Potassium Nutrition in *Lilium*: Critical Concentrations, Photosynthesis, Water Potential, Leaf Anatomy, and Nutrient Status

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Additional index words. cut flowers, hydroponics, plant nutrition, segmented analysis, soilless culture

Abstract. The present study was conducted to determine the critical optimum and toxic concentrations of potassium (K) using segmented analysis and its relationship with some physiological, anatomical, and nutritional responses to increasing K in hydroponically grown *Lilium* sp. L. cv. Arcachon. Plants were fertigated with nutrient solutions containing K (K<sub>ext</sub>) at 0, 2.5, 5.0, 7.5, 12.5, 17.5, 22.5, and 30 mmol·L<sup>-1</sup>. Maximum flower diameter occurred when, on a dry mass basis, shoot K (K<sub>int</sub>) ranged from 504 to 892 mmol·kg<sup>-1</sup>; however, a lower K<sub>int</sub> was required to obtain maximum biomass accumulation and shoot length (384 and 303 mmol·kg<sup>-1</sup>, respectively). Potassium increased in all plant organs as K in the nutrient solution increased. Nitrogen increased in young leaves and magnesium (Mg) decreased as K<sub>int</sub> increased. Concentrations of K<sub>ext</sub> from 5 to 17.5 mmol·L<sup>-1</sup> increased the size of chlorenchyma and occlusive cells; however, metaxylem vessels were unaffected. Net photosynthetic rate was higher in young leaves, whereas water potential increased in both young and mature leaves when K<sub>ext</sub> was greater than 22.5 mmol·L<sup>-1</sup>. Critical concentrations varied according to the growth parameter. Optimum K<sub>int</sub> ranged from 303 to 384 mmol·kg<sup>-1</sup> for vegetative parts, whereas parameters related with flower growth ranged from 427 to 504 mmol·kg<sup>-1</sup>. Concentration of 504 mmol·kg<sup>-1</sup> K<sub>int</sub> was associated with optimum growth for all the parameters assessed, whereas a K<sub>int</sub> greater than 864 mmol·kg<sup>-1</sup> was associated with a decline in growth; thus, these concentrations were considered as the critical optimum and critical toxicity levels, respectively. The optimum and toxicity critical K<sub>int</sub> were estimated when K<sub>ext</sub> in the nutrient solutions was 5.6 and 13.6 mmol·L<sup>-1</sup>, respectively.

Received for publication 26 Aug. 2013. Accepted for publication 15 Oct. 2013.

Potassium plays a key role in plant growth and physiology, specifically in the activation of enzymes, stomata regulation, plant water relations, and mobility of ions and other solutes within the plant (Mengel and Kirkby, 2001). Potassium deficiency affects primary and secondary metabolism (Armengaud et al., 2009), leading to increased susceptibility to pest and disease (Amtmann et al., 2008), leaf edge scorching, and reduced growth and marketability of a range of ornamental species (Karimi et al., 2009; Wang, 2007; Yi Lin and Ming Yeh, 2008).

Knowledge of critical nutrient demands is of major importance for the design of sustainable horticultural production systems. Nutrient requirement is defined in terms of a critical concentration derived from growth or yield response curves over a wide range of nutrient supply (Genc et al., 2002). The response curves are usually separated into four phases: 1) a deficiency phase in which plant growth increases markedly with slight incremental increases in nutrient concentration; 2) a sufficiency phase in which growth is maximized (Salifu and Timmer, 2003); 3) an adequate phase in which further growth is not achieved despite the increase in nutrient availability as a result of luxury consumption; and 4) a toxicity phase in which nutrient concentration continues to increase but plant growth declines (Isaac and Kimaro, 2011; Marschner, 1995; Salifu and Timmer, 2003). Nutrient concentration is defined as sufficient or as the critical optimum concentration (Marschner, 1995) when plants exhibit 90% to 95% of maximum growth or yield (Ulrich and Hills, 1993), whereas the concentration at which growth declines is considered as the critical toxicity level (Marschner, 1995).

