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ENHANCING NITROGEN USE EFFICIENCY OF POTATO AND CEREAL CROPS BY OPTIMIZING TEMPERATURE, MOISTURE, BALANCED NUTRIENTS AND OXYGEN BIOAVAILABILITY

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ENHANCING NITROGEN USE EFFICIENCY OF POTATO AND CEREAL CROPS BY OPTIMIZING TEMPERATURE, MOISTURE, BALANCED NUTRIENTS AND OXYGEN BIOAVAILABILITY

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□ Enhancement of nutrient use efficiency is imperative for increasing economic returns and reducing environmental pollution caused by fertilizer use in crop production systems. In this paper, we have demonstrated at a given soil temperature and nitrogen (N) rate, N loss via ammonia emission at 80% field capacity (FC) soil water regime in potato production was decreased by 58 to 81% compared to that at 20% FC, in two soils. In another study, N uptake by flooded corn (genotype: FR27 × FRMO17) seedlings with oxygen fertilization was 8-fold greater than that without oxygen fertilization. Nitrogen utilization efficiency of wheat (cv. ‘Yanzhong 144’) seedlings grown in a complete nutrient solution was 10-fold greater than that of the seedlings under low-phosphorus stress. It is concluded that appropriate management of soil water, oxygen fertilization, and of well-balanced nutrients supply significantly enhance N uptake and utilization efficiencies of corn and wheat, and minimize N loss.

Keywords: corn, oxygen fertilization, soil moisture, soil temperature, wheat

INTRODUCTION

After Liebig’s *Chemistry in Its Applications to Agriculture and Physiology* was first published in 1843 (Liebig, 2002), mineral fertilization gradually became a common practice in crop productions in the 1920s. It has become a routine practice in crop productions since 1950. Mineral fertilization has

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increased cereal yield from 2 metric tons (MT) per hectare in 1900 to 7.5 MT per hectare in 2000 (Roy et al., 2006). Fertilizer application contributes 43 percent of the 70 million MT of the nutrients taken up by crop production across the world. As the native fertility of the soils depletes the above percentage will increase to 84 percent (Fresco, 2003a, 2003b). Thus, the world's crop production will become increasingly dependent on mineral fertilization (Fresco, 2003b). In 2009, the mineral fertilizer use of the world is 163.2 MT nutrients [nitrogen (N), 101.0; phosphorus pentoxide (P_2O_5), 37.2; potassium oxide (K_2O), 25.0 MT] (Heffer and Prud'homme, 2009) and the world population is 6.8 billion including 139 million newly born babies (Population Reference Bureau, 2009). This means the average use of mineral fertilizer is 24 kg per human this year. If we convert this average value into materials such as 10-10-10 fertilizers that indicates every person used 80 kg of fertilizers in 2009. However, mineral resources used for fertilizer production are being rapidly depleted. For example, some predictions indicate phosphate rock will be depleted in another 70 years (Raghothama, 1999). As the need for food production increases with an increasing population growth, it is important that strategies are developed to enhance the nutrient uptake and utilization efficiencies.

Last decade, nitrogen (N) fertilizer price increased by fivefold but cereal grain price increased only a little. In 1999, selling one MT of paddy rice was able to purchase 4 MT of urea, but in 2008, the same amount of paddy rice was able to buy only 0.9 MT of urea (FAOSTAT, 2008). The producers have to face low profit challenges in crop production systems. On the other hand, application of fertilizers causes negative environmental impacts in excess of crop requirement in addition to depletion of non-renewable mineral resources.

Environmental factors significantly affect nutrient influx and use efficiency by various crops. Nutrients retained in the soil particles after fertilization can be absorbed and used by plants. Among the plant nutrients applied to the soil, N is the only essential element that volatilizes into the atmosphere as ammonia (NH_3). Consequently, NH_3 is the third most abundant N gas [after dinitrogen (N_2) and nitrous oxide (N_2O)] in the atmosphere (Liu et al., 2007c). Ammonia volatilization from fertilizers applied to crops and from livestock waste, contributes about 90% of global NH_3 emission (Schlesinger and Hartley, 1992; Ferm, 1998). Thus, NH_3 volatilization not only causes N loss, reduction in N influx and use efficiencies but also exacerbates air quality and human well-being. Soil pH, water regimes, and temperature are important factors influencing NH_3 volatilization from agricultural soils (FAO, 2001; Fenn and Hossner, 1985; Fenn and Kissel, 1973; He et al., 1999; Liu et al., 2007b). Thus, soil water and fertilizer management is important for enhancing N uptake and utilization efficiency via reducing NH_3 volatilization.

