Potassium and nitrogen poising: Physiological changes and biomass gains in rice and barley

D. T. Britto, K. D. Balkos, A. Becker, D. Coskun, W. Q. Huynh, and H. J. Kronzucker[1]

University of Toronto, Department of Biological Sciences, 1265 Military Trail, Toronto, Ontario, Canada M1C 1A4.

Britto, D. T., Balkos, K. D., Becker, A., Coskun, D., Huynh, W. Q. and Kronzucker, H. J. 2014. **Potassium and nitrogen poising: Physiological changes and biomass gains in rice and barley**. Can. J. Plant Sci. **94**: 1085–1089. Soil nitrogen, potassium, and water are three of the most important factors influencing, often interdependently, the growth of plants. Maximizing plant growth is not simply a matter of maximizing the availability of these and other nutrients; indeed, excess supply can be deleterious to plant performance. Rather, optimal performance may come about by adjusting the supply of each of the disparate factors required for plant growth, not only individually, but in relation to one another. In our work investigating the nutritional maximization of plant growth, we have found that altering the ratios of N and K provided to seedlings of cereal grasses can result in very substantial increases in vegetative biomass accrual, e.g., $>220\%$ of low-K^+ controls, in short-term studies with rice, the world's most important cereal grain, and even greater gains in grain yield, in the longer term. Hence, the findings in our laboratory are of direct relevance to the aim of NSERC's Green Crop Network, which was to contribute to the amelioration of climate change by improvement of carbon capture and sequestration in crop plants. In addition, these findings may help to increase the world's food supply, the security of which is sometimes at odds with proposed means to thwart climate change. Our work in this area has also led to a potential breakthrough of a more fundamental sort in plant nutritional biology, which may in itself have important practical implications: evidence that aquaporin-type transport proteins conduct rapid NH_3 fluxes into roots at toxic levels of external ammonia/ammonium.

Key words: Yield, water-use efficiency, nitrogen, potassium, cereals, aquaporins

Britto, D. T., Balkos, K. D., Becker, A., Coskun, D., Huynh, W. Q. et Kronzucker, H. J. 2014. **Équilibrage du potassium et de l'azote : modifications physiologiques et augmentation de la biomasse chez le riz et l'orge**. Can. J. Plant Sci. **94**: 1085–1089. L'azote, le potassium et l'eau présents dans le sol sont les trois paramètres les plus importants à influer, souvent de façon interdépendante, sur la croissance des plantes. Optimiser la croissance des végétaux ne se borne pas à mettre la plus grande quantité de ces éléments nutritifs à leur disposition; à dire vrai, un excès a parfois des effets néfastes sur la performance de la plante. On parviendra plutôt à un rendement optimal en ajustant les apports de chaque facteur dont la plante a besoin pour croître, non seulement séparément, mais aussi en rapport les uns avec les autres. Dans leurs recherches sur l'optimisation de la croissance des plantes par la nutrition, les auteurs ont découvert qu'en modifiant le ratio de N et de K dont disposent les plantules de céréales, on peut augmenter de façon très appréciable la biomasse végétative accumulée, à savoir plus de 220 % comparativement aux cultures témoins recevant peu de K^+ dans les études à court terme sur le riz, principale céréale cultivée dans le monde; les gains peuvent même être supérieurs à plus longue échéance. Les constatations réalisées en laboratoire par les auteurs ont une pertinence directe pour les objectifs du Réseau des cultures vertes du CRSNG, programme qui vise à freiner le changement climatique par un captage plus important et une meilleure séquestration du carbone par les cultures. De plus, ces constatations pourraient contribuer à améliorer les approvisionnements d'aliments sur le globe, approvisionnements dont la sécurité se bute parfois aux moyens envisagés pour contrer le changement climatique. Enfin, les travaux des chercheurs dans ce domaine pourraient déboucher sur une percée de nature plus fondamentale en biologie de la nutrition des plantes, ce qui aurait éventuellement d'importantes répercussions d'ordre pratique: la preuve que les protéines de transport comme l'aquaporine amènent rapidement le NH_3 acheminé aux racines à un taux de toxicité externe pour l'ammoniac/ammonium.

Mots clés: Rendement, efficacité de l'utilisation de l'eau, azote, potassium, céréales, aquaporines

N SOURCE, K SUPPLY, AND PLANT GROWTH

In the case of the nitrogen nutrition of plants, a special complication is that there are numerous possible sources of N. In particular, of the two major inorganic N sources, ammonium (NH_4^+) and nitrate (NO_3^-), the former can be deleterious to many plant species when present in the high levels that can be found in both natural and man-made ecosystems, while, less commonly, the latter cannot be utilized (or only poorly) by some species of agronomic and silvicultural importance

[1]*Corresponding author (e-mail: herbertk@utsc.utoronto.ca).*

Abbreviations: GS, glutamine synthetase; **PEPcase**, phosphenol pyruvate carboxylase; **WUE**, water-use efficiency

(Kronzucker et al. 1997, 2003; Magalhaes and Huber 1989; Britto and Kronzucker 2002). Various hypotheses have been advanced to explain ammonium toxicity in plants, but none appears to be completely satisfactory (Britto and Kronzucker 2002; Qin et al. 2008; Li et al. 2010, 2011; Zou et al. 2012). A decade ago, we discovered a new piece in the puzzle of ammonium toxicity, that of rapid, futile cycling of NH_4^+ across the membranes of root (Britto et al. 2001; Kronzucker et al. 2003) and leaf (Britto et al. 2002) cells, which occurs in the presence of elevated (toxic) levels of ammonium. Indeed, the apparent flux of NH_4^+ into root cells exceeds virtually all known ion fluxes across the plasma membrane (for a given substrate concentration), and, moreover, is accompanied by a concomitant efflux