*Lilium* (*Lilium* sp.) is a widely cultivated ornamental geophyte. Studies on *Lilium* nutrition have been reported (Argo and Biembaum, 1994) and tissue nutrient levels (mmol·kg<sup>-1</sup>) of high-quality lilium plants are 1700 to 2900 nitrogen (N), 32 to 226 phosphorus (P), 512 to 1279 K, 50 to 100 calcium (Ca), and 125 to 833 Mg (Dole and Wilkins, 2005). However, there is little information available on lilium cultivation for cut flower purposes in hydroponic systems. Ornamental geophytes pose a challenge for plant nutrition research because the bulb stores reserves of carbohydrates and mineral elements; thus, the response to external nutrient concentrations may not be comparable to that of non-geophytic species. The present study was conducted to determine the response of *Lilium* sp. L cv. Arcachon to varying K levels in the nutrient solution with the objective of defining the critical internal and external K concentration. Because no reports have been published, on the present research we also assessed the relationship of K nutrition with leaf water potential (ψ<sub>W</sub>), photosynthetic rate, leaf anatomy, and plant nutritional status.

Materials and Methods

Cultural conditions and plant material. The study was conducted under greenhouse conditions in northeast México (lat. 25°27’ N, long. 101°02’ W, 1610 m above sea level); average minimum/maximum temperature and relative humidity for experiment duration
were 12.4/27.2 °C and 46%/75%, respectively, and average photosynthetically active radiation (PAR) measured at solar noon was 461 μmol·m⁻²·s⁻¹.

Twelve, previously disinfect ed (benomyl; 1 g·L⁻¹), lilium (Lilium sp. cv. Arcachon) bulbs, 16 to 18 cm in circumference, were planted in 39-L rigid plastic containers with a drainage hole for retrieval of the nutrient solution. Each container was considered an experimental unit. In the container, the bulbs were uniformly distributed on a ≈7.5-cm bed of perlite and covered to a height of ≈7.5 cm above the bulb tip. Water-holding capacity of perlite was 33% (v/v), air-filled porosity space 64%, and an apparent density 0.25 g·cm⁻³.

**Potassium application.** Experimental units were fertigated with nutrient solutions prepared with distilled water to supply K at 0, 2.5, 5.0, 7.5, 12.5, 17.5, 22.5, and 30 mmol·L⁻¹. Compositions, pH, and electrical conductivity (EC) of the nutrient solutions are shown in Table 1 and were prepared with Ca(NO₃)₂·3H₂O (Fisher Scientific, Pittsburgh, PA), CaSO₄·2H₂O (Sigma, St. Louis, MO), KNO₃ (Sigma), KH₂PO₄ (Sigma), K₂SO₄ (Sigma), Mg(NO₃)₂·6 H₂O (Sigma), MgSO₄·7H₂O (Sigma), Fe-DTPA (Becker Underwood, Inc., Ames, IA), CuSO₄·5H₂O (Fisher Scientific, Fair Lawn, NJ), ZnSO₄·5H₂O (Matheson Coleman & Bell Manufacturing Chemists), MnSO₄·H₂O (Sigma), and H₂BO₃ (Spectrum Chemical Mfg. Corp., Gardena, CA).

Fertigation was applied through a drip irrigation system (six emitters per experimental unit) designed to collect the leachate for reuse. Initially, plants were irrigated for 10 min (≈3.6 L) three times a day, however, as the plants increased in size, irrigation frequency was increased to six times a day. Evapotranspired water was replenished daily to each stock tank of nutrient solution with distilled water and the nutrient solutions were replaced at weekly intervals.

**Photosynthesis and leaf water potential.** Net photosynthesis was measured (LI-6200; LI-COR, Inc., Lincoln, NE) at 1200 h on 54 d after planting on young (the third fully developed leaf from top to bottom) and mature (sampled in the lower third of plant canopy) leaves. Average PAR, CO₂ concentration, and temperature were 400 μmol·m⁻²·s⁻¹, 355 ppm, and 25.5 °C, respectively. Three measurements on each leaf from one plant per experimental unit were recorded. Water potential of two young and two mature leaves per plant were measured (Scholander Pressure Chamber; Soil Moisture Equipment Corp., Santa Barbara, CA). Relative chlorophyll content (SPAD index; Konica Minolta, Japan) was measured in three mature (lower two-thirds of plant canopy) and three young leaves (upper one-third of plant canopy) per plant.

