ISSN 0367-6315 (Print) / ISSN 2288-2162 (Online)
Korean J. Soil Sci. Fert. 46(5), 351-358 (2013)
http://dx.doi.org/10.7745/KJSSF.2013.46.5.351

Article

Effect of Suboptimal Nutritional Status on Mineral Uptake and Carbohydrate Metabolism in Tomato Plants

Jwakyung Sung[1], Sangmin Lee[2†], Suyeon Lee[1], Rogyoung Kim[3], Yejin Lee[1], Hongbae Yun[1], Sangkeun Ha[1], and Beomheon Song[4]*

[1]Division of Soil and Fertilizer, NAAS, RDA, Suwon, 441-707, Korea
[2]Division of Planning and Coordination, NAAS, RDA, Suwon, 441-707, Korea
[3]Department of Biological Environment, Kangwon National University, Chuncheon, 200-710, Korea
[4]Department of Crop Science, Chungbuk National University, Cheongju, 361-763, Korea

(Received: August 30 2013, Accepted: September 27 2013)

A suitable supply of mineral elements into shoot via a root system from growth media makes plants favorable growth and yield. The shortage or surplus of minerals directly affects overall physiological reactions to plants and, especially, strongly influences carbohydrate metabolism as a primary response. We have studied mineral uptake and synthesis and translocation of soluble carbohydrates in N, P or K-deficient tomato plants, and examined the interaction between soluble carbohydrates and mineral elements. Four-weeks-old tomato plants were grown in a hydroponic growth container adjusted with suboptimal N (0.5 mmol L^{-1} $Ca(NO_3)_2 \cdot 4H_2O$ and 0.5 mmol L^{-1} KNO_3), P (0.05 mmol L^{-1} KH_2PO_4), and K (0.5 mmol L^{-1} KNO_3) for 30 days. The deficiency of specific mineral element led to a significant decrease in its concentration and affected the concentration of other elements with increasing treatment period. The appearance of the reduction, however, differed slightly between elements. The ratios of N uptake of each treatment to that in NPK sufficient tomato shoots were 4 (N deficient), 50 (P deficient), and 50% (K deficient). The P uptake ratios were 21 (N deficient), 19 (P deficient), and 28% (K deficient) and K uptake ratios were 11 (N deficient), 46 (P deficient), and 7% (K deficient). The deficiency of mineral elements also influenced on carbohydrate metabolism; soluble sugar and starch was substantially enhanced, especially in N or K deficiency. In conclusion, mineral deficiency leads to an adverse carbohydrate metabolism such as immoderate accumulation and restricted translocation as well as reduced mineral uptake and thus results in the reduced plant growth.

Key words: Mineral, Carbohydrate, mineral deficiency, Tomato

Correlation analysis between soluble carbohydrates and macro elements

	Sugar	Starch	N	P	K	Ca	Mg
Sugar	-	0.29*	-0.39***	-0.15	-0.64***	0.25*	0.16
Starch		-	-0.56***	-0.18	-0.25*	0.28*	-0.27*
N			-	-0.19	0.05	0.01	0.40***
P				-	0.23*	-0.35**	-0.26*
K					-	-0.20	0.01
Ca						-	0.26*
Mg							-

Our data report that the suboptimal status of minerals greatly affects the synthesis, translocation and accumulation of soluble carbohydrates, and, finally, influences adversely photosynthesis, mineral uptake and plant growth.

*Corresponding author : Phone: +82-43-261-2511, Fax: 82-43-273-2242, E-mail: bhsong@chungbuk.ac.kr
†An author contributed equally to this work and is considered as a co-first author.
§Acknowledgement: This study was supported financially by a grant from the research project (No. PJ008596) of National Academy of Agricultural Science, Rural Development Administration, Republic of Korea