Also, different abiotic or biotic stresses during the plant growth and development influence nutrient uptake ability to store nutrients regardless of the soils (Hirt, 2009). For example, hypoxia caused by flooding due to heavy rainfall or over irrigation is a world-wide stress affecting crop production systems (Athar and Ashraf, 2009). Hypoxic stress reduces crop growth and decreases N uptake by crop plants and hence, reduces N utilization efficiency.

Additionally, nutrient imbalances in the root environment influences uptake of a single nutrient which may be abundant. Very recently, Vitousek et al. (2009) concluded that “nutrient additions to intensive agricultural systems range from inadequate to excessive and both extremes have substantial human and environmental costs”. Their findings show that nutrient imbalance is a serious problem in soils in the Midwest USA, North China, or Western Kenya. But how much do nutrient imbalances influence N use efficiency? In this paper, we discuss the role of (i) optimal soil water regime for minimizing N loss via NH_3 volatilization from fertilized soils for potato production systems; (ii) oxygen fertilization to enhance N influx in hypoxic conditions; and (iii) balanced nutrient availability on N utilization efficiency.

MATERIALS AND METHODS

Affects of Soil Temperature and Moisture on NH_3 Volatilization

Warden Silt Loam (WSL, Coarse-silty, mixed, mesic, Xerollic Camborthids, dark grayish-brown soil) soil was sampled (0–15 cm) from the Columbia Basin potato production region in south central Washington. This area of the state is well known for production of high potato yields in the nation and the world, as evident from high yield of 70 to 80 Mg ha^{-1} and a mean yield of 60 Mg ha^{-1} (Liu et al., 2007b). The soils are sandy (sand content $\geq 95\%$), well drained and the growing period is characterized by lack of cloud cover, high day time temperature followed by cool nights. The mean annual precipitation is about 150 mm, therefore, highly dependent on irrigation for crop production. Krome Gravelly Loam (KGL, loamy-skeletal carbonic, hyperthermic Lithic Udorthents) was collected (0–15 cm) from a commercial potato farm in South Florida. The annual rainfall of this region is 980 to 1651 mm. For a given soil (as described above), 300 g (dry weight) of the soil was placed in an incubation bottle (Figure 1). The surface area of the bottle was $\sim 60 \text{ cm}^2$.

The experiment had a factorial design with two soils \times four N sources (including the control without fertilization) \times three temperatures (maximum, mean, and minimum temperatures in the Columbia Basin potato production region) \times two water regimes (20% and 80% FC) \times three replications which resulted in 144 total incubation bottles. Each of the incubation bottles with the above treatments was placed in a sealed plastic Ziploc storage bag

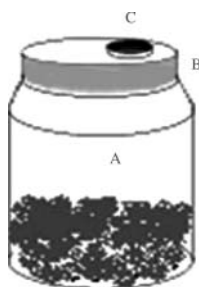


FIGURE 1 A schematic diagram of the apparatus used to trap ammonia emission from fertilized soils (Liu et al., 2007b). A: N was applied using a stock solution of either $(\text{NH}_4)_2\text{SO}_4$, $(\text{NH}_2)_2\text{CO}$, or NH_4NO_3 on equivalent to 75 kg ha^{-1} . Soil water content was adjusted to either 20% or 80% field capacity (FC) of the respective soil. B: A sponge moistened with $800 \mu\text{l}$ NH_3 trapping solution (He et al., 1999) was inserted in the mouth of the bottle to trap the volatilized ammonia. C: A small sponge spiked with $150 \mu\text{l}$ NH_3 trapping solution was inserted into a short pour spout of the screw cap on the bottle to protect the bottle from any contaminations from the outside air. The bottles were incubated at either 11, 20, or 29°C . Ammonia volatilization was measured on Day 1, 3, 7, 14, or 28 of incubation (Liu et al., 2007b).

($23 \text{ cm} \times 30 \text{ cm}$) and maintained in incubators (Precision Incubator, 6DM, THELCO[®] High Performance Incubators, Precision, Ottawa, Canada).