**Assessment of plant growth and nutrient status.** Growth measurements were recorded at harvest (60 d after planting) in five randomly selected plants per experimental unit, including shoot length (substrate to the top of the inflorescence), flower diameter (measured when the first two flowers were fully expanded), and leaf area (LI-3100; LI-COR, Inc.). In addition, five plants per experimental unit were separated into roots, bulbs, stems, young and mature leaves, and flowers; washed twice with distilled water; and placed in an oven at 75 °C for 72 h (120 h for bulbs). Dry mass (DM) was recorded for each plant part and shoot DM was calculated by adding the DM of stems, leaves, and flowers. Plant tissues were ground to pass a 40-mesh sieve (A-10; Tekmar, IKA Labortecnik, Germany). Tissues were digested in a 2:1 mixture of H₂SO₄: HClO₄ and 2 mL 30% H₂O₂. The digested samples were analyzed for N with the Micro-Kjeldahl procedure (Bremner, 1996) and for K, P, Ca, and Mg with an inductively coupled plasma emission spectrometer (Model Liberty; VARIAN, Santa Clara, CA) (Soltanpour et al., 1996).

**Effect of potassium concentration on leaf anatomy.** The transversal middle portion of young leaves from plants irrigated with solutions containing 0, 5, 12.5, 17.5, and 30 mmol·L⁻¹ K were sampled at experiment termination, processed, and cut into 10-μm transversal slices with a rotary microtome (Jung Histocut, Model 820; Leica, Rankin Biomedical Co., Holly, MI). Leaf thickness, number, and diameter of metaxylem vessels and the number of spongy parenchyma cells were measured with an optic microscope (Olympus BX60; Olympus Co., Japan) and an image analyzer (Image-PRO Plus Version 7.0; Media Cybernetics, Bethesda, MD). Stomata density, length, and width of occlusive cells were measured on epidermal samples close to the central vein on the abaxial surface of the same leaves. Leaf thickness was measured at a distance of 780 μm from the center of the first vascular bundle closest to the central vein, whereas the number and diameter of metaxylem vessels were measured on the same vascular bundle. The number of spongy parenchyma cells was measured close to the leaf margin.

**Statistical design.** Four replicates of each experimental unit (container with 12 bulbs) were distributed in a complete randomized block design with eight levels of K. Significance of K in the nutrient solution (K_ext) on leaf anatomy, nutrient status, and leaf ψₛ was determined using analysis of variance and linear, quadratic, or cubic trend analysis. Remaining data were modeled with piecewise segmented analysis (NLIN procedure; SAS Version 8.0; SAS Institute, Cary, NC) to define the responses of plants to the resulting K shoot concentration (K_int). The models estimated the optimum and toxicity critical levels at which the highest and lowest K internal concentrations were associated with increasing or toxic effects on plant growth, respectively.

Results

Potassium in the shoot increased linearly when K_int increased from 0 to 12.5 mmol·L⁻¹ (Fig. 1); however, higher K_ext induced an additional increase in K_int but at a lower rate. The inflection point at which the rate of K_int concentration shifted was estimated at 12 mmol·L⁻¹ (K_kn). Maximum flower diameter was estimated by segmented analysis at 24.7 cm when K_int ranged from 504 to 892 mmol·kg⁻¹ (Fig. 2A). Shoot K less than 504 mmol·kg⁻¹ and greater than 892 mmol·kg⁻¹ were associated with decreased flower size. Maximum shoot DM was estimated at 42.9 g when K_int ranged from 384 to 864 mmol·kg⁻¹ (Fig. 2B); concentrations below and above this range were associated with decreased shoot DM accumulation.

Maximum shoot length was estimated when K_int ranged from 303 to 949 mmol·kg⁻¹ (Fig. 2C). Internal K less than 303 mmol·kg⁻¹ or greater than 949 mmol·kg⁻¹ were associated with decreased shoot length. Other growth attributes such as leaf area and flower dry mass were also affected by K_int (models not shown). Maximum flower DM, shoot length, leaf area, shoot DM, and flower diameter were observed at varying K_int concentrations (Fig. 2D).