Introduction

Physiological and biochemical approaches have been used to determine the specific roles of nitrogen (N), phosphorus (P) and potassium (K) in responses to plant growth and crop yields. Plant responses to nitrogen, phosphorus and potassium limitations differ (de Groot et al., 2003a; de Groot et al., 2003b; Epstein and Bloom, 2005) and this may be due to the different roles of these nutrients in plants. The N limitation is associated with decreased enzyme activities that are required for energy metabolism such as photosynthesis and respiration (Marschner, 1995; de Groot et al., 2003b). The decrease in CO_2 fixation is due to direct effects on N-rich photosynthetic structures such as chlorophyll, light-harvesting complex and Rubisco (Evans and Poorter, 2001). Phosphorus has direct impacts on plant functions and productivity (Hell and Hillebrand 2001, Epstein and Bloom, 2005). The K starvation leads to retarded growth through the lack of osmoticum (Epstein and Bloom, 2005) and to impaired sugar and N balance through inhibition of protein synthesis and long-distance transport (Marschner, 1995; Epstein and Bloom, 2005). In the case of N starvation, two distinct changes in carbon utilization are commonly observed: (a) the starch accumulation and (b) the translocation of available carbohydrates from leaves into roots, resulting in a general decline in the shoot to root weight ratio (Ariovich and Cresswell, 1983; Huber and Akazawa, 1986, Thomas et al., 1988). The accumulation of shoot-derived carbohydrates is an early response to phosphorus starvation and has been observed in many plant species (Cakmak et al., 1994; Ciereszko et al., 1996; Ciereszko and Barbachowska, 2000; Ciereszko et al., 2005). The P starvation also impacts on the export of triose-Pi from the chloroplast, subsequently converted to starch. Low K can result in an adverse effect on leaf photosynthesis and thus destabilize the source-sink relationship (Zhao et al., 2001) but the effect was not due to impairment of tugor-induced regulation of stomatal conductance (Behboudian and Anderson, 1990). The mild K deficiency suppresses the translocation of assimilates with affecting photo synthesis at the source and metabolism at the sink (Mengel and Viro, 1974; Mengel, 1980; Beringer and Haeder, 1981). The effects of nutrient deficiency have been widely implemented with tomato plants while a number of contradictions are still in argument regarding mineral distribution, carbohydrate translocation, and the interaction between both factors. Tomato (*Lycopersicon esculentum*) is one of the most popular vegetable crops cultivated commercially around the world and film houses-based cultivation area (the 5th in vegetable crops) throughout South Korea has been expanded year by year. The objective of this study was to examine the effects of N, P or K deficiency on the daily changes in uptake and accumulation of mineral elements, production and translocation of soluble carbohydrates, and the interaction between each mineral element and soluble carbohydrate in soilless grown tomato plants.

Materials and Methods

Plant materials and growth conditions The present study was performed at a green house in National Academy of Agricultural Science in Suwon, South Korea in 2012 for tomato (*Lycopersicon esculentum* cv. Seonmyoung). Seeds were germinated in a tray filled with pearlite supplied with distilled-deionized water. Seedlings were transplanted into aerated containers with 1/3 strength of Hoagland nutrient solution. Four-week-old tomato plants were subjected to 12 holes-aerated 20 L capacity containers with Hoagland nutrient media [5 mmol L^{-1} $Ca(NO_3)_2 \cdot 4H_2O$, 5 mol L^{-1} KNO_3, 2 mmol L^{-1} Mg $SO_4 \cdot 7H_2O$, 0.5 mmol L^{-1} KH_2PO_4, 1.5 mmol L^{-1} Fe-EDTA, 1 mmol L^{-1} NH_4NO_3, and 1 mL of micro-elements mixture (H_3BO_3, 2.86 g L^{-1}; $MnCl_2 \cdot 4H_2O$, 1.81 g L^{-1}; $ZnSO_4 \cdot 7H_2O$, 0.22g L^{-1}; $CuSO_4 \cdot 5H_2O$, 0.051 g L^{-1}; $H_2MoO \cdot 4H_2O$, 0.09 g L^{-1})]. For N, P or K deficiency, nutrient solution was adjusted as followed; N (0.5 mmol L^{-1} $Ca(NO_3)_2 \cdot 4H_2O$ and 0.5 mmol L^{-1} KNO_3), P (0.05 mmol L^{-1} KH_2PO_4), and K (0.5 mmol L^{-1} KNO_3). The equivalents of calcium chloride and potassium chloride were added to fill in the lack of nitrate of N and K deficient conditions. Tomato plants were constantly exposed for 30 days at average day temperature of 28 ± 3℃ and night temperature of 18 ± 3℃. Mid-day photosynthetic photon flux density was 800-1,200 μmol m^{-2} s^{-1}. The nutrient solution was replaced every 3 days in order to ensure a consistent nutrient supply. Plants were harvested between 10:00 and 14:00 at 1, 5, 15 and 30 days after treatment (DAT) and immediately separated into leaves, stem and roots for further analysis.