Ammonia Analyses

The concentration of $\text{NH}_4\text{-N}$ was determined in AutoAnalyzer III (Bran+Luebbf GmbH, Werkstrasse, Norderstedt, Germany) according to Environmental Protection Agency (EPA), Method 350.1 (Alpkem Corporation, 1989; EPA, 1993).

Oxygen Bioavailability vs. N Use Efficiency

Culture Methods

Corn seeds (genotype: FR27 \times FRMO17) were germinated and the corn plants grown in aeroponics in Yan's recipe (Yan et al., 1998) with a little modification: the full-strength nutrient solution had the following composition: 1 mM ammonium nitrate (NH_4NO_3), 0.2 mM sodium phosphate (NaH_2PO_4), 1 mM potassium sulfate (K_2SO_4), 2 mM calcium chloride (CaCl_2), 3 mM magnesium sulfate (MgSO_4), $0.2 \mu\text{M}$ boric acid (H_3BO_3), $0.2 \mu\text{M}$ copper sulfate (CuSO_4), $0.01 \mu\text{M}$ ammonium molybdate [$(\text{NH}_4)_6\text{Mo}_7\text{O}_{24}$], $5 \mu\text{M}$ manganese sulfate (MnSO_4), $0.2 \mu\text{M}$ zinc sulfate (ZnSO_4), $200 \mu\text{M}$ iron (Fe)-ethylenediaminetetraacetic acid (EDTA), and 0.3 mM silicon (Si) (as sodium silicate, Na_2SiO_3 , Epstein, 1994) for 5 days at 26°C , 60% relative humidity and at light density of $550 \mu\text{mol photon m}^{-2}\text{s}^{-1}$ (photosynthetically active radiation, PAR) in the growth cabinet manufactured by Percival Scientific, Inc. (Perry, IA, USA). The day/night regime was 14 hr light/10 hr dark. The uniform seedlings were chosen and divided into two groups. Each plant was

transferred into hydroponics in a plastic pot with 1800 mL measuring solution containing 1 mM NH_4NO_3 and 0.2 mM CaCl_2 with or without oxygen fertilizer (OF, 0.1 mL 1 mM H_2O_2) for two days before scanning a root.

Root Scanning

The roots were then scanned along approximately 16 mm from the root tip using a pH sensitive microelectrode. The microelectrodes were made using glass capillaries. Untreated 1.5 mm borosilicate glass capillaries, 10 cm long, were pulled into two microelectrodes each using a Flaming & Brown type micropipette puller (Sutter P-97, Novato, CA, USA) at 545°C. The tip of the microelectrode was approximate 2 to 3 microns in diameter. The freshly pulled microelectrodes were silanized with N, N-Dimethyltrimethylsilylamine in oven at 200°C over night (Porterfield, 2002). Microelectrodes were back-filled with H^+ probe backfilling solution containing 50 mmol L^{-1} KCl and 50 mmol L^{-1} HK_2PO_4 (Porterfield, 2002). Then hydrogen ionophore I - Cocktail B was drawn into the tip with a minimal negative pressure under a binocular compound microscope. For the microelectrode system (Applicable Electronics, Forestdale, MA, USA), the values of $[\text{H}^+]_1$ and $[\text{H}^+]_2$ are proton concentration of either near root surface or far root surface and calculated by the automated scanning electrode technique (ASET) software (Science Wares, Inc., Falmouth, MA, USA) using the following equations (Porterfield et al., 2009):

$$[\text{H}^+]_1 = 10^{E_1 - \frac{b}{s}} \quad (1)$$

$$[\text{H}^+]_2 = 10^{E_2 - \frac{b}{s}} \quad (2)$$

$$[\text{H}^+]_{ef} = [\text{H}^+]_1 - [\text{H}^+]_2 \quad (3)$$

where E_1 and E_2 is potential measured at near root surface, and far root surface, respectively (mV), b is y -intercept of the Nernst plot (mV), and s slope of the Nernst plot ($\text{mV} \log[\text{H}^+]^{-1}$). $[\text{H}^+]_{ef}$ is effluxed proton concentration from root surface.

