This article was downloaded by: [Moskow State Univ Bibliote]
On: 09 December 2013, At: 17:55
Publisher: Taylor & Francis
Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Plant Nutrition
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/lpla20

Effect of Oxygen Deficiency on Mineral Nutrition of Excised Tomato Roots

Philippe Morard [a] , Ludovic Lacoste [a] & Jérôme Silvestre [a]
[a] Laboratoire d'Agronomie Environnement Ecotoxicologie , Ecole Nationale Supérieure Agronomique de Toulouse , Castanet-Tolosan, France
Published online: 16 Aug 2006.

To cite this article: Philippe Morard , Ludovic Lacoste & Jérôme Silvestre (2004) Effect of Oxygen Deficiency on Mineral Nutrition of Excised Tomato Roots, Journal of Plant Nutrition, 27:4, 613-626, DOI: 10.1081/PLN-120030371

To link to this article: http://dx.doi.org/10.1081/PLN-120030371

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at http://www.tandfonline.com/page/terms-and-conditions

JOURNAL OF PLANT NUTRITION
Vol. 27, No. 4, pp. 613–626, 2004

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Effect of Oxygen Deficiency on Mineral Nutrition of Excised Tomato Roots

Philippe Morard,* Ludovic Lacoste, and Jérôme Silvestre

Laboratoire d'Agronomie Environnement Ecotoxicologie,
Ecole Nationale Supérieure Agronomique de Toulouse,
Castanet-Tolosan, France

ABSTRACT

The influence of oxygen deficiency on uptake of water and mineral elements through root system was studied on detopped tomato plants for 48 h. The root exudates and the nutrient solutions were collected and analyzed every two hours after decapitation of the shoots at the early fruiting stage. The lack of oxygen in the nutrient solution induced the appearance of nitrite ions in the nutrient medium and in the xylem sap. Nitrites were derived from nitrate reduction by tomato root cells. This mechanism, called ''nitrate respiration'', should be an alternative pathway to have oxygen as electron acceptor during root anoxia and could be a transient adaptation to hypoxic conditions. The lack of oxygen in the nutrient medium caused a

*Correspondence: Philippe Morard, Laboratoire d'Agronomie Environnement Ecotoxicologie, Ecole Nationale Supérieure Agronomique de Toulouse, B.P. 107, Castanet-Tolosan 31326, France; E-mail: morard@ensat.fr.

DOI: 10.1081/PLN-120030371 0190-4167 (Print); 1532-4087 (Online)
Copyright © 2004 by Marcel Dekker, Inc. www.dekker.com

ORDER REPRINTS

42% reduction of water consumption by excised tomato roots during the experiment. The deprivation of oxygen induced also an efflux of potassium, magnesium, phosphate and sulfate in the nutrient solution. So, this experimentation allows to obtain information about macronutrient uptake mechanisms by excised tomato roots. The uptake of potassium, magnesium, phosphate and sulfate is an ''active process'', directly linked to the energetic catabolism. On the opposite, the absorption of calcium is a ''passive process'', in the pathway of the electrochemical gradient via the water xylem flow.

Key Words: Anoxia; Hydroponics; Mineral contents; Mineral uptake; Tomato plants; Xylem sap.

INTRODUCTION

Oxygen deficiency in soils and in nutrient solutions of soilless culture has unfavorable effects on water uptake[1,2] and on mineral elements such as potassium,[3–5] nitrate,[6] and phosphate.[7] These unfavorable effects on water and mineral uptake of plants reduce their growth.[8] In addition, the appearance of anoxic conditions entails ethylene production,[9] fermentation processes[10] accompanied by an accumulation of a released carbon dioxide[11] and ethanol production.[12] Moreover, investigations have revealed that, in anoxia, the pathway of nitrate utilization is partially or completely blocked at the nitrite reduction step.[13,14] Resulting increase of intracellular nitrite concentration is associated with release of NO_2^- in the surrounding medium.[15,16] The presence of nitrite in the nutrient solution of soilless culture of tomato plants at flowering stage was detected in the nutrient medium after an asphyxia period of the roots.[2]

All these works confirm the essential role of oxygen in the water and mineral uptake but few of them have studied the influence of a root asphyxia period on the mineral uptake and the translocation via xylem sap. In this objective, the plant exudates must be collected directly from the root system after decapitation of the aerial part. Out of shoot transpiration, the xylem sap collected results from the root pressure, which is particularly important in tomato, plant test used in this study.[17–19]

The aim of this work was (i) to study the adaptative behavior of excised roots to anoxic conditions, (ii) to study the influence of oxygen deprivation on the flux and on the mineral composition of the xylem sap, (iii) to analyze the evolution of macronutrient concentrations in the

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

ORDER REPRINTS

nutrient solution during anoxia period to obtain information about uptake mechanisms of detopped tomato plants.