Measurement of nutrient elements Fresh plants were

separated into shoot and root tissues and then washed with tap water followed by distilled water. Seedlings were oven-dried at 80℃ for 48 h and weighed. The dry samples (0.3 g) of shoots or roots were soaked in 5 mL of 368 mM salicylic acid in 84.7 % sulfuric acid (H_2SO_4) for 24 h then digested in a digestion system, heated to 300℃ for 3 h, followed by several drops of hydrogen peroxide (H_2O_2). The extracted solution was transferred to 100 mL volumetric flasks and then diluted to 100 mL with deionized water for mineral assays. The N concentration was colorimetrically determined using the automatic flow injection analyzer (BRAN LUBBE, Germany). The P concentration was measured using the molybdate-blue colorimetry method (UV-2450, Shimadzu, Japan) and cation concentrations were determined with ICP-OES (INTEGRA XMP, GBC, Australia). The uptake ratio of each N, P, and K of each treatment was calculated as a ratio of each nutrient concentration in each treatment to that in NPK sufficient condition.

Measurement of soluble carbohydrates Soluble sugars from fresh leaves and roots were determined by the reaction of 1.0 mL of the alcoholic extract with 2.0 mL fresh 0.2% anthrone in sulfuric acid (w/v); the absorbance was read at 630 nm. After the extraction of the soluble fractions, the solid fraction was used for starch analysis. Starch was extracted with 9.3 mol L^{-1} perchloric acid followed by 4.6 N. The extracts were combined and starch concentration was determined after reaction with the anthrone reagent. Glucose was used as the standard for soluble sugars.

Calculation and statistical analysis The ANOVA was conducted to find effects of treatments using version 9.01 of SAS (SAS Institute Inc, Cary, NC). The significance of the treatment effect was determined using Fisher's protected test. Least significant difference (LSD) was performed to determine the significance of the difference between the means of treatments.

Results

Dry mass accumulation Significant difference was found between the dry weights of tomato plants with increasing period of four nutrient treatments (Fig. 1). The significant reduction in dry mass was initiated on 15 DAT. N-deficient plants were the lowest in weight at 30 DAT. The shoot dry weight of N, P, and K deficiency accounted for 78, 36, and 34%, respectively, of that in the NPK sufficient condition.

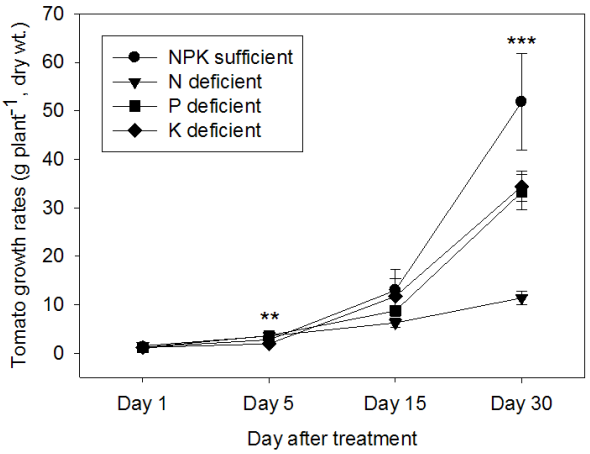

Fig. 1. The effects of N, P or K deficiency on shoot dry weight of tomato plants. Four week-old tomato seedlings were exposed to one tenth of Hoagland nutrient solution for 30 days. Different symbols (*, **, and *) indicate significant differences (*P*<0.05, 0.01, and 0.001) between treatments according to ANOVA test.**

The ratio of monovalent to divalent cations The ratio of K to the sum of calcium (Ca) and magnesium (Mg) in tomato plants grown under NPK sufficient condition ranged from 1.5 to 2.0 in leaves and from 4.0 to 5.0 in stem and roots during the whole period of the experiment (Fig 3). The deficiency of N, P, and K led to the significant decrease in the ratio and was the highest in K deficiency due to the shortage of K absorbed from media. The ratio in leaves, stem, and roots under K deficiency on 30 DAT was 0.15, 0.33, and 0.18, respectively, which accounts for 11, 6 and 5% of that in NPK sufficiency.

NPK uptake The contents of mineral N, P and K were clearly influenced by N, P and K-deficient plants, respectively (Fig. 2). Among the plant organs under N deficiency, the N concentration relative to dry matter was highest in the roots and lowest in stem. The N deficiency decreased the concentration of N in all the parts during the initial 30 days after treatment. The N deficiency also influenced the gradual reduction in the contents of P and K in all plant parts, especially higher for K. The reduction ratio of N concentration relative to that in NPK