Active uptake nutrients by plants are considered to occur via antiporter or symporter (Pinton and Varanini, 2007). For example, uptake of one NH_4^+ or K^+ ion by a plant leads to uptake of one hydroxyl (OH^-) or bicarbonate (HCO_3^-) ion (through a symporter) or extrusion of one H^+ (through an antiporter) in order to maintain electrical neutrality of cells. The net result of either symport or antiport is the same: medium is acidified and hence pH goes down. Thus, ammonium (NH_4^+) or K^+ uptake is considered to be closely associated with and reflected reduced pH of growth medium. Therefore, changes in growth medium pH can be an indirect indicator of $\text{NH}_4\text{-N}$ or K^+ absorbance. Changes in growth medium pH were used to evaluate and identify potassium efficient barley genotypes from crop gene

banks (Glass et al., 1981). Taylor and Bloom (1998) reported that there was a strong correlation between net proton extrusion and net uptake of NH_4^+ on corn. Therefore, this ad hoc index is used to compare with $\text{NH}_4\text{-N}$ uptake by corn seedlings with or without oxygen fertilization.

Soil Nutrient Balancing vs. N Use Efficiency

Split Root Experiment

Wheat seeds (cv. 'Yanzhong 144') were soaked for 24 hr in MilliQ water for germination and 3 days at 25°C in a growth chamber until the root length was about 5 cm. Twenty four pots each with a volume of 1200 mL were assembled in twelve pairs. One seedling was planted in each pair of pots. For this purpose 12 uniform and healthy seedlings were chosen and their primary roots were arranged into essentially two equal parts, and each part was placed into one of a pair of pots. The seedlings were stabilized with plastic foam board, which covered the openings of the pair of pots. The pots in each pair were kept about 5 mm apart from each other in order to avoid contamination. The left and right pots had different contents. Hence, there were four treatments including the control: (i) The control: $[\text{CNS}][\text{H}_2\text{O}]$; (ii) treatment 1: $[\text{CNS-P}][\text{H}_2\text{O}]$; (iii) treatment 2: $[\text{CNS-P} + \text{TCP}][\text{H}_2\text{O}]$; and (iv) treatment 3: $[\text{CNS-P}][\text{H}_2\text{O} + \text{TCP}]$. CNS = Complete nutrient solution, CNS-P = Complete nutrient solution without phosphorus, TCP = Tri-calcium phosphate. The CNS solution was used based on Ponnampereuma's recipe (Ponnampereuma, 1976) with silicon (Epstein, 1994) in mM: 1.429 NH_4NO_3 , 0.323 $\text{NaH}_2\text{PO}_4\cdot\text{H}_2\text{O}$, 1.026 K_2SO_4 , 1.000 CaCl_2 , 1.646 $\text{MgSO}_4\cdot 7\text{H}_2\text{O}$, 0.090 Fe(II)EDTA , 0.020 $\text{MnCl}_2\cdot\text{H}_2\text{O}$, 5.21×10^{-4} $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24}\cdot 4\text{H}_2\text{O}$, 1.07×10^{-3} $\text{ZnSO}_4\cdot 7\text{H}_2\text{O}$, 1.85×10^{-2} H_3BO_3 , 1.57×10^{-4} CuSO_4 , and 0.356 Na_2SiO_3 . The application rate for TCP was approximate 100 mg per pot.

Each wheat seedling was grown hydroponically in 2400 ml of culture solution (1200 ml per pot) for three weeks (Liu et al., 2007a) (Figure 2).

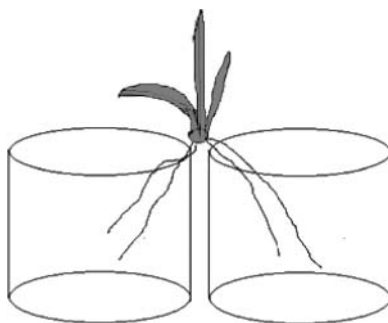


FIGURE 2 Setup of the split root experiment. Both left and right pots had different contents: culture solution or water with or without TCP.

One ml of nutrient stock solution was added to the left-side pot of each pair of pots on the 1st, 8th, and 15th day. Sodium dihydrogen phosphate (SDP) was the soluble P source added to the left-side for the control. Tricalcium phosphate (TCP) was the insoluble phosphate compound used for the treatments. One ml extra mM Ca^{2+} as CaCl_2 was always added with TCP to further reduce the solubility of TCP. There were four treatments including the control. The setup of the split root experiment is shown in Figure 2. On the 21st day, all the seedlings were oven-dried for biomass measurement, and then submitted to P analysis.