Trend analysis suggests that N increased in roots and mature and young leaves (Table 2; Fig. 3A), but in the bulbs, there was a decreasing trend as K_ext increased in the

| K in the nutrient solution (mmol·L⁻¹) | pH | EC (dSm⁻¹) | NO₃-N | H₃PO₄ | K | Calcium | Magnesium | SO₄²⁻ | Boron | Manganese | Zinc | Copper | Iron |
|-------------------------------------|----|------------|-------|--------|---|---------|-----------|-------|-------|------------|------|--------|------|
| 0                                   | 6.2| 1.52       | 15     | 0.5    | 0.0| 9.0     | 7.0       | 1.0   | 0.5   | 0.5        | 0.05 | 0.02   | 5    |
| 2                                   | 6.2| 1.60       | 15     | 0.5    | 2.0| 9.0     | 6.0       | 1.5   | 0.5   | 0.05       | 0.05 | 0.02   | 5    |
| 2.5                                 | 6.2| 1.65       | 15     | 0.5    | 2.5| 9.0     | 6.0       | 2.0   | 0.5   | 0.05       | 0.05 | 0.02   | 5    |
| 5                                   | 6.3| 1.77       | 15     | 0.5    | 2.5| 9.0     | 6.0       | 4.5   | 0.5   | 0.05       | 0.05 | 0.02   | 5    |
| 7.5                                 | 6.4| 2.04       | 15     | 0.5    | 2.5| 9.0     | 6.0       | 4.5   | 0.5   | 0.05       | 0.05 | 0.02   | 5    |
| 17.5                                | 6.5| 2.49       | 15     | 0.5    | 17.5| 9.0    | 6.0       | 17.0  | 0.5   | 0.05       | 0.05 | 0.02   | 5    |
| 22.5                                | 6.5| 2.88       | 15     | 0.5    | 22.5| 9.0    | 6.0       | 22.0  | 0.5   | 0.05       | 0.05 | 0.02   | 5    |
| 30                                  | 6.6| 3.30       | 15     | 0.5    | 30.0| 9.0    | 6.0       | 29.5  | 0.5   | 0.05       | 0.05 | 0.02   | 5    |
nutrient solution. Highest N concentrations were observed in mature and young leaves when \( K_{\text{ext}} \) was 12.5 to 22.5 mmol·L\(^{-1} \); however, increasing \( K_{\text{ext}} \) to 30 mmol·L\(^{-1} \) decreased leaf N (Fig. 3A).

Phosphorus increased after a quadratic trend in roots, bulbs, and stems as \( K_{\text{ext}} \) concentration increased (Table 2; Fig. 3B); however, young leaves exhibited a linear decrease at high \( K_{\text{ext}} \) concentrations. Potassium increased in all plant parts (Table 2); however, the increase was marginal in bulbs and greatest in young leaves (Fig. 3C).

Calcium was higher in roots of plants irrigated with solutions containing high \( K_{\text{ext}} \); however, Ca increased at higher \( K_{\text{ext}} \) levels in mature leaves, whereas in young leaves, it increased when \( K_{\text{ext}} \) increased from 5 to 12.5 mmol·L\(^{-1} \) (Table 2; Fig. 3D). Increasing internal Ca concentration was associated with an increase in Mg (\( \text{Ca} = 33.6 + 0.85 \text{Mg}, R^2 = 0.601 \)) and N (\( \text{Ca} = 39.5 + 0.15 \text{N}, R^2 = 0.780 \)), whereas an increase in \( K_{\text{ext}} \) was associated with an increase in N (\( \text{N} = 162 + 48.7 \text{K}, R^2 = 0.840 \)) in young leaves.

In all plant parts, there was a linear or quadratic decrease in Mg as \( K_{\text{ext}} \) was increased from 0 to 7.5 mmol·L\(^{-1} \) in bulbs, stems, and roots or from 0 to 12.5 mmol·L\(^{-1} \) in mature and young leaves (Table 2; Fig. 3E). There were no further decreases at higher \( K_{\text{ext}} \) concentration.