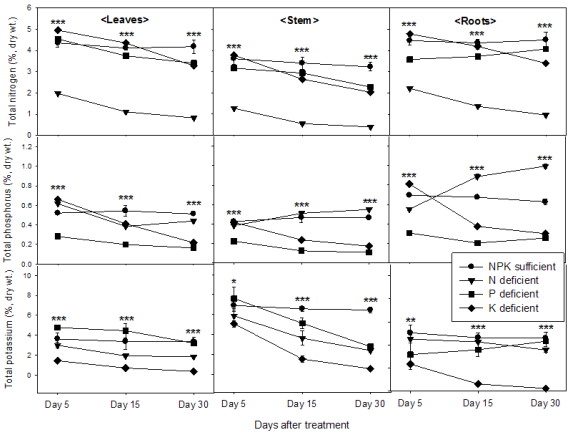

Fig. 2. Temporal changes in N, P and K contents of leaves, stem and roots of tomato plants grown under mineral deficient conditions; N (0.5 mol m^{-3}), P (0.05 mol m^{-3}) and K (0.5 mol m^{-3}). Different symbols (*, **, and *) indicate significant differences (*P*<0.05, 0.01, and 0.001) between treatments according to ANOVA test.**

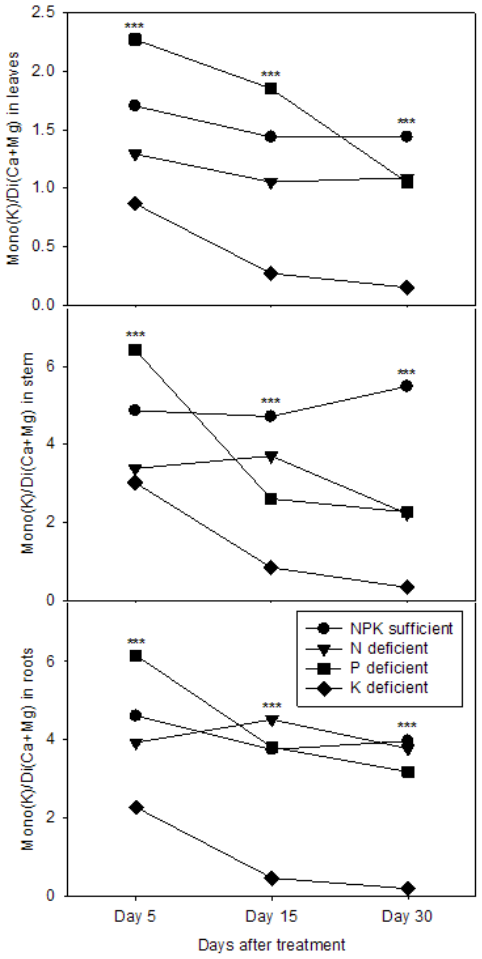

Fig. 3. The ratios of mono- (K) to di-valents (Ca + Mg) of tomato plants grown under mineral deficient conditions; N (0.5 mol m^{-3}), P (0.05 mol m^{-3}) and K (0.5 mol m^{-3}). Different symbols (*, **, and *) indicate significant differences (*P*<0.05, 0.01, and 0.001) between treatments according to ANOVA test.**

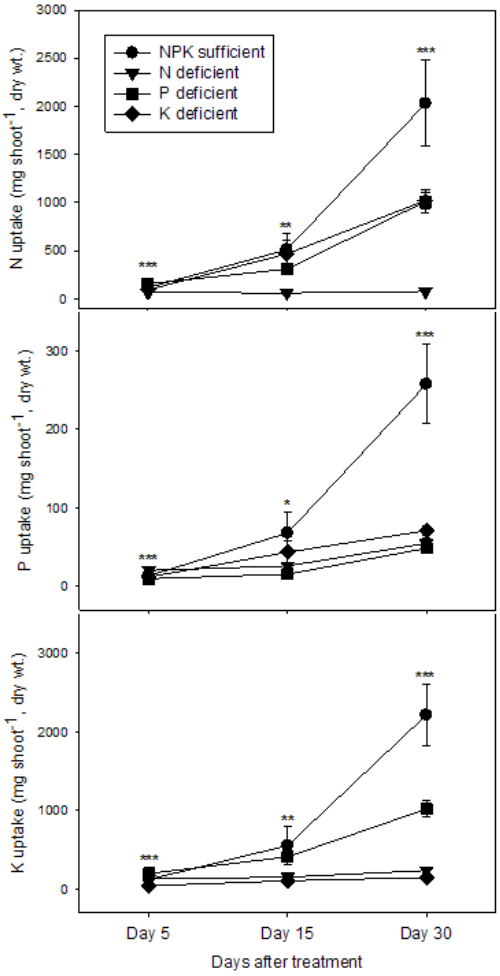

Fig. 4. Uptake rates of N, P and K of tomato plants grown under mineral deficient conditions; N (0.5 mol m^{-3}), P (0.05 mol m^{-3}) and K (0,5 mol m^{-3}). Different symbols (*, **, and *) indicate significant differences (*P*<0.05, 0.01, and 0.001) between treatments according to ANOVA test.**