Phosphorus Analysis

Plant materials were dried at 75°C for 48 hr, ground and digested using the wet method, and the P concentration was measured colorimetrically (Shimogawara and Usuda, 1995) with spectrophotometer (Model, DU 640, Beckman Instruments Inc., Fullerton, CA, USA). The culture solution was sampled for P-analysis on the 3rd day after the third addition of nutrient solution.

Nitrogen Use Efficiency Calculation

$$\text{AE}(\text{mg} \cdot \text{mg}^{-1}) = \frac{\text{B}}{\text{F}} \quad (4)$$

where AE means apparent use efficiency (mg mg^{-1}) of N, B is net biomass (mg) of an entire wheat plant and F denotes applied amount (mg) of fertilizer N.

$$\text{RE}(\%) = \frac{\text{TAE}}{\text{CAE}} \times 100 \quad (5)$$

where RE represents relative use efficiency of N (%), TAE means apparent use efficiency of N of the treatments, CAE is the apparent use efficiency of N of the control.

All the measurements were replicated three times.

Statistical Analysis

The Statistical Analysis System (SAS) package (version 9.1.3, SAS Institute, Cary, NC, USA) was used. The data were tested by Duncan's Multiple Range Test ($\text{LSD}_{2, 0.05}$) with a statistical significance of $P \leq 0.05$.

TABLE 1 Ammonia volatilization as percentage of applied N from various N sources applied to two soils under different water regimes and soil temperatures

N source/ Temperature	Krome gravelly loam			Warden silt loam		
	20% (A)	80% (B)	A/B	20% (A)	80% (B)	A/B
(NH ₄) ₂ SO ₄						
11°C	20.1 b*	4.3 b	4.7	1.1 c	0.4 b	2.5
20°C	25.7 a	6.3 a	4.1	1.6 b	0.3 b	4.8
29°C	23.8 a	6.7 a	3.6	8.0 a	3.4 a	2.4
LSD _{2, 0.05}	3.02	0.74		0.37	0.20	
(NH ₂) ₂ CO						
11°C	12.3 c	2.2 b	5.5	12.1 a	1.8 b	6.8
20°C	24.2 a	3.1 a	7.8	10.7 b	1.7 b	6.1
29°C	16.8 b	3.5 a	4.9	10.5 b	3.3 a	3.2
LSD _{2, 0.05}	1.75	0.65		1.08	0.60	
NH ₄ NO ₃						
11°C	7.9 b	1.9 c	4.1	0.8 c	0.3 b	3.1
20°C	13.1 a	3.0 b	4.4	1.4 b	0.2 c	6.7
29°C	12.0 a	3.7 a	3.2	8.5 a	1.5 a	5.8
LSD _{2, 0.05}	1.49	0.31		0.34	0.02	

*The mean followed by different letters under the same fertilizer in the same column differs significantly at $P < 0.05$.

RESULTS

Soil Temperature and Moisture vs. N Use Efficiency

Ammonia volatilization at 20% FC soil water regime was 3- to 8-fold and 2- to 7-fold greater than that at 80% FC, in the KGL and WSL soils, respectively (Table 1). N loss at 11°C was significantly ($P < 0.05$) lower than that at 29°C across both water regime and soils except the WSL soil amended with urea at 20% FC. Similarly, in most of the cases, percentage of N loss at 11°C was significantly lower than that at 20°C. In the KGL soil, NH₃ emission was greater from (NH₄)₂SO₄ than that from the other two fertilizer sources. In the WSL soil, both (NH₄)₂SO₄ and urea were always more volatile than NH₄NO₃ except one case amended with (NH₄)₂SO₄ with at 29°C and 20%. Urea always volatilized more NH₃ than (NH₄)₂SO₄ except the one at 29°C and 80%. Additionally, between the two soils, the KGL soil emitted up to 19-, 2-, and 14-fold more NH₃ than the WSL soil amended with (NH₄)₂SO₄, urea and NH₄NO₃ across the three temperatures.

