

Effects of Nitrogen, Phosphorus, Potassium, Calcium, or Magnesium Deficiency on Growth and Photosynthesis of *Eustoma*

Chang-Tsern Chen, Ching-Lung Lee, and Der-Ming Yeh¹

Department of Horticulture and Landscape Architecture, National Taiwan University, Taipei, Taiwan

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Abstract. Growth and photosynthetic parameters were measured in *Eustoma grandiflorum* (Raf.) Shinn. ‘Umihonoka’ grown hydroponically under nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), or magnesium (Mg) deficiency in 1/2 strength of modified Johnson’s solution. Plant height, node number, and leaf area were all reduced under N, P, K, and Ca deficiencies but not under Mg deficiency as compared with plants grown in the complete nutrient solution. Shoot and root dry weight were reduced in the N-, P-, K-, and Ca-deficient treatments, whereas root but not shoot dry weight was lowered by Mg-deficient treatment. Shoot-to-root dry weight ratio decreased under N and P deficiencies, increased under K and Mg deficiency, but was not altered under Ca deficiency. Decreased net photosynthetic rate (P_n) of N-, P-, and K-deficient leaves was all related to lower stomatal conductance (g_s), whereas N-deficient leaves also accompanied by a higher intercellular carbon dioxide concentration (C_i). The Mg-deficient treatment did not alter chlorophyll fluorescence F_v/F_m , maximal fluorescence (F_m), or minimal fluorescence (F_o). Decreased F_v/F_m of N-, P-, K-, and Ca-deficient leaves was all related to lower F_m , whereas N- and P-deficient leaves also accompanied by lower F_o . A key was developed for the identification of N, P, K, Ca, and Mg deficiency symptoms.

Eustoma grandiflorum (Raf.) Shinn. is native to the alkaline soils in Texas, Arizona, and Colorado (Croft and Nelson, 1998), and its cultivation has extended worldwide. Many growers in Taiwan and Japan reduce irrigation before harvesting the flowers to decrease g_s for a better water balance and a longer vase life. However, preharvest-deficit irrigation may limit nutrient supply or availability because *Eustoma* plants require high nutrient levels (Frett et al., 1988; Marchese et al., 2005) and continue to accumulate dry matter and minerals after flower bud visibility (de Camargo et al., 2004; Ushio and Fukuta, 2010). Small yellow specks are often seen on the lower leaves in *Eustoma* after flower bud visibility, suggesting a certain level of nutrient deficiency. Characterization of plant development and nutrient deficiency symptoms could aid in diagnosing nutrient disorders and distinguishing nutrient imbalances from other disorders caused by pathogens, chemical damage, or other stresses.

Frett et al. (1988) reported that N deficiency reduced lateral branches and chlorophyll concentration, whereas Ca deficiency reduced

shoot dry weight and caused abortion of the apical meristem and young flower buds in four *Eustoma* cultivars. *Eustoma* with 50 g·m⁻³ N had lower P_n , g_s , and transpiration rates (E), and higher C_i than those with 250 or 300 g·m⁻³ N (Marchese et al., 2005). No information is available on effects of other macronutrient deficiencies on growth and photosynthesis for *Eustoma*. In other plant species, nutrient deficiencies not only reduce the provision of photosynthates, but also alter the shoot–root partitioning of photoassimilates (Farhat et al., 2016; Hermans et al., 2006).

The objectives of this study were to measure growth and photosynthesis of *Eustoma* under N, P, K, Ca, or Mg deficiency in a nutrient solution. We also investigated nutrient deficiency on visual deficiency symptoms and shoot–root ratios, which are important aspects of *Eustoma* used as a cut flower or potted flowering plant.

Materials and Methods

Plug seedlings of *Eustoma* ‘Umihonoka’ were selected for uniformity at the three to four leaf-pair stage and rinsed several times with deionized water to remove the root medium, with the least possible injury to the roots. The plants were then placed into the various nutrient-deficient treatments in 3-L plastic containers fitted with Styrofoam lids with holes to support the plants.