MATERIALS AND METHODS

Plant Material and Growth

Tomato seeds (*Lycopersicon esculentum* cv. Rondello) were germinated on filter paper moistened with distilled water at 25°C in the dark. After 7 d, plants were grown individually in PVC tank containing 6L of noncirculating nutrient solution. The nutrient solution contained macronutrients (meq/L: K^+ 2.6, Ca^{++} 0.5, Mg^{++} 0.15, NO_3^- 2.35, $H_2PO_4^-$ 0.35, SO_4^- 0.15) and micronutrients (mg/L: Fe 15, Mn 0.49, Cu 0.06, Zn 0.11, B 0.26, Mo 0.01). The formulation of macronutrients was elaborated according to the mineral needs of the plants during the relatively brief duration of the experiment.[20] The nutrient solution was replaced twice a week. The electric conductivity of the nutrient solution was 0.42 mS cm^{-1} and the pH varied from 5.2 for fresh solution to 6.0 for spent solution.

Aeration/Asphyxiating Experiment

The culture systems were located in a greenhouse (16 h of photoperiod, day/night air temperatures of $24/18 \pm 6$°C, $50\% \pm 10\%$ of relative humidity). Asphyxiating experiments were conducted on excised roots at 17/18 leaf stage of tomato plant (2nd thrush). At the beginning of the experiment, plants were detopped at collar level. Root anoxia was obtained progressively by sealing the PVC tank with an airtight cover at the beginning of the experiment while aeration was stopped and an airtight seal between shoot and root was also set-up.[21] Oxygen dissolved in nutrient solution was depleted by root respiration. By contrast, control plants remained continuously bubbled with air. Two treatments were applied, tomato roots were placed either in an aerated nutrient solution (Treatment A), or non-aerated (Treatment NA). Each experiment was conducted over a 48 h period. Before each measurement, transpirational water losses were compensated with deionized and degasified water. The oxygen concentration in the medium was monitored with an Orion oxygen electrode 97-08-99 connected to an Orion ionometer 960 (Cambridge, MA, USA). Every 2 h, water consumption was measured

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

ORDER REPRINTS

and nutrient solution samples (2 mL) were collected to determine mineral nutrient absorption.

At the beginning of the experiment and 24 h after excision, the isolated root systems of 5 plants at the same stage of development and cultivated under the same conditions were collected and analyzed to serve as reference values (Treatment C).

Sampling and Analysis

The volume and mineral composition of xylem sap were recorded every two hours during two days. The flux of xylem sap was expressed in milliliters per gram of root dry weight (measured at harvest) and per hour ($mL\,g^{-1}\,h^{-1}$) and calculated for each nyctemeral period (D1, D2 in daytime and N1, N2 in night hours). The samples of xylem sap and nutrient solution were analyzed by high pressure liquid ionic chromatography (Dionex DX-100, ionpac CS-12A, and AS4A-SC, Dionex Co., Sunnyvale, CA, USA). The cumulative quantities of cations absorbed by the plants were determined in milliequivalent of ion per 100 g of root dry weight (meq $100\,g^{-1}$ DW) and calculated according to the nychtemeral period after the beginning of the experiment D1, D2 in daytime and N1, N2 during night hours. The composition of the xylem sap was determined in milliequivalent of ion per liter (meq L^{-1}). The cumulative flux of xylem sap was determined in milliliters of sap per gram of root dry weight (mL sap g^{-1}) and calculated for each nychtemeral period D1, D2 in daytime and N1, N2 during night hours.

The extraction of water soluble carbohydrates (saccharose, glucose and fructose) from the excised root systems was conducted on 1 g of dry matter shaken during 30 min with 25 mL of boiling demineralized water.[22] The analysis of the water soluble carbohydrates (WSC) was conducted by high pressure liquid ionic chromatography (Dionex® Dx-300, Carbopac® PA_1). The results for the water soluble carbohydrates (WSC) were expressed in milligrams of carbohydrates per gram of dry weight ($mg\,g^{-1}$). Before the aerial part was excised, the WSC content were analyzed in root system of the tomato plants (Treatment C) to serve as reference value. The results were expressed in milligrams of WSC per gram of dry matter.

After drying, grinding and calcination at 550°C, macronutrient content (K, Ca, Mg, Na, $P_{H_2PO_4^-}$) was analyzed in every complete root systems from A and NA treatments by high pressure liquid ionic chromatography (Dionex DX-100, ionpac CS-12A and AS4A-SC, Dionex Co., Sunnyvale, CA, USA). The total nitrogen ($N_{NO_3^-}$)

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

ORDER REPRINTS

was measured after a sulfuric acid mineralization and the total sulfur ($S_{SO_4^{2-}}$) after a nitric acid mineralization. The results were expressed in milliequivalent of ion per 100 grams of dry matter (meq $100\,g^{-1}$) and in dry matter percentage (% DM).