A quadratic or cubic increase in leaf thickness and length of occlusive cells was observed when \( K_{\text{ext}} \) increased from 5 to 12.5 or 17.5 mmol·L\(^{-1} \) (Table 3); however, stomata and chlorenchyma cell count decreased when \( K_{\text{ext}} \) was increased, suggesting larger cells per unit area. At 30 mmol·L\(^{-1} \) \( K_{\text{ext}} \), the number of both cell types was similar to that of plants with 0 mmol·L\(^{-1} \) of \( K_{\text{ext}} \). The number and diameter of metaxylem vessels as well as occlusive cells width were unaffected by \( K_{\text{ext}} \) (Table 3).

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**Fig. 1.** Segmented analysis of the effect of external potassium (K) concentration on internal K in shoots of *Lilium* sp. L. cv. Arcachon. Segmented analysis showed an inflection point where K accumulation changed slopes at 12 mmol·L\(^{-1} \) of external K (\( X_0 \)). Linear models that apply when X is lower or higher than the inflection point are shown. Arrows indicate the predicted critical optimum and toxicity internal concentrations and the corresponding external K. Bars represent the SEM.

**Fig. 2.** Predicted response curves with segmented analysis of growth parameters as affected by internal potassium (K) in shoots of *Lilium* sp. L. cv. Arcachon fertigated with 0 to 30 mmol·L\(^{-1} \) K (A–C). Sufficiency zones are indicated by the plateau of the line; critical optimum (\( X_O \), left side of the plateau) and critical toxicity (\( X_1 \), right side of the plateau) concentrations are also delineated. Bars represent the SEM. Potassium sufficiency zones are predicted for all the growth parameters assessed (D).
Net photosynthetic rate was affected by K_{ext} in both young and mature leaves but no significant trend was observed in mature leaves, whereas in young leaves, photosynthetic rate increased as K_{ext} increased from 0 to 5 mmol·L^{-1} (Table 4). When averaged across K_{ext} concentration, photosynthetic rates were greater in young leaves when compared with mature leaves at K_{ext} less than 7.5, 12.5, and 30 mmol·L^{-1}. Leaf ψw increased in both young and mature leaves with K_{ext} increased after a linear or quadratic trend (Table 4). Higher chlorophyll content (SPAD index) was detected on young leaves; however, increasing K on the nutrient solution was associated with a linear decrease in young leaves, whereas it was unaffected in mature leaves (Table 4).

### Discussion

In this study, K_{int} concentration was a function of K external supply; however, when K_{ext} was greater than 12 mmol·L^{-1}, the accumulation rate of K in the shoot decreased sharply, which corresponded very closely with the K_{ext} concentration at which the toxicity critical levels was estimated.

Decreased K accumulation at high K_{int} may be the result of a decreased uptake rate, probably related with a high-affinity and low-affinity K-uptake system (Britto and Kronzucker, 2008; Rengel and Damon, 2008).

The two critical concentrations in the shoot were defined in the present study by segmented analysis using K_{crit} because plant responses better fit the models when compared with models using K_{ext} concentrations. Critical concentrations varied according to the growth parameter selected; optimum K_{int} ranged from 303 to 384 mmol·kg^{-1} for vegetative plant parts, whereas optimum flower growth (diameter and DM) ranged from 427 to 504 mmol·kg^{-1}. Thus, higher K is required for maximum flower quality.

Internal K at 504 mmol·kg^{-1} was associated with optimum growth for all the parameters assessed; however, K_{int} greater than 864 mmol·kg^{-1} was associated with a decline in all growth parameters. Thus, these may be considered as the critical optimum and toxicity concentrations, respectively. The high K_{int} concentrations were achieved with nutrient solutions with the highest K and EC; however, we suggest that the growth decline is not the result of the osmotic effects because plants irrigated with these solutions had the highest leaf ψw. In addition, when the data for plants grown with solutions containing K at 30 mmol·L^{-1} were removed from the segmented analysis to avoid the possibility of osmotic effects or excess sulfate resulting from high K_{ext} concentrations, the estimated models (not shown) were poor in detecting the critical toxic level. The models for shoot K in response to K_{crit} indicate that optimum and toxic levels of K_{crit}, 504 and 864 mmol·kg^{-1}, are achieved at 5.6 and 13.6 mmol·L^{-1} of K in the nutrient solution, respectively.

