral imaging and two laser-induced fluorescence instruments for the detection of zinc stress and chlorophyll concentration in bahia grass (Paspalum notatum Flugge.). Remote Sens. Environ. 84:572–588.

Song, H., X. Xu, H. Wang, and Y. Tao. 2011. Protein carbolylation in barley seedling roots caused by aluminum and proton toxicity is suppressed by salicylic acid. Russ. J. Plant Physiol. 58:653–659.

Szafranska, K., S. Gilska, and K.M. Janas. 2013. Ameliorative effect of melatonin on meristematic cells of chilled and...
re-warmed *Vigna radiata* roots. Biol. Plant. 57:91–96.

Tanimoto, E. 2012. Tall or short? Slender or thick? A plant strategy for regulating elongation growth of roots by low concentrations of gibberellin. Ann. Bot. (Lond.) 110:375–381.

Tischler, C.R. and B.L. Burson. 1995. Evaluating different bahiagrass cytotypes for heat tolerance and leaf epicuticular wax content. Euphytica 84:229–235.

Tomas, K., S. Zdenek, M. Ali, A.R. Stephen, and F. Martin. 2009. Boron-regulated hypocotyl elongation is affected in *Arabidopsis* mutants with defects in light signaling pathways. Environ. Exp. Bot. 67:101–111.

Wang, H., J. Huang, W. Liang, X. Liang, and Y. Bi. 2013. Involvement of putrescine and nitric oxide in aluminum tolerance by modulating citrate secretion from roots of red kidney bean. Plant Soil 366:479–490.

Wu, T., S. Gu, F. Yan, M. Wu, C. Wang, and M. Yu. 2013. Effect of NaCl stress on root characteristics of three clones of *Catalpa bungei* at seedling stage. J. Plant Res. Environ. 22:67–71.

Wu, Y. and W.H. Hendershot. 2010. Effect of calcium and pH on copper binding and rhizotoxicity to pea (*Pisum sativum* L.) root: Empirical relationships and modeling. Arch. Environ. Contam. Toxicol. 59:109–119.

Yoshimitsu, Y., K. Tanaka, W. Fukuda, T. Asami, S. Yoshida, K. Hayashi, Y. Kamiya, Y. Jikumaru, T. Shigeta, Y. Nakamura, T. Matsuo, and S. Okamoto. 2011. Transcription of DWARF4 plays a crucial role in auxin-regulated root elongation in addition to brassinosteroid homeostasis in *Arabidopsis thaliana*. PLoS One 6:e23851.

Yun, H.R., S. Joo, C.H. Park, S. Kim, S.C. Chang, and S.Y. Kim. 2009. Effects of brassinolide and IAA on ethylene production and elongation in maize primary roots. J. Plant Biol. 52:268–274.

Zhang, J., W. Gao, J. Wang, and P. Xiao. 2011. Affect of Ag⁺ and La⁺⁺ elicitors on growth and accumulation of adventitious roots of *Periploca sepium*. Zhongguo Zhong Yao Za Zhi 36:11–15.

Zhang, N., H. Zhang, B. Zhao, Q. Sun, Y. Cao, R. Li, X. Wu, S. Weeda, L. Li, S. Ren, R.J. Reiter, and Y. Guo. 2014. The RNA-seq approach to discriminate gene expression profiles in response to melatonin on cucumber lateral root formation. J. Pineal Res. 56:39–50.

Zhang, N., B. Zhao, H. Zhang, S. Weeda, C. Yang, Z. Yang, S. Ren, and Y. Guo. 2013. Melatonin promotes water-stress tolerance, lateral root formation, and seed germination in cucumber (*Cucumis sativus* L.). J. Pineal Res. 54:15–23.

Zheng, H., Z. Zhao, C. Zhang, J. Feng, Z. Ke, and M. Su. 2000. Changes in lipid peroxidation, the redox system and ATPase activities in plasma membranes of rice seedling roots caused by lanthanum chloride. Biometals 13:157–163.