Oxygen Bioavailability and N Use Efficiency

Flooding, waterlogging, or hydric soil condition is a common hypoxic or even anoxic stress crop plants have to deal with in fields. The stressful condition not only impact growth and development of crop plants but also greatly reduces N and other nutrient uptake. The proton micro-measurements with

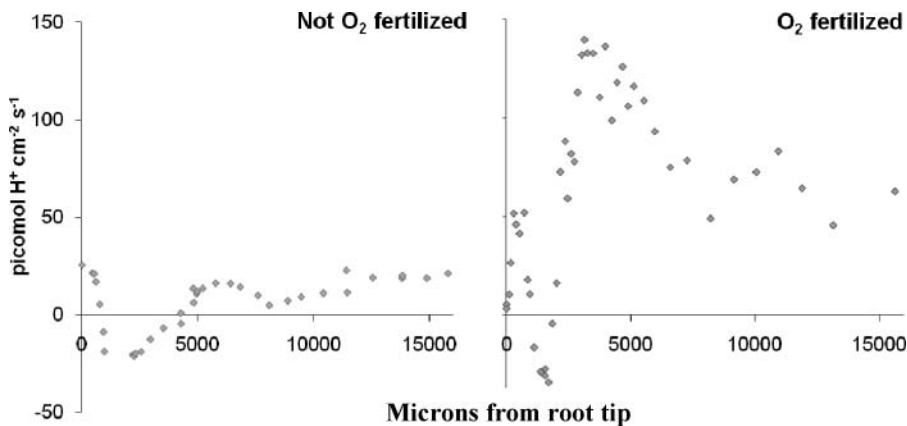


FIGURE 3 Dynamic changes in proton efflux of flooded corn roots with or without oxygen fertilization.

a self-referencing ion selective (SRIS) electrode show that hydroponic corn seedlings without aeration or oxygen fertilization have extruded only 20 picomol $\text{H}^+ \text{cm}^{-2} \text{s}^{-1}$ around 5000 microns from the root tip because the hypoxic seedlings cannot make enough ATP (Nicholls and Ferguson, 2002) to absorb ammonium (NH_4^+) from the growth medium. However, the seedlings with oxygen fertilization have extruded 150 picomol $\text{H}^+ \text{cm}^{-2} \text{s}^{-1}$ (Figure 3) around 5000 microns from the root tip (Liu et al., 2005). Furthermore, the uptake pattern with oxygen fertilization was different from that without oxygen fertilization. The uptake peak zone was after 5000 microns from the root tip without oxygen fertilization but that with oxygen fertilization was before 5000 microns (Figure 3).

Soil Nutrient Balancing vs. N Use Efficiency

Balancing soil nutrients is one of the key factors to nutrient use efficiency. Our split-root experiment with or without P indicates that N use efficiency of P-sufficient plants is up to 10 fold greater than that of P-deficient plants (Figure 4) grown in hydroponics (Liu et al., 2007a). Furthermore, P bioavailability of insoluble phosphates depends on the placement of this P source. P bioavailability was 253-fold greater when placed with the other nutrients than when placed separately (Figure 4). Correspondingly, the difference in their relative N use efficiency was 2.1 fold.

DISCUSSIONS

Nitrogen is an essential element required in abundance for plant growth and development. Among all the essential plant nutrients, N is the only one that has both extreme redox statuses, i.e., highly reduced (NH_4^+) and