Apart from the complete nutrient solution (control), nutrient-deficient treatments

comprised –N, –P, –K, –Ca, and –Mg in 1/2 strength of modified Johnson’s solution (Johnson et al., 1957). Nutrient solutions were formulated to eliminate the particular nutrients, without changing the concentration of others. This was achieved by replacing the associated missing anions or cations using an appropriate sodium or chloride compound (Table 1). To prevent salt accumulation or nutrient depletion, nutrient solutions were changed weekly. The pH and electrical conductivity (EC) of all nutrient solutions were measured using a pH and conductivity meter (IQ170; IQ Scientific Instruments, Carlsbad, CA) and adjusted to pH 6.5 ± 0.2 following the methods described by Kirkby and Mengel (1967). The EC of nutrient solutions in this study ranged from 0.99 to 1.03 dS·m⁻¹. All plants were grown in a greenhouse with an average noon photosynthetic photon flux (PPF) of 777 μmol·m⁻²·s⁻¹. The air temperature during the experimental period ranged from 18 to 23 °C, as recommended for *Eustoma* growth (Harbaugh, 1995; Harbaugh and Woltz, 1991; Islam et al., 2004).

Plant growth (height, node number, leaf area, longest root length, shoot, and root dry weights), relative chlorophyll concentration, and photosynthetic parameters were measured after treatment for 56 d. Total leaf area was determined by a leaf area meter (LI-COR 3000; LI-COR, Lincoln, NE). Relative chlorophyll concentration of the recently fully expanded leaves was gauged in situ with a chlorophyll meter (SPAD-502; Minolta Camera, Tokyo, Japan). Shoots and roots were oven-dried at 68 °C for 72 h to determine their dry weights.

The recently fully expanded leaf was used to measure the photosynthetic parameters. A portable photosynthesis system (LI-6400 XT; LI-COR) was used to measure P_n , g_s , and C_i under 1000 μmol·m⁻²·s⁻¹ PPF. Carbon dioxide concentration entering the leaf chamber and the leaf temperature were 380 μmol·mol⁻¹ and 25 ± 0.2 °C, respectively. Minimal fluorescence was determined after 30 min dark adaptation at 20 °C, whereas F_m was measured after saturation pulse with a modulated light MiniPam (Teaching-PAM chlorophyll fluorometer; Heinz Walz, Effeltrich, Germany). The fluorescence ratio F_v/F_m , with $F_v = F_m - F_o$ being the variable fluorescence, was calculated.

The nutrient treatments were arranged in a completely randomized design, with three replications per treatment and six plants per replication. Means of growth and photosynthetic parameters were separated by *t* test for comparison of means with the control.

Results and Discussion

Complete nutrient solution (control). *Eustoma* plants with the complete nutrient solution had maximum growth as measured by plant height, node number, total leaf area, SPAD-502 reading, and plant dry weights (Tables 2 and 3). Plants grew well and without any deficiency symptoms (Fig. 1),

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¹Corresponding author. E-mail: dmyeh@ntu.edu.tw.

Table 1. Nutrient formulations used to induce nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), or magnesium (Mg) deficiencies in *Eustoma* 'Umihonoka'.

Nutrient formulation	Rate (mM)	Treatment					
		Control	-N	-P	-K	-Ca	-Mg
NaNO ₃	3	—	—	+	+	+	—
KNO ₃	3	+	—	+	—	+	+
NH ₄ NO ₃	1	—	—	+	—	+	—
Ca(NO ₃) ₂	2	+	—	—	+	—	+
NH ₄ H ₂ PO ₄	1	+	—	—	+	—	—
(NH ₄) ₂ SO ₄	0.5	—	—	—	—	—	+
NaH ₂ PO ₄	1	—	+	—	—	+	+
KCl	3	—	+	—	—	—	—
MgSO ₄	0.5	+	+	+	+	+	—
CaCl ₂	2	—	+	+	—	—	—
H ₃ BO ₃	0.025	+	+	+	+	+	+
MnSO ₄	0.005	+	+	+	+	+	+
ZnSO ₄	0.002	+	+	+	+	+	+
CuSO ₄	0.0005	+	+	+	+	+	+
H ₂ MoO ₄	0.0001	+	+	+	+	+	+
FeSO ₄	0.004	+	+	+	+	+	+
Fe-EDTA	0.004	+	+	+	+	+	+

Table 2. Effects of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), or magnesium (Mg) deficiencies on plant height, node number, leaf area, SPAD-502 reading of the recently fully expanded leaves, and root length in *Eustoma* 'Umihonoka' grown hydroponically.