Each experiment (one plant for each treatment A or NA) was replicated 5 times. The results were analyzed statistically with ANOVA (Sigmastat v. 2.03, SPSS Inc., 1997). Each point on the curves of the water, of the nutrient consumption and of the xylem sap content was subjected to a variance analysis: significant difference (s) or nonsignificant difference (ns) at the 5% threshold was specified at the head of each figure.

RESULTS AND DISCUSSION

Nitrate Respiration: Adaptative Behavior of Excised Roots to Anoxic Conditions

After the PVC tanks were closed hermetically, root system consumed the oxygen dissolved in the nutrient solution until it was depleted.[21] The rate of oxygen decrease was 1.90 mg $O_2\,g^{-1}\,h^{-1}$ (DW tomato roots); total depletion was obtained 5 h after the start of the experiment. This anoxic condition (treatment NA) induced nitrite appearance in nutrient solution after 16 h (Fig. 1) and in root xylem sap after 22 h (Fig. 2). No nitrite was detected in aerated nutrient solution (treatment A). Some hours after the beginning of oxygen deprivation, root tissues were able to reduce nitrate ions to nitrite ions: $NO_3^- \rightarrow NO_2^- + \frac{1}{2}\,O_2$. During the second day after the beginning of the experiment (D2 and N2, Fig. 1), about 2 meq/L of nitrate ions disappeared and about 1 meq/L of nitrite ions appeared in the nutrient solution of treatment NA (versus no modification of the concentration of these ions in the A medium). This important quantitative phenomenon would be an adaptation of tomato roots to unfavorable conditions when oxygen becomes limiting. The oxygen produced could take place exogenous oxygen essential for the terminal electron acceptor of mitochondrial electron transport. This mechanism, called ''nitrate respiration'', is known in certain facultatively anaerobic microorganisms and was suggested for the asphyxia process of barley roots[13] and of wheat.[23] As far as we know, it was the first time it was found in excised tomato roots and confirmed our previous results on intact tomato plants at flowering stage of development.[2] Nitrite appearance could not be related to microorganism activity, NO_2^- was not detected in oxygen deprivated medium of excised tomato roots cultivated in sterile conditions (unpublished data).