sufficient condition was 80, 88 and 79% in leaves, stem and roots, respectively. The P concentration under P deficiency was in order of roots, leaves and stem. The deficiency of P also resulted in the drastic reduction of K concentrations after 5 DAT, whereas N concentration increased in the same period. The P concentration decreased to 68, 77 and 59% of that in NPK sufficient condition in leaves, stem and roots, respectively. The K concentration also revealed a significant decrease under K deficiency. Its tendency of the reduction, however, was different with N and P. The K reduction in leaves already appeared on 5 DAT while it was initiated after 5 DAT in stem and roots. The K deficiency also negatively affected N and K concentrations in stem. The K concentration decreased to 89, 91 and 95% of that in NPK sufficient condition in leaves, stem and roots, respectively.

The deficiency of N, P and K affected their uptake into the shoot of tomato plants (Fig. 4) and a significant reduction of mineral (N, P and K) uptake was apparent after 15 DAT ($P<0.05$). The ratios of N uptake was 4 (N deficient), 50 (P deficient) and 50% (K deficient), P uptake ratios were 21 (N deficient), 19 (P deficient) and 28% (K deficient), and K uptake ratios were 11 (N deficient), 46 (P deficient) and 7% (K deficient).

Soluble carbohydrates The lack of minerals led to the significant accumulation of soluble sugars in leaves and roots of tomato plants with the experimental period (Fig. 5). The difference in soluble carbohydrate concentration was apparent from 15 DAT ($P<0.01$) and was the highest in K deficiency followed by N deficiency. However, P deficiency had no significant effect on soluble sugar concentration in both tissues. The mineral deficiency also resulted in accumulation of starch in the leaves ($P<0.01$, Fig. 6), and the level was the highest in N deficiency (13.9 fold higher), followed by P (1.9 fold higher), and the lowest in K (1.6 fold higher). The N deficiency also affected accumulation of starch in roots ($P<0.05$), whereas no significant effect was found in P and K deficiency.

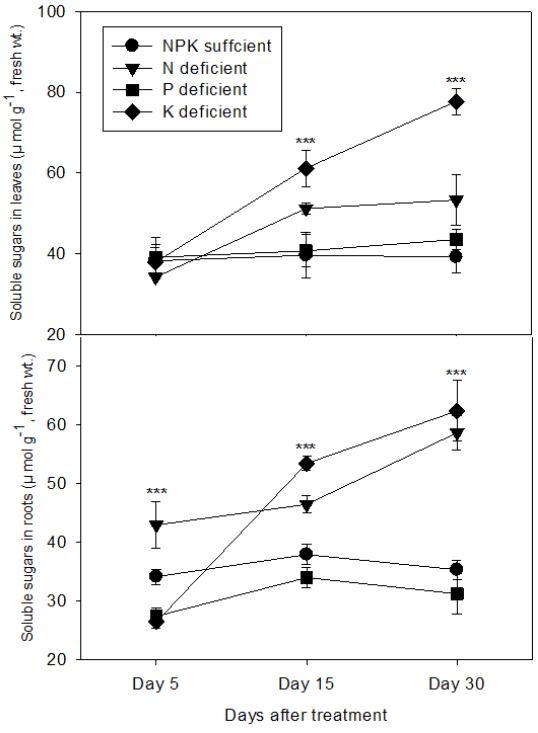

Fig. 5. Total soluble sugar contents expressed as μmol g^{-1} of glucose equivalents in leaves and roots of tomato plants grown under mineral deficient conditions; N (0.5 mol m^{-3}), P (0.05 mol m^{-3}) and K (0.5 mol m^{-3}). Different symbols (*, **, and *) indicate significant differences ($P<0.05$, 0.01, and 0.001) between treatments according to ANOVA test.**