Treatment	Ht (cm)	Node number	Leaf area (cm ²)	SPAD-502 reading	Root length (cm)
Control	18.5	12.6	225.30	55.3	24.1
-N	2.2***	5.0***	24.00***	29.9***	42.5***
-P	5.3***	7.0***	39.60***	52.4 NS	51.6***
-K	9.5***	11.0***	137.35**	44.3**	19.6 NS
-Ca	7.3***	8.4***	57.75***	23.5***	7.0**
-Mg	17.6 NS	11.8*	272.61 NS	53.8 NS	21.3 NS

NS, *, **, ***Nonsignificant or significantly different from the control by *t* test at *P* < 0.05, 0.01, or 0.001, respectively.

Table 3. Effects of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), or magnesium (Mg) deficiencies on shoot and root dry weight, and shoot–root dry weight ratio of *Eustoma* 'Umihonoka' grown hydroponically.

Treatment	Shoot dry wt (g/plant)	Root dry wt (g/plant)	Shoot–root dry wt ratio
Control	1.78	0.50	3.61
-N	0.09***	0.17***	0.54***
-P	0.32***	0.21***	1.52***
-K	0.65***	0.13***	5.45**
-Ca	0.40***	0.14***	2.98 NS
-Mg	1.75 NS	0.34*	5.27**

NS, *, **, ***Nonsignificant or significantly different from the control by *t* test at *P* < 0.05, 0.01, or 0.001, respectively.

Table 4. Effects of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), or magnesium (Mg) deficiencies on net photosynthetic rate (*P_n*), stomatal conductance (*g_s*), and intercellular carbon dioxide concentration (*C_i*) of the recently fully expanded leaves of *Eustoma* 'Umihonoka' grown hydroponically.

Treatments	<i>P_n</i> (μmol CO ₂ /m ² /s)	<i>g_s</i> (mol·m ⁻² ·s ⁻¹)	<i>C_i</i> (μmol·mol ⁻¹)
Control	14.7	0.56	320
-N	2.2***	0.29**	352*
-P	1.4***	0.17***	325 NS
-K	7.5*	0.33*	345 NS
-Ca	7.4*	0.38 NS	335 NS
-Mg	14.7 NS	0.58 NS	318 NS

NS, *, **, ***Nonsignificant or significantly different from the control by *t* test at *P* < 0.05, 0.01, or 0.001, respectively.

indicating that the EC and pH range adopted was appropriate.

The net CO₂ assimilation rate of *Eustoma* plants with the complete nutrient solution was 14.7 μmol·m⁻²·s⁻¹ (Table 4), slightly higher than 9.6–12.2 μmol·m⁻²·s⁻¹ as reported previously (Hernández-Pérez et al., 2016; Takezaki et al., 2004). By contrast,

Marchese et al. (2005) recorded *P_n* of 4–5 μmol·m⁻²·s⁻¹ in nutrient-sufficient *Eustoma* plants, probably because of reduced carboxylation efficiency as it was associated with an increase in *C_i* (380–390 μmol·mol⁻¹ CO₂).

The average *F_v/F_m* of *Eustoma* plants with the complete nutrient solution was 0.84 (Table 5), within the range from 0.75 to 0.85

for nonstressed plants (Bolhar-Nordenkamp et al., 1989).

Nitrogen deficiency. Nitrogen deficiency resulted in stunted growth, with reduced leaf area and SPAD-502 reading, as well as slender roots (Fig. 1; Table 2). Leaf initiation appeared to have stopped. Young and recently developed leaves became uniformly chlorotic, whereas the lower leaves were yellowish. The N deficiency symptoms are similar to those described for *Spathiphyllum* (Yeh et al., 2000). Shoot and root dry weight, and shoot–root ratio were all significantly reduced by the -N treatment (Table 3). Similar examples for preferential partitioning of photosynthetic carbon to the roots and decrease in shoot–root ratio are well documented for other species under N deficiency (Hermans et al., 2006).

Nitrogen-deficient *Eustoma* plants had lower *P_n* and *g_s* but higher *C_i* than that of the control (Table 4), similar to previous reports (Cechin and Fumis, 2004; Mak and Yeh, 2000; Marchese et al., 2005). Nitrogen-deficient plants had lower *F_v/F_m* and *F_m*, but higher *F_o* than the control plants (Table 5), indicating that N deficiency causes damage to photosystem II functioning in *Eustoma*. Similar results have been reported for rice (*Oryza sativa* L.) (Huang et al., 2004).