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

ORDER REPRINTS

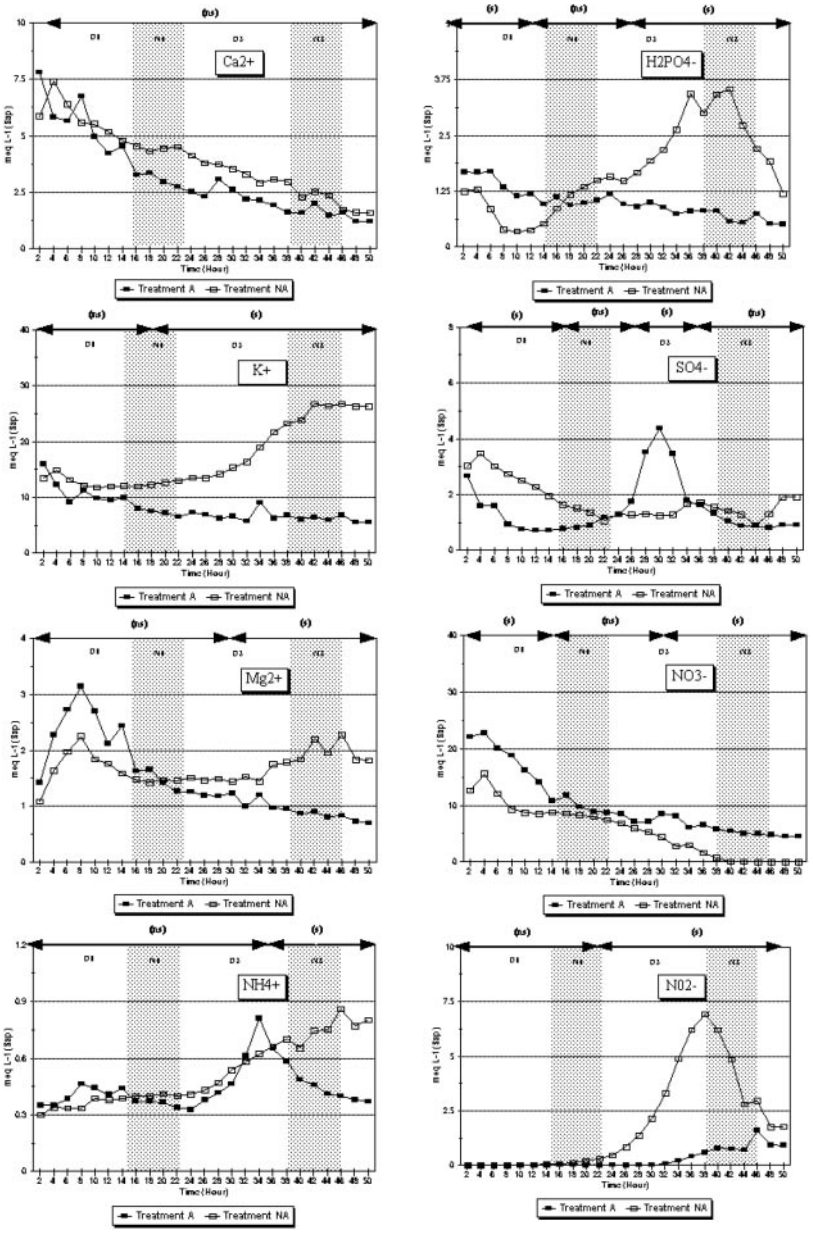


Figure 1. Evolution of mineral composition of the nutrient solution after decapitation of tomato soilless culture with aerated (A) and nonaerated (NA) roots. (*D1 − D2 = day period*; *N1 − N2 = night period represented by shaded area*; *s = significant difference*; *ns = nonsignificant difference*)

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

ORDER REPRINTS

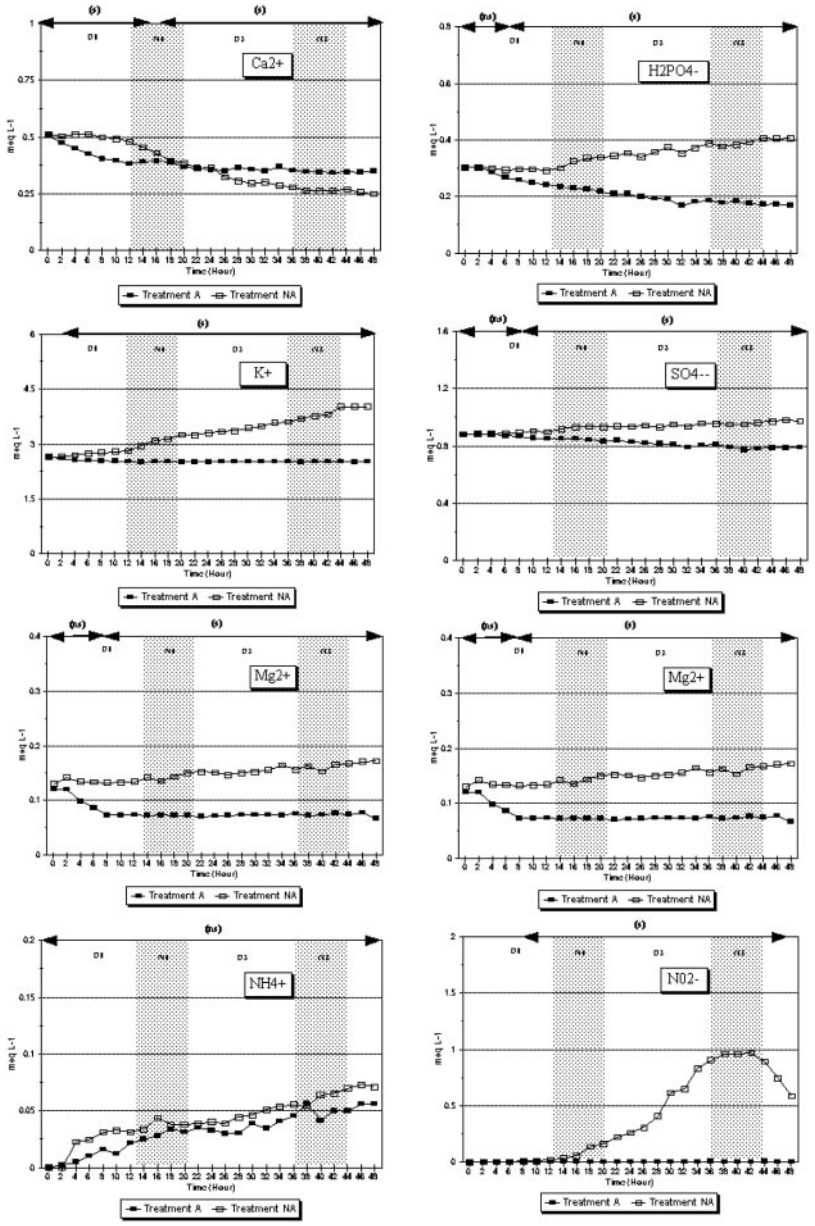


Figure 2. Evolution of mineral composition of xylem sap after decapitation of tomato soilless culture with aerated (A) and nonaerated (NA) roots. (*D1 − D2 = day period*; *N1 − N2 = night period represented by shaded area*; *s = significant difference*; *ns = nonsignificant difference*)

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

ORDER REPRINTS

Moreover, the evidence of nitrate respiration was corroborated in this experiment with nitrite appearance in xylem sap 22 h after the start of the experiment (Fig. 2). So, nitrite ions were derived from nitrate reduction by root cells and rejected in apoplastic zone out of roots (nutrient solution or xylem sap). Nitrite appearance was also related to an enhancement of nitrate reductase activity (unpublished data), according other investigations on the stimulation of NR activity under flooding and low oxygen conditions.[14,16,24] Finally, at the end of the experiment, total N content in NA roots was lesser significant than A roots (Table 1).