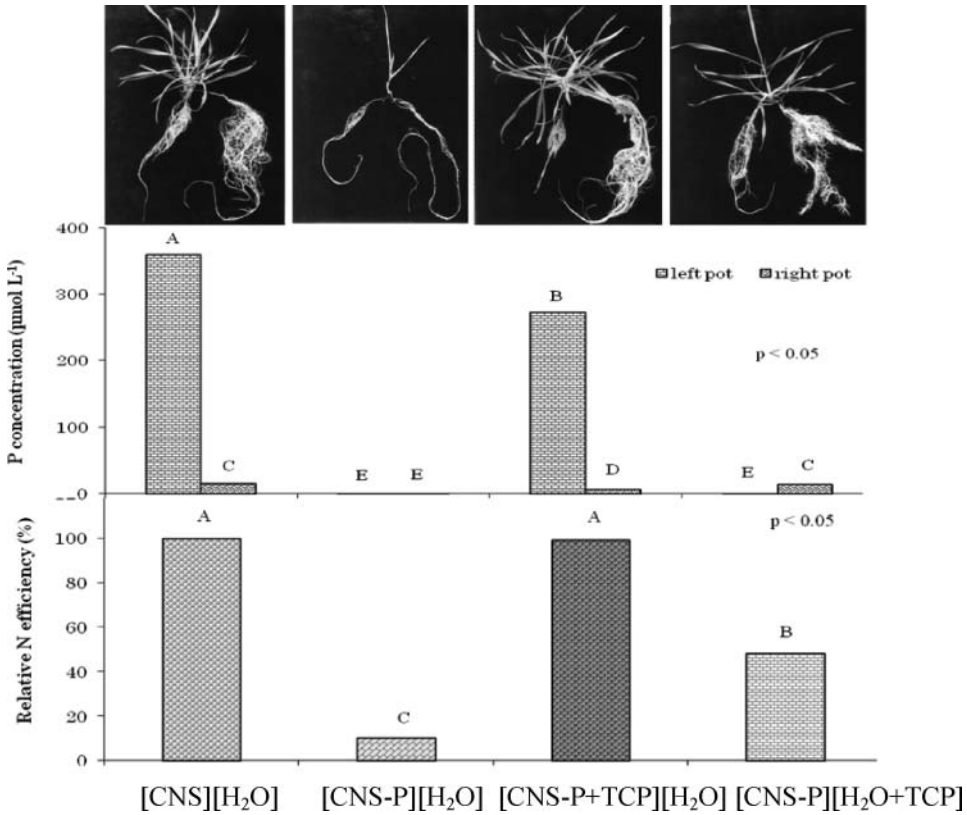


FIGURE 4 Relative N use efficiencies of wheat seedlings grown in a split root system and mobilization of an insoluble phosphate, tri-calcium phosphate as $\text{Ca}_3(\text{PO}_4)_2$ (TCP) by imbalance between cation and anion influxes by wheat plants. CNS = complete nutrient solution, TCP = tri-calcium phosphate.

oxidized (NO_3^-) with transformation from the former to the latter that occurs in the soil. Nitrogen loss can occur as gaseous emissions and as leaching of the ionic form. Both modes of loss negatively impact N uptake and utilization efficiency. These N losses occur in soil solutions, plant-soil interfaces, soil-air interfaces, and soil solution-air interfaces. Therefore, soil moisture, temperature, and oxygen bioavailability influence N uptake and utilization efficiency.

Soil Temperature and Moisture vs. N Use Efficiency

Optimal soil water regime significantly reduced N loss via NH_3 volatilization in both soils (Table 1) and thus could significantly enhance N use efficiency. Moisture quotient analysis showed that the real-time rate of NH_3 volatilization at 20% FC was up to 110 times greater than that at 80% FC in the identical soil condition (Liu et al., 2007c). Moisture quotient is defined

as a ratio of NH_3 emission rate at 20% FC to that at 80% FC at the same soil under the same temperature (Liu et al., 2007c). Compared to 20% FC soil water regime, 80% FC soil water regime ensured relatively low NH_4^+ concentration in the soil solution and favored less NH_3 volatilization from soil after N fertilization. Temperature effect on NH_3 volatilization was soil dependant. Temperature dependence was greater in the WSL soil than that in the KGL soil. The temperature quotients of NH_3 emission of the WSL soil were significantly different from those of the KGL soil (Liu et al., 2007d) among the three incubation temperatures. Temperature quotient is defined as a ratio of NH_3 volatilization rate at a higher soil temperature to that at a lower soil temperature (Liu et al., 2007d). Additionally, the KGL soil always has greater N loss than the WSL soil at each soil water regime or temperature. Principal component analysis (PCA) showed that soil type was the top factor governing NH_3 emission rate (Liu et al., 2011).