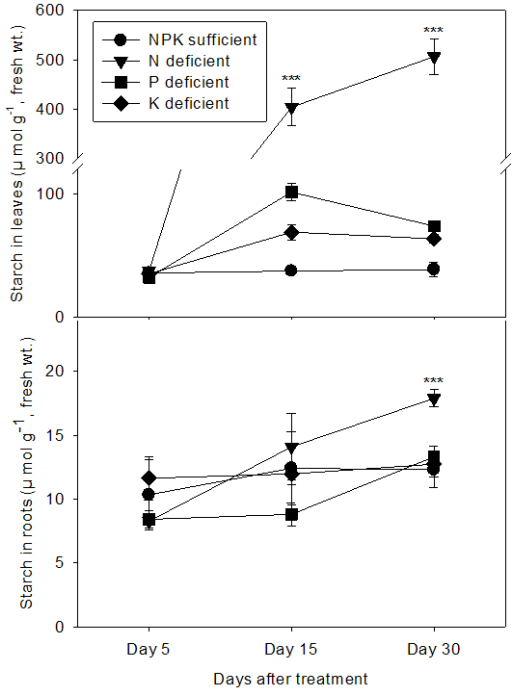

Fig. 6. Starch contents expressed as μmol g^{-1} of glucose equivalents in leaves and roots of tomato plants grown under mineral deficient conditions; N (0.5 mol m^{-3}), P (0.05 mol m^{-3}) and K (0.5 mol m^{-3}). Different symbols (*, **, and *) indicate significant differences ($P<0.05$, 0.01, and 0.001) between treatments according to ANOVA test.**

Interaction between minerals and soluble carbohydrates Soluble carbohydrates appeared to be closely related with mineral status (Table 1) and showed negative correlation with N ($P<0.001$), K ($P<0.001$ with sugar and $P<0.05$ with starch), and Mg ($P<0.05$ with starch). Calcium, however, represented positive correlation with soluble carbohydrates ($P<0.05$).

Discussion

The mineral (N, P or K) limitation imposed in this study resulted in great limitation of mineral uptake and growth, and rapid adjustments in carbohydrate formation and utilization in leaves and roots of tomato plants. The restriction of shoot development in mineral-deficient plants revealed a delayed sink leaf initiation and decreased expansion of growing leaves. Therefore, a decline in dry weight of shoot was predicted on 15 DAT in all treatments

Table 1. Pearson's correlation coefficients between soluble carbohydrates and mineral elements.

	Sugar	Starch	N	P	K	Ca	Mg
Sugar	-	0.29*	-0.39***	-0.15	-0.64***	0.25*	0.16
Starch		-	-0.56***	-0.18	-0.25*	0.28*	-0.27*
N			-	-0.19	0.05	0.01	0.40***
P				-	0.23*	-0.35**	-0.26*
K					-	-0.20	0.01
Ca						-	0.26*
Mg							-

Different symbols (*, **, and ***) indicate significant differences (P<0.05, 0.01, and 0.001) between treatments according to ANOVA test.

(Fig. 1). Similar responses to minerals-starved conditions were observed in many crops (Kanai et al., 2007; Pujos and Morard, 1997; Guidi et al., 1997; Rufty et al., 1988; Zaho et al., 2001) while extents of responses are various depending on plant species, age, nutrition composition, etc. Visual symptoms such as necrosis, chlorosis and growth reduction appear much later when plants are exposed to a long period of the stress (Besford, 1978a, b; Pujos and Morard, 1997). In this study, we found that the limitation of growth was relatively late response with considering mineral uptake and carbohydrate metabolism; a gap of 10 days was found between both factors. It is well known that the shortage of mineral element leads to a dramatic decline of mineral uptake by plants. The reduction of elements in this study reached to approximately 50% on 5 DAT irrespective of plant parts and elements (Fig. 2). This can be a good example for predicting an elapsed time and required dose of mineral deficiency through growth reduction. The starvation of N and P as well as K appeared significantly negative for K uptake, and thus led to a great decline in the ratio of K to Ca+Mg (Fig. 3). A temporal decrease in the ratio of K to Ca+Mg was observed. The P deficiency on 5 DAT, interestingly, resulted in a great increase in the ratio of K to Ca+Mg in all tissues. In this study, N deficiency affected negatively the uptake of K, Ca and Mg. On the other hand, P deficiency induced their uptake and K deficiency only resulted in an increase in Mg uptake. The sodium (Na) concentration in all treatments did not show any significance because of the lack of Na in growth media. Therefore, N was an antagonistic relationship with cations (K, Ca and Mg), whereas P was a synergistic with them.

In general, plant growth was closely related with mineral uptake, and thus estimating the uptake rates of mineral elements can be helpful to comprehensively understand the status of plant growth, mineral concentration, etc. The difference in mineral uptake rates appeared distinctly after 15 DAT representing similar tendency to growth rates (Fig. 4). On 30 DAT, the amount of N, P and K uptake in N deficiency entirely corresponded to growth rates. The N and K uptake rates also represented the similar tendency in P deficiency, whereas their uptake rates were greatly influenced by P concentration of tissues in P deficiency which was similarly described in previous report (Wang and Tillberg, 1997). In K deficiency, the uptake of N was affected by growth rates while the uptake of P and K was dependent upon their concentrations in tissues. Our study suggests that the potential of N uptake was considerably associated with plant growth whereas P uptake was highly reflected by the concentration in tissues.