All these observations indicate that nitrate respiration improves tomato survival to transient hypoxic conditions. When medium conditions become favorable again, the plant return to a normal respiratory process.[21]

Table 1. Total uptake, mineral root content and mineral composition of xylem sap, after decapitation of tomato grown in soilless culture with aeration (Treatment A) or no aeration (Treatment NA). (*Each value is the mean of five individual samples* $\pm$ *SE*; $p = 0.05$; *values followed by the same letter are not statistically different at* $p < 0.05$)

Element	Treatment	Total uptake meq $100\,g^{-1}$ d.w (1)	Root contents meq $100\,g^{-1}$ d.w	Xylem sap meq $100\,g^{-1}$ d.w
K^+	A	−11.60 b	125.29 a	15.10 a
	NA	153.09 a	22.76 b	20.10 b
Ca^{2+}	A	−13.22 a	47.73 a	8.51 a
	NA	−27.18 b	57.88 a	6.32 a
Mg^{2+}	A	−3.96 b	21.99 a	3.69 a
	NA	4.36 a	18.09 a	2.30 a
$N\text{-}NO_3^-$	A	−42.23 a	57.10 a	29.13 a
	NA	−271.78 b	37.58 b	10.80 b
$N\text{-}NO_2^-$	A	0.27 b	—	0.16 b
	NA	84.90 a	—	1.68 a
$P\text{-}PO_4H_2^-$	A	−10.74 b	10.83 a	2.39 a
	NA	10.77 a	5.98 b	2.04 a
$S\text{-}SO_4^{2-}$	A	−9.12 b	34.96 a	2.97 a
	NA	9.70 a	27.06 b	2.79 a

(1) Total uptake: decrease of nutrient uptake is indicated as negative value; increase of nutrient uptake is indicated as positive value.

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

ORDER REPRINTS

Influence of Oxygen Deprivation on Xylem Sap Flux

The effects of oxygen deprivation on root systems of detopped tomato plants were studied on the exudation rates (Fig. 3). The tomato root system asphyxia (Treatment NA) induced a strong reduction of the xylem sap flow on the first day of the experiment (D1: 0 to 14 h). The flux decrease of the xylem sap was statistically significant: 0.56 mL $g^{-1} h^{-1}$ for Treatment NA versus 0.96 mL $g^{-1} h^{-1}$ for Treatment A. This reduction (42%) of water consumption during this period could be related to a reduced water permeability of the asphyxiated roots.[8] Oxygen root deprivation carried out on intact tomato plants with the same experimental design revealed a lesser reduction (20–30%) of water uptake.[2] The comparison of water consumption between this experiment with excised roots and the previous results with intact tomato plants

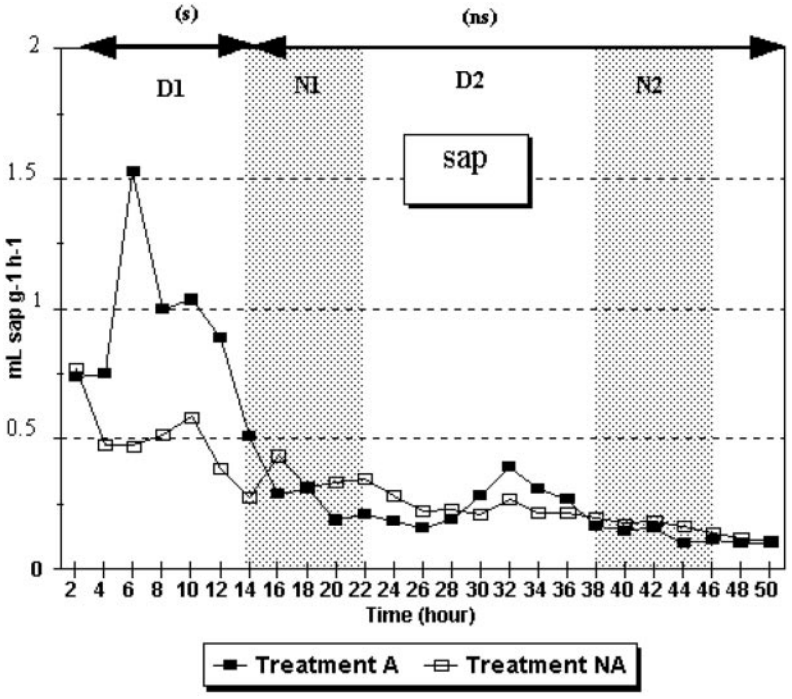


Figure 3. Xylem sap flow after decapitation of tomato soilless culture with aerated (A) and nonaerated (NA) roots. (*D1 – D2 = day period*; *N1 – N2 = night period represented by shaded area*; *s = significant difference*; *ns = nonsignificant difference*)