Phosphorus deficiency. The P-deficient *Eustoma* plants were shorter and produced fewer nodes, smaller leaf area, but longer roots than those with the complete nutrient solution (Fig. 1; Table 2). The -P treatment reduced 80% shoot dry weight and 58% root dry weight and resulted in a decreased shoot–root ratio as compared with the control (Table 3). These results are consistent with Mollier and Pellerin (1999) showing that P deficiency quickly and severely reduces leaf growth. Leaf demand for assimilates by leaves is decreased and, thus, more assimilates become available for root growth in a short time. Hermans et al. (2006) showed that the P-deficient plants improve their ability to acquire P by altering their carbon partitioning to favor root growth, which serves to decrease shoot–root ratio.

Phosphorus-deficient plants had lower *P_n* and *g_s* than those with complete nutrient solution (Table 4). However, the SPAD-502 reading and *C_i* was comparable with that of the control plants (Tables 2 and 4). These results suggest that decreased *P_n* of P-deficient leaves in *Eustoma* was mainly through stomatal limitation and not caused by reduced chlorophyll concentration. Similar results were reported for sugar beet (*Beta vulgaris* L.) (Terry and Ulrich, 1973).

Phosphorus-deficient *Eustoma* plants had lower *F_v/F_m* and *F_m* but higher *F_o* than the control plants (Table 5). Similar P deficiency effects on chlorophyll fluorescence parameters were reported for rice (Xu et al., 2007).

Potassium deficiency. Potassium-deficient resulted in reduced plant height, node number, leaf area, and SPAD-502 reading (Fig. 1; Table 2). Small chlorotic specks and marginal necrosis were expressed on the lower



Fig. 1. Growth of *Eustoma* 'Umihonoka' under 1/2 strength of complete Johnson's solution (control), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), or magnesium (Mg) deficiencies. Bar = 10 cm.

Table 5. Effects of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), or magnesium (Mg) deficiencies on F_v/F_m , F_o , and F_m values of the recently fully expanded leaves of *Eustoma* 'Umihonoka' grown hydroponically.

Treatments	F_v/F_m	F_o	F_m
Control	0.844	254.2	1,632.4
-N	0.729***	328.3***	1,215.8***
-P	0.622***	431.5***	1,218.1***
-K	0.607**	286.8 NS	1,004.9***
-Ca	0.002***	256.2 NS	256.4***
-Mg	0.841 NS	261.6 NS	1,648.7 NS

NS, **, ***Nonsignificant or significantly different from the control by t test at $P < 0.01$ or 0.001 , respectively.

leaves, similar to K deficiency symptoms described for *Phalaenopsis* (Wang, 2007) and *Spathiphyllum* (Yeh et al., 2000). Such symptoms are often seen in Taiwan and Japan when harvesting *Eustoma* cut flowers, proba-

bly because growers adapt preharvest-deficit irrigation, which may limit K supply or availability, whereas *Eustoma* plants require high K, particularly during and after visible bud stage (de Camargo et al., 2004; Ushio and Fukuta, 2010). Reproductive growth of *Phalaenopsis* takes on priority for K that is already in other parts of a plant, resulting in necrosis and even death of the lower leaves and roots (Wang, 2007).

Shoot and root dry weight were significantly reduced, but shoot-root ratio was significantly increased by the -K treatment (Table 3). Hermans et al. (2006) proposed that in contrast to N and P deficiencies, the -K plants are less able to translocate sucrose to the root via the phloem and, thus, exhibit increased shoot-root ratio. Examples of increased shoot-root ratio under K deficiency are well documented for other species (Hafsi et al., 2014).

Potassium-deficient plants had lower P_n and g_s , but C_i did not differ significantly, as compared with plants with complete nutrient solution (Table 4). Decreased P_n of K-deficient leaves in *Eustoma* was not only related to lower chlorophyll concentration and marginal necrosis but also to lower g_s (Tables 2 and 4), similar to reports for K-deficient *Brassica napus* L. (Lu et al., 2016). Potassium-deficient plants had lower F_v/F_m and F_m than the control plants (Table 5). Decreased F_v/F_m and F_m of K-deficient leaves were reported for sweetpotato [*Ipomoea batatas* (L.) Lam.] (Liu et al., 2017).

Calcium deficiency. Plant growth was strongly suppressed by the Ca-deficient treatment. Root growth was poor and roots were short, thickened, and brittle (Fig. 1; Table 2). Calcium deficiency induced shoot tip injury and loss of apical dominance. Tip injury was followed by the development of axillary shoots, with necrotic young leaves. The expressed Ca deficiency symptoms are similar to those described for other species (Hao and Papadopoulos, 2003; Yeh et al., 2000).