Oxygen Bioavailability and N Uptake Efficiency

As a common hypoxic or even anoxic stress crop plants have to deal with in fields under some production regimes, flooding, waterlogging, or hydric soil condition not only impacts growth and development of crop plants but also greatly reduces N and other nutrient uptake. The results of the proton micro-measurements with a self-referencing ion selective (SRIS) electrode showed that at 5000 microns from the root tip, the rate of proton extrusion by hydroponic corn seedlings without oxygen fertilization extruded protons was only a seventh that of the oxygen fertilized plants. This is probably the result of need for the hypoxic seedlings to run anaerobic respiration. Anaerobic respiration not only produces little ATP but also probably accumulates toxic products such as alcohol (Figure 5) (Angulo-Brown et al., 1995). Such effects would reduce the ability of the roots to absorb NH_4^+ from the growth medium (Liu et al., 2005). Oxygen fertilization ensures that the seedlings can produce ATP (Nicholls and Ferguson, 2002) which is prerequisite for NH_4^+ absorption. The ATP drives the electrogenic proton extrusion pump which results in a negative electropotential inside the cells relative to the soil solution. This electropotential gradient is an essential component in driving the absorption of NH_4^+ ions (Marschner, 1995). Ammonium transport across the plasma membrane into the cytoplasm in antiport or symport is therefore associated with the proton concentration in the growth medium. Thus, SRIS can indirectly measure NH_4^+ uptake via determining the proton concentration in the growth medium. The SRIS measurements reported here suggest that oxygen fertilization can greatly increase NH_4^+ uptake of flooded corn seedlings suffering from oxygen deficiency and hence enhance N uptake efficiency.

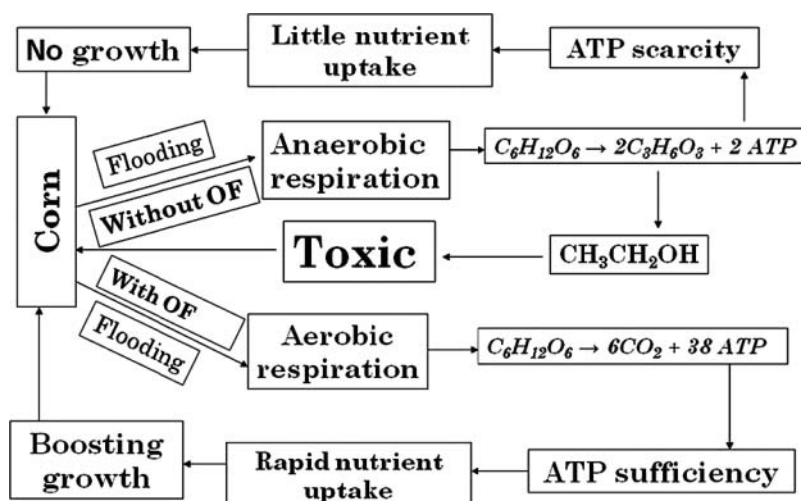


FIGURE 5 Possible mechanisms of ammonium uptake enhanced by oxygen fertilized corn plants under hypoxic stress. Oxygen fertilizer is abbreviated as OF. Theoretically, one mole of glucose can produce 36 to 38 moles of ATP in aerobic respiration but only two moles of ATP in anaerobic respiration (Angulo-Brown et al., 1995; Porter and Brand, 1995).

Soil Nutrient Balance and N Use Efficiency

Balanced nutrient availability in the root environment is a key factor influencing nutrient use efficiencies. In practice, nutrient imbalance is common. For example, in both the Midwest USA and North China, the ratio of applied N to P is about 7:1 and 6:1 (Vitousek et al., 2009). The imbalance seriously reduces N use efficiency. The results of this root-split experiment with or without P indicated that N use efficiency of P-balanced wheat plants was significantly greater than that of the P-imbalanced plants (Figure 4). Additionally, P bioavailability of insoluble phosphates depends on the placement of the applied fertilizer (Liu et al., 2007a). Insoluble phosphates have greater P bioavailability when they are placed with the other nutrients than they are separated from the other nutrients (Figure 4). In crop production practices, synchronous application of fertilizers with various nutrients can ensure placing phosphorus with other nutrients. This may not only enhance P bioavailability and utilization efficiency but also benefit N utilization efficiency. Thus, the data of this study may suggest that application of complex fertilizers is advantageous both in improving N and P use efficiencies and in mobilizing insoluble phosphates over that of single nutrient fertilizers in crop productions if they are not applied together.

CONCLUSIONS

Soil water regime, oxygen bioavailability, and fertility are important factors in enhancing nutrient use efficiency to optimize crop production and

quality. Based on the data presented above, we conclude that: (i). Low soil water regime significantly increased NH_3 volatilization from applied N fertilizers. Optimal water management is a key to reduce N loss via NH_3 emission and hence improves N use efficiency; (ii). Oxygen fertilization significantly improved NH_4^+ influx of hypoxic corn plants and thus can significantly enhance N uptake efficiency; (iii). Balanced application of all nutrients significantly enhanced N uptake and utilization efficiency as compared to that in the absence of a single nutrient.

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