The association between mineral status and carbohydrates metabolism has been reported by many researches in various plant species. However, many studies have been investigated on the effect of an individual element on the accumulation and utilization of soluble carbohydrates rather than comparative analysis. The accumulation of soluble sugars increased in both leaves and roots under N or K deficiency with increasing period of treatment, whereas it was not affected by P deficiency (Fig. 5). The dramatic elevation of soluble sugars in N or K deficiency was on 5 DAT and appeared to be associated with reduced entry of soluble sugars, especially sucrose, into the transport pool or decreased phloem loading. This pattern of response associated with soluble sugar accumulation of the tomato plant to N or K deficiency is identical to the response of soybean (Thomas et al., 1988) and tobacco (Paul and Stitt, 1993; Paul and Driscoll, 1997) to N

stress, of tomato (Kanai et al., 2007) and cotton (William, 1999; Zhao et al., 2001) to K stress. Soluble sugars under P deficiency remained constant and similar result was observed in barley (Wang and Tillberg. 1997; Alejandro et al., 2001). However, other researchers have reported general accumulation of soluble sugars in shoots and/or roots affected by low P condition in bean, barley, spinach, tobacco and soya plants (Paul and Stitt, 1993; Cakmak et al., 1994; Ciereszko et al., 1996; Ciereszko et al., 2005: Ciereszko and Barbachowska, 2000). In our study, constant levels of soluble sugars throughout the experiment appear to be moderately responsive to P deficiency, which sustained photosynthetic activity and phloem loading to transport them to the roots. However, further study is required to elucidate why soluble sugars remain unchanged in both leaves and roots. The accumulation of starch in both tissues was similar tendency to that of soluble sugars with an increment of treatment period and was the highest in K deficiency, which showed markedly elevation throughout the experiment (Fig. 6). These data coincide with many previous reports showing that the suboptimal levels and withdrawal of mineral supply have resulted in an accumulation of soluble carbohydrates in shoots and roots (Paul and Stitt, 1993; Guidi et al., 1997; Paul and Driscoll, 1997; William, 1999). According to the result of soluble carbohydrates on the mineral stresses in our study, K had the strongest influence on soluble carbohydrates metabolism, followed by N and P, although N was most responsible for the reduction in plant growth and photosynthesis (data not shown) compared to P and K. These imply that K deficiency suppresses assimilated translocation due to enzyme activities related with phloem loading and unloading without affecting photosynthesis at the source, and thus led to an accumulation of soluble carbohydrates in both shoot and roots. We also investigated the responses on soluble carbohydrates of each mineral element (Table 1). The N and K had negatively correlated with soluble sugars and starch while P did not affect their metabolism. Unlike N and K, Ca appeared to be a positive relationship with them. This could also be the strong evidence that N or K deficiency influences adversely, and thus results in huge accumulation of soluble carbohydrates. In conclusion, the reduction in plant growth and mineral uptake in tomato plant was more sensitive in N deficiency, whereas K deficiency was more responsible for soluble carbohydrate metabolism. These results indicate the difference in reaction time between plant growth and carbohydrate metabolism such as feedback and end-product effects and it substantially differs from mineral elements.

References

Ariovich, D., and C. F. Cresswell. 1983. The effect of nitrogen and phosphorus on starch accumulation and net photosynthesis in two variants of Panicum maximum. Jacq. Plant Cell Environ. 6: 657-664.

Behboudian, M. H., and D. R. Anderson. 1990. Effect of potassium deficiency on water relations and photosynthesis of tomato plants. Plant and Soil. 127: 137-139.

Beringer, H. and H. E. Haeder. 1981. Influence of potassium nutrition on starch synthesis in barley grains. Zeitschrift für Pflanzenernähring Bodenkunde. 144: 1-7.

Besford, R. T. 1978a. Effect of replacing nutrient potassium by sodium on uptake of and distribution of sodium in tomato plants. Plant Soil 50: 399-409.

Besford, R. T. 1978b. Effect of sodium in the nutrient medium on the incidence of potassium-deficiency symptoms in tomato plants. Plant Soil 50: 427-432.

Cakmak, I., C. Hengeler, and H. Marschner. 1994. Changes in phloem export of sucrose in leaves in response to phosphorus, potassium and magnesium deficiency in bean plants. J. Exp. Bot. 45: 1251-1257.