The increased K in the younger leaves may have been associated with increased ψw as a result of the effect of K on uptake, transport, and compartmentalization of water and solutes (Marschner, 1995). In turn, water accumulation may have increased turgor pressure and allowed maximum cell extension, leading to increased flower and cell size, as suggested by the lower number of chlorenchyma and occlusive cells observed per unit area. Potassium has been reported to contribute to cell enlargement and leaf expansion (Fricke et al., 1994; Fricke and Flowers, 1998; Shabala, 2003; Shabala et al., 2000). An increase in leaf size in Guazania lingulata (L.) Mez (Yi Lin and Ming Yeh, 2008), Olea europea L. (Karimi et al., 2009), and Phalaenopsis Blume (Wang, 2007) as well as a higher ψw in Hibiscus rosa-sinensis L. (Egilla et al., 2005) have been reported with supplementary K application. Young leaves exhibited increased N as K_{ext} 12.5 mmol·L^{-1} or greater. Higher N in young leaves at a K sufficient range was probably the result of the requirement of K for the translocation of NO_{3} from the root to the aboveground portions of the plant (Mengel and Kirkby, 2001).

Our results showed that N concentrations in mature and young leaves were comparable to the recommended nutrient status for..
good-quality lilium plants, as stated previously (Dole and Wilkins, 2005). However, N content reported for all other plant parts was below recommended levels. Phosphorus was within the recommended range (Dole and Wilkins, 2005) in all plant parts, except for roots, and K was within the recommended range when Kext was 7.5 mmol L−1 or higher. Calcium in the mature and young leaves was above suggested concentrations, whereas Mg was within the range in the mature and young leaves and stems at lower Kext levels.

Potassium increased in young leaves and roots when Kext was 12.5 mmol L−1 or greater. Higher K in young leaves was associated with higher chlorophyll content, as suggested by the higher SPAD index, whereas the mature leaves exhibited a decrease in Mg as K increased, probably as a result of antagonism between these nutrients (Qi and Spalding, 2004; Rus et al., 2004; Spalding et al., 1999) as observed in our study.

Photosynthetic rates were higher in young leaves when compared with mature leaves, which was probably the result of the higher chlorophyll content; however, this was not observed in plants supplemented with Kext concentrations close to the estimated optimum levels (7.5 mmol L−1). Plants with a limited supply of Kext exhibited a lower photosynthetic rate in mature leaves, which may be associated with the lower concentration of K in roots as a result of K mobilization to the younger organs when deficiency levels of Kext were imposed. Photosynthetic rate did not exhibit a clear tendency in response to Kext, probably as a result of the nutrient imbalances that resulted from either low or excessive K uptake as well as the interaction of K with the uptake of other nutrients such as Mg, P, and NO3−.

Conclusions

Under the experimental conditions in which this study was conducted, the critical optimum K concentration in the shoots of Lilium was estimated at 504 mmol·kg−1, whereas the critical toxicity level was at 864 mmol·kg−1; these internal K concentrations were estimated to occur when K in the nutrient solution was at 5.6 and 13.6 mmol·L−1, respectively. Optimum growth at the critical optimum level was associated with increased cell enlargement as a result of increased leaf ψps. Photosynthetic rates were lower in mature leaves when compared with the younger leaves, which may be the result of decreased K when plants were subjected to suboptimal K or decreased Mg.

Literature Cited

Amtmann, A., S. Troufflard, and P. Armengaud. 2008. The effect of potassium nutrition on pest and disease resistance in plants. Physiol. Plant. 133:682–691.

Argo, W.R. and J.A. Biernbaum. 1994. Irrigation requirements, root-medium pH, and nutrient concentrations of easter lilies grown in five peat-based media with and without an evaporation barrier. J. Amer. Soc. Hort. Sci. 119:1151–1156.

Armengaud, P., R. Sulpic, A.J. Miller, M. Stitt, A. Amtmann, and Y. Gibon. 2009. Multilevel analysis of primary metabolism provides new insights into the role of potassium nutrition for glycolysis and nitrogen assimilation in Arabidopsis roots. Plant Physiol. 150:772–785.

Bremner, J.M. 1996. Nitrogen-total, p. 1085–1121. In: Bigham, J.M. (ed.). Methods of soil analysis. Soil Science Society of America, Madison, WI.