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

ORDER REPRINTS

Table 2. Water Soluble Carbohydrate (WSC) content after decapitation of tomato grown in soilless culture at 0, 24 h (Treatment Control) and at 48 h with aeration (Treatment A) or no aeration (Treatment NA); results expressed in mg g^{-1} of dry weight root. (*Each value is the mean of five individual samples* ± *SE*; *p* = *0.05; values followed by the same letter are not statistically different at p < 0.05*)

Time (h)	Treatment	Sucrose (mg g^{-1})	Glucose (mg g^{-1})	Fructose (mg g^{-1})	Total (mg g^{-1})
0	Control	4.29 ± 0.78 a	0.36 ± 0.21 a	0.58 ± 0.25 a	5.23 ± 0.90 a
24 h	Control	2.54 ± 0.29 b	0.16 ± 0.06 b	0.14 ± 0.03 b	2.84 ± 0.24 b
48 h	A	0.66 ± 0.14 a	0.19 ± 0.03 a	0.04 ± 0.02	0.88 ± 0.16 a
	NA	0.08 ± 0.08 b	0.07 ± 0.06 b	0.04 ± 0.02 ns	0.19 ± 0.16 b

cultivated in the same conditions allows to estimate root pressure (about 15% of water flow) versus leaf transpiration (85%).

At the start of the first nocturnal period and until the end of the experiment (N1, D2, N2), a strong reduction of the exudation rates from root systems was observed. During this phase, the oxygen deprivation did not induce any significant difference in the sap flow between treatments A and NA (Fig. 3). The reduction of xylem flux could be related to the of water soluble carbohydrate (WSC) stock in root tissues (Table 2). WSC contents (5.23 mg g^{-1} at the beginning of the experiment on plant control, Treatment C) were nearly totally depleted after 48 h (0.88 mg g^{-1} Treatment A; 0.19 mg g^{-1} Treatment NA).

In both A and NA treatments, the xylem sap flow is more important during the diurnal periods (D1, D2) than during the nocturnal periods (N1, N2). A 24 h rhythm is therefore conserved independently of the influence of the aerial part. This observation has already been made for tomatoes.[17,18,25] It has been attributed to the osmotic pressure of the root[26] in relation to the mineral element composition of the nutrient medium[27] or to the mineral composition of the caulinary exudates.[28] The different nychtemeral rhythm of the flux observed without tomato aerial part could be related to xylem sap viscosity during day/night temperature in the greenhouse.

Macronutrient Uptake Mechanisms on Excised Roots

Nutrient solution composition and mineral concentration of root xylem sap were regularly and simultaneously analyzed for the two

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

ORDER REPRINTS

treatments (A and NA) during the experiment. Information about root uptake mechanism of macronutrients could be drawn from these data. Active process mechanism are related to ATP energy and chemical oxidized power (NAD) coupled with oxygen electron acceptor. So, in anoxic conditions, the lack of oxygen in root tissues blocks mitochondrial respiration and disturbs the active uptake of nutrients. In the opposite, passive process are decoupled from energetic catabolic and depends directly from the electrochemical gradient in relation to water flow. Potassium, magnesium, phosphate and sulfate were characterized by similar behavior: (i) oxygen deprivation induced a greater concentration of these elements (except sulfate) in the xylem sap of treatment NA as compared to treatment A, 22 h after the beginning of the experiment (Fig. 2); (ii) when oxygen was depleted about 5 h after the beginning of the experiment, the concentration of these ions increased in the nutrient solution (Fig. 1) related to ion efflux from roots back to nutrient medium (Table 1); (iii) at the end of experiment (48 h), K, P, and S content in roots were significantly less in A treatment than in NA treatment (Table 1). Under anoxia conditions, the depolarization of cellular membrane of the root cells caused an efflux of potassium and magnesium (antiport), phosphate and sulfate (symport), from the root cell cytosol into the apoplastic zone of the root tissue. Then, these ions were thrown either out of the roots and their concentration increased in the nutrient solution, or in the xylem vessels and therefore increased in the collected xylem sap. These results confirm that the uptake mechanism is an active process: potassium,[4] phosphate,[29] and sulfate[30] uptake are directly linked to the metabolic activity of the root cells. Magnesium uptake is generally considered to be a passive mechanism.[31] These experiment results on excised roots confirm our previous hypothesis for intact tomato plant:[2] two uptake mechanisms would exist for this ion, a passive process with high concentration and an active process of magnesium uptake with low concentration in nutrient medium. In this experimentation, the concentration scale chosen was low (0.15 meq L^{-1}) and the mechanism uptake of magnesium observed was an active type.

The mechanism of nitrate uptake is known as an active process. This experiment cannot give any information because nitrate are also utilized in the nitrate respiration.