Ciereszko, I. and A. Barbachowska. 2000. Sucrose metabolism in leaves and roots of bean (*Phaseolus vulgaris* L.) during phosphate deficiency. J. Plant Physiol. 156: 640-644.

Ciereszko, I., A. Gniazdowska, M. Mikulska, and A. M. Rychter. 1996. Assimilate translocation in bean plants (*Phaseolus vulgaris* L.) during phosphate deficiency. J. Plant Physiol. 149: 343-348.

Ciereszko, I., H. Johansson, and L. A. Kleczkowski. 2005. Interactive effects of phosphate deficiency, sucrose and light/dark conditions on gene expression of UDP-glucose pyrophosphorylase in Arabidopsis. J. Plant Physiol. 162: 343-353.

de Groot, C. C., L. F. M., Marcelis, R. van der Boogaard, W. M. Kaiser, and H. Lambers. 2003a. Interaction of nitrogen and phosphorus nutrition in determining growth. Plant Soil 248: 257-268.

de Groot, C. C., R. van der Boogaard, L. F. M., Marcelis, J. Harbinson, and H. Lambers. 2003b. Contrasting effects of N and P deprivation on regulation of photosynthesis in tomato plants in relation to feedback limitation. J. Exp. Bot. 54: 1957-1967.

Epstein, E. and A. J. Bloom. 2005. Mineral nutrition of plants: Principles and Perspectives, 2nd ed. Sinauer Associates, Inc., Sunderland, MA.

Evans, J. R. and H. Poorter. 2001. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. Plant Cell Environ. 24: 755-767.

Guidi, L., G. Lorefice, A. Pardossi, F. Malorgio, F. Tognoni, and G. F. Soldatini. 1997. Growth and photosynthesis of *Lycopersicon esculentum* (L.) plants as affected by nitrogen deficiency. Biologia Plantarum 40: 235-244.

Hell, R. and H. Hillebrand. 2001. Plant concepts for mineral acquisition and allocation. Curr. Opin. Biotechno. 12: 161-168.

Huber, S. C. and T. Akazawa. 1986. A novel sucrose synthase pathway for sucrose degradation in cultured sycamore cells. Plant Physiol. 81: 1008-1013.

Kanai, S., K. Ohkura, J. J. Adu-Gyamfi, P. K. Mohapatra, N. T. Nguyen, H. Saneoka, and K. Fujita. 2007. Depression of sink activity precedes the inhibition of biomass production in tomato plants subjected to potassium deficiency stress. J. Exp. Bot. 2007: 2917-2928.

Marschner, A. 1995. Mineral nutrition of higher plants. Academic Press, San Diego, CA

Mengel, K. 1980. Effect of potassium on the assimilate conduction of storage tissue. Berichte der Deutschen Botanischen Gesellschaft. 93: 353-362.

Mengel, K. and M. Viro. 1974. Effect of potassium supply on the transport of photosynthates to the fruits of tomatoes (*Lycopersicon esculentum*). Physiol. Plantarum. 30: 295-300.

Paul, M. J. and S. P. Driscoll. 1997. Sugar repression of photosynthesis: the role of carbohydrates in signaling nitrogen deficiency through source:sink imbalance. Plant Cell Environ. 20: 110-116.

Paul, M. J. and M. Stitt. 1993. Effects of nitrogen and phosphorus deficiencies on levels of carbohydrates, respiratory enzymes and metabolites in seedlings of tobacco and their response to exogenous sucrose. Plant Cell Environ. 16: 1047-1057.

Pujos, A. and P. Morard.1997. Effect of potassium deficiency on tomato growth and mineral nutrition at the early production stage. Plant Soil 189: 189-196.

Rufty, T. W., S. C. Huber, and R. J. Volk. 1988. Alterations in leaf carbohydrate metabolism in response to nitrogen stress. Plant Physiol. 88: 725-730.

Wang, C., and J. E. Tillberg. 1997. Effects of short-term phosphorus deficiency on carbohydrate storage in sink and source leaves of barley (*Hordeum vulgare*). New Phytol. 136: 131-135.

William, T. P. 1999. Potassium deficiency increases specific leaf weights and leaf glucose levels in field-grown cotton. Agronomy J. 91: 962-968.

Zhao, D., D. M. Oosterhuis, and C. W. Bednarz. 2001. Influence of potassium deficiency on photosynthesis, chlorophyll content, and chloroplast ultra-structure of cotton plants. Photosynthetica. 39: 103-109.