Britto, D.T. and H.J. Kronzucker. 2008. Cellular mechanism of potassium transport in plants. Physiol. Plant. 133:637–650.

Dole, J.M. and H.F. Wilkins. 2005. Floriculture, principles and species. 2nd Ed. Prentice Hall, NJ.

Egilla, J.N., F.T. Davies, and T.W. Boutton. 2005. Drought stress influences leaf water content, photosynthesis, and water-use efficiency of Hibiscus rosa-sinensis at three potassium concentrations. Photosynthetica 43:135–140.

Fricke, W. and T.J. Flowers. 1998. Control of leaf cell elongation in barley. Generation rates of osmotic pressure and turgor, and growth-associated water potential gradients. Planta 206:53–65.

Fricke, W., R.A. Leigh, and A.D. Tomos. 2002. Critical deficiency concentration of zinc and its relation to growth responses. J. Plant Nutr. 25:545–560.

Isaac, M.E. and A.A. Kimaro. 2011. Diagnosis of nutrient imbalances with vector analysis in agroforestry systems. J. Environ. Qual. 40:860–866.
Karimi, E., A. Abdolzadeh, and H.R. Sadeghipour. 2009. Increasing salt tolerance in Olive, *Olea europaea* L. plants by supplemental potassium nutrition involves changes in ion accumulation and anatomical attributes. Intl. J. Plant Prod. 3:49–60.

Marschner, H. 1995. Mineral nutrition of higher plants. 2nd Ed. Academic Press, Inc., London, UK.

Mengel, K. and E.A. Kirkby. 2001. Principles of plant nutrition. 5th Ed. Kluwer Academic Publishers, The Netherlands.

Qi, Z. and E.P. Spalding. 2004. Protection of plasma membrane K⁺ transport by the salt overly sensitive1 Na⁺-H⁺ antiporter during salinity stress. Plant Physiol. 136:2548–2555.

Rengel, Z. and P.M. Damon. 2008. Crops and genotypes differ in efficiency of potassium uptake and use. Physiol. Plant. 133:624–636.

Rus, A., B. Lee, A. Muñoz-Mayor, A. Sharkhuu, K. Miura, J.K. Zhu, R.A. Bressan, and P.M. Hasegawa. 2004. AtHKT1 facilitates Na⁺ homeostasis and K⁺ nutrition in planta. Plant Physiol. 136:2500–2511.

Salifu, K.F. and V.R. Timmer. 2003. Optimizing nitrogen loading of *Picea mariana* seedlings during nursery culture. Can. J. For. Res. 33:1287–1294.

Shabala, S. 2003. Regulation of potassium transport in leaves: From molecular to tissue level. Ann. Bot. (Lond.) 92:627–634.

Shabala, S., O. Babourina, and I. Newman. 2000. Ion-specific mechanisms of osmoregulation in bean mesophyll cell. J. Expt. Bot. 51:1243–1253.

Soltanpour, P.N., G.W. Johnson, S.M. Workman, J. Benton Jones, and R.O. Miller. 1996. Inductively coupled plasma emission spectrometry and inductively coupled plasma-mass spectrometry, p. 91–139. In: Bigham, J.M. (ed.). Methods of soil analysis. Soil Science Society of America, Madison, WI.

Spalding, E., R.E. Hirsch, D.R. Lewis, Z. Qi, M.R. Sussman, and B.D. Lewis. 1999. Potassium uptake supporting plant growth in the absence of AKT1 channel activity: Inhibition by ammonium and stimulation by sodium. J. Gen. Physiol. 113:909–918.

Ulrich, A. and F.J. Hills. 1993. Principles and practices of plant analysis, p. 11–24. In: Westerman, R.L. (ed.). Soil testing and plant analysis. Part II. Soil Sci. Soc. Amer., Madison, WI.

Wang, Y.T. 2007. Potassium nutrition affects growth and flowering of *Phalaenopsis* grown in a bark mix or sphagnum moss substrate. HortScience 42:1563–1567.

Yi Lin, C. and D. Ming Yeh. 2008. Potassium nutrition affects leaf growth, anatomy, and macroelements of *Guzmania*. HortScience 43:146–148.