The calcium concentration of the xylem sap was not influenced by the aeration of the culture medium (Fig. 2). The deprivation of oxygen was not related to an efflux of this ion in the nutrient medium (Fig. 1). No significant difference was observed in calcium root contents between A and NA treatments after 48 h of experiment (Table 1). The absorption process would be a passive process. Moreover, the calcium

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

ORDER REPRINTS

concentration in xylem sap (2 to 8 meq L^{-1}) was higher than in nutrient solution (0.5 meq L^{-1}). The high level of calcium in xylem sap was derived from the apoplastic root stores.[19] After 48 h of experiment, calcium destorage was over at the end of the experiment because the concentration in xylem sap was near to that of the nutrient solution.

CONCLUSIONS

Oxygen deficiency applied during 48 h to the root system of decapitated tomatoes induced nitrite appearance in the nutrient solution and in xylem sap. Nitrites were derived from nitrate reduction by tomato root cells. This mechanism, called nitrate respiration, should be an alternative pathway to have oxygen as electron acceptor during root anoxia. This mechanism could be a transient adaptation of root system metabolism in hypoxic conditions.

Asphyxiating conditions disturb uptake of water and mineral nutrients. Lack of oxygen in the nutrient solution caused a 42% reduction of the xylem flux sap.

These experimentation on excised roots indicate that uptake mechanism of potassium, magnesium, phosphates and sulfates are an "active process" directly linked to the energetic catabolism. The uptake of calcium is a "passive process" in pathway of the electrochemical gradient via to the water xylem flow.

REFERENCES

1. Bradford, K.J.; Hsiao, T.C. Stomatal behavior and water relations of waterlogged tomato plants. Plant Physiol. **1982**, *70*, 1508–1513.
2. Morard, P.; Lacoste, L.; Silvestre, J. Effect of oxygen deficiency on uptake of water and mineral nutrients by tomato plants in soilless culture. J. Plant Nutr. **2000**, *23*, 1063–1978.
3. Buwalda, F.; Thompson, C.J.; Steigner, W.; Barrett-Lennard, E.G.; Gibbs, J.; Grennway, H. Hypoxia induces membrane depolarization and potassium loss from wheat roots, but does not increase their permeability to sorbitol. J. Exp. Bot. **1988**, *39*, 1169–1183.
4. Morard, P.; Maertens, C.; Bertoni, G.; Boisseau, Y. Influence de la respiration des racines sur l'absorption du potassium et des nitrates chez le blé. C. R. Acad. Sci. Fr. **1990**, *311*, 103–108.

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

ORDER REPRINTS

5. Bousqué, I.; Morard, P.; Silvestre, J.; Maertens, C. Influence de l'hypoxie racinaire localisée sur l'absorption minérale et la croissance racinaire du blé. C. R. Acad. Agric. Fr. **1992**, *3*, 81–92.
6. Bertoni, G.; Silvestre, J.; Llorens, J.M.; Morard, P.; Maertens, C. Effect of a transient anoxia on potassium uptake in cucumber. In *Optimization of Plant Nutrition*; Fragoso, M., Van Beusichem, M.L., Eds.; Kluwer Academic Publishers: Dordrecht, The Netherlands, 1993; 203–206.
7. Atwell, B.J.; Steer, B.T. The effect of oxygen deficiency on uptake and distribution of nutrients in maize plants. Plant Soil **1990**, *122*, 1–8.
8. Throught, M.C.T.; Drew, M.C. The development of waterlogging damage in wheat seedlings (*Triticum aestivum* L.). II. Accumulation and redistribution of nutrients by the shoot. Plant Soil **1980**, *56*, 187–90.
9. Tonutti, P.; Ranina, A. Oxygen concentration and ethylene production in roots and leaves of wheat: short term reaction in air after anoxic and hypoxic treatments. Physiol. Plant. **1991**, *81*, 295–300.
10. Waters, I.; Morelle, F.; Greenway, H.; Colmer, T.D. Effects of anoxia on wheat seedlings. J. Exp. Bot. **1991**, *42*, 1437–1447.
11. Schapira, A.; Morard, P.; Maertens, C. Echanges gazeux racinaires du concombre et de la tomate en culture hydroponique. C. R. Acad. Agric. Fr. **1990**, *76*, 59–66.
12. Drew, M.C. Oxygen deficiency and root metabolism: Injury and acclimation under hypoxia and anoxia. Annu. Rev. Plant Physiol. Plant Mol. Biol. **1997**, *78*, 223–250.
13. Lee, R.B. Inorganic nitrogen metabolism in barley root under poorly aerated conditions. J. Exp. Bot. **1978**, *29*, 693–708.
14. Botrel, A.; Magné, A.; Kaiser, W.M. Nitrate reduction, nitrite reduction and ammonium assimilation in barley roots in response to anoxia. Plant Physiol. Biochem. **1996**, *34*, 645–652.
15. Lee, R.B. The release of nitrite from barley roots in response to metabolic inhibitors, uncoupling agents, and anoxia. J. Exp. Bot. **1979**, *30*, 119–133.
16. Glaab, J.; Kaiser, W.M. Rapid modulation of nitrate reductase in pea roots. Planta **1993**, *191*, 173–179.
17. Ferrario, S.; Agius, I.; Morisot, A. Daily variations of xylemic exudates in tomato. J. Plant Nutr. **1992**, *15*, 69–83.
18. Ferrario, S.; Agius, I.; Morisot, A. Daily variations of the mineral composition of xylemic exudates in tomato. J. Plant Nutr. **1992**, *15*, 85–98.