High relative humidity (RH) inhibits the translocation of Ca to the tip of the young developing leaves, resulting in tipburn of *Eustoma* in the greenhouse. Increased Ca in the nutrient solution increased leaf Ca concentration but had little or no effect on the incidence of tipburn (Islam et al., 2004). Severe tipburn symptoms of *Eustoma* are seen primarily in 1–2 weeks before flower buds become visible under 90% RH (Islam et al., 2004), suggesting that the developing flower buds might compete with the young leaves for Ca, as reported for Chinese cabbage [*Brassica rapa* L. subsp. *pekinensis* (Lour.) Hanelt] (Pressman et al., 1993). Thus, the cause and/or severity of Ca deficiency might differ between the young vegetative *Eustoma* as shown in this study and the reproductive plants as reported by Islam et al. (2004).

Calcium deficiency reduced shoot and root dry weight by 78% and 72%, respectively, as compared with plants with complete nutrient solution (Table 3). Increased Ca in the nutrient solution (Frett et al., 1988) or medium (Harbaugh and Woltz, 1991) resulted in increased *Eustoma* dry weight. The Ca-deficient *Eustoma* had lower P_n , F_v/F_m , and F_m than the control plants (Tables 4 and 5). Our results indicate that Ca plays a vital role for the growth, especially for *Eustoma* plants native to the alkaline soils. Gómez-Pérez et al. (2014) also reported that supplementary Ca can ameliorate *Eustoma* tolerance to alkalinity in irrigation water.

Magnesium deficiency. The Mg-deficient treatment resulted in plants with fewer nodes and did not alter plant height, leaf area, SPAD-502 reading, and root length (Fig. 1; Table 2). Symptoms of slight interveinal chlorosis were observed only on lower leaves, similar to reports for other species (Farhat et al., 2016; Yeh et al., 2000).

Magnesium deficiency did not affect shoot dry weight and photosynthetic parameters measured in this study, but decreased

Table 6. A diagnostic key to nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), or magnesium (Mg) deficiencies in *Eustoma* 'Umihonoka'.

a. The symptoms are expressed on the whole plant and mainly on the lower leaves.	
b. The symptoms are developed on the whole plant.	
c. Plant growth is strongly affected. Uniformly chlorotic young leaves, whereas the lower leaves were yellow.	N
cc. Plants grow slowly. No visual deficiency symptoms.	P
bb. The symptoms are expressed on the lower leaves.	
c. Yellow specks developed on lower leaves and/or marginal necrosis.	K
cc. Slightly interveinal chlorosis on lower leaves.	Mg
aa. The symptoms are expressed on the upper leaves.	
b. Shoot tip injury. Development of axillary shoots with necrotic young leaves.	Ca

root dry weight and thereby increased shoot-root ratio as compared with the control (Tables 2–5). Cakmak and Kirkby (2008) reported that, at early stage of Mg deficiency, phloem export of sucrose was severely impaired, an effect that occurred before any noticeable changes in shoot growth, chlorophyll concentration, or photosynthetic activity. As Mg is a highly mobile nutrient in plants, it is preferentially transported to source leaves to prevent severe decreases in photosynthesis. Plants lacking Mg are less able to translocate sucrose to the root via the phloem (Farhat et al., 2016; Hermans et al., 2006). de Camargo et al. (2004) showed that a small amount of Mg accumulated in young *Eustoma* plant, however, a relatively high Mg accumulation, only next to N and K, for plants at 120 d after transplanting. We suggest that results in this study (Tables 2–5) were early effects of Mg deficiency and the prolonged Mg-deficient effects require further research.

Nutrition deficiencies of *Eustoma* may result from improper fertilizer application and preharvest-deficit irrigation. Visual differences in response to N, P, K, Ca, and Mg deficiencies were used to create a key (Table 6), which should be a valuable diagnostic tool to identify the nutritional deficiencies of *Eustoma*. Growers may adopt the complete hydroponic nutrient solution for an alternative production for *Eustoma* to avoid soil sickness, resulting from successive cropping in greenhouses all year round. It should be recognized that under field conditions, it is rare that one element would be completely deficient as in controlled studies. Therefore, the diagnosis of the cause of an injury symptom may be more complicated than looking at the deficiency symptoms of a single element. Nevertheless, the results in this study provide a good reference for correcting the nutrition of the *Eustoma* being produced.

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