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

ORDER REPRINTS

19. Morard, P.; Lacoste, L.; Silvestre, J. Effect of calcium deficiency on nutrient concentration of xylem sap of excised tomato plants. J. Plant Nutr. **2000**, *23*, 1051–1962.
20. Morard, P. *Les Cultures Végétales Hors Sol*; Publications Agricoles: Agen, France, 1995.
21. Morard, P.; Silvestre, J. Plant injury due to oxygen deficiency in the root environment of soilless culture: A review. Plant Soil **1996**, *184*, 243–254.
22. Chanprame, S.; Kuo, T.M.; Widholm, J.M. Soluble carbohydrate content of soybean (Glycine *max* Merr.) somatic and zygotic embryos during development. In Vitro Cell. Biol. Plant **1998**, *34*, 64–68.
23. Chirkova, T.V.; Belonogova, V.A. Nitrate reductase activity and productivity of grain crops under waterlogged conditions. Soviet Soil Sci. **1991**, *22*, 19–29.
24. Kaiser, W.M.; Huber, S.C. Post-translational regulation of nitrate reductase: Mechanism, physiological relevance and environmental triggers. J. Exp. Bot. **2001**, *52*, 1981–1989.
25. Urrestarazu, M.; Sanchez, A.; Lorente, F.A.; Guzman, M. Chronophysiological rhythm model for daily ionic variation of xylematic exudates in tomato plants. Commun. Soil Sci. Plant Anal. **1996**, *27*, 1843–1858.
26. Armstrong, M.J.; Kirkby, E.A. Estimation of potassium recirculating in tomato plants by comparison of the rates of potassium and calcium accumulation in the tops with their fluxes in the xylem stream. Plant Physiol. **1979**, *63*, 1143–1148.
27. Ho, L.C.; Adams, P. The physiological basis for high fruit yield and susceptibility to calcium deficiency in tomato and cucumber. J. Hort. Sci. **1994**, *69*, 367–376.
28. Monard, J.F. Variations au cours du cycle journalier de la composition minérale de l'exsudat caulinaire chez le lycopersicum racemigerum (Lange). C. R. Acad. Sc. Paris **1976**, *282*, 1519–1522.
29. Haynes, R.J. Active ion uptake and maintenance of cation-anion balance: A critical examination of their role in regulating rhizosphere pH. Plant Soil **1990**, *126*, 247–264.
30. Marschner, H. *Mineral Nutrition of Higher Plants*; Academic Press: London, UK, 1995.
31. Mengel, K.; Kirkby, E.A. Magnesium in physiology: Uptake and translocation. In *Principles of Plant Nutrition*; International Potash Institute: Bern, Switzerland, 1987; 482–488.

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Copyright © Marcel Dekker, Inc. All rights reserved.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

Downloaded by [Moskow State Univ Bibliote] at 17:55 09 December 2013

Request Permission or Order Reprints Instantly!

Interested in copying and sharing this article? In most cases, U.S. Copyright Law requires that you get permission from the article's rightsholder before using copyrighted content.

All information and materials found in this article, including but not limited to text, trademarks, patents, logos, graphics and images (the "Materials"), are the copyrighted works and other forms of intellectual property of Marcel Dekker, Inc., or its licensors. All rights not expressly granted are reserved.

Get permission to lawfully reproduce and distribute the Materials or order reprints quickly and painlessly. Simply click on the "Request Permission/ Order Reprints" link below and follow the instructions. Visit the U.S. Copyright Office for information on Fair Use limitations of U.S. copyright law. Please refer to The Association of American Publishers' (AAP) website for guidelines on Fair Use in the Classroom.

The Materials are for your personal use only and cannot be reformatted, reposted, resold or distributed by electronic means or otherwise without permission from Marcel Dekker, Inc. Marcel Dekker, Inc. grants you the limited right to display the Materials only on your personal computer or personal wireless device, and to copy and download single copies of such Materials provided that any copyright, trademark or other notice appearing on such Materials is also retained by, displayed, copied or downloaded as part of the Materials and is not removed or obscured, and provided you do not edit, modify, alter or enhance the Materials. Please refer to our Website User Agreement for more details.

Request Permission/Order Reprints

Reprints of this article can also be ordered at

http://www.dekker.com/servlet/product/DOI/101081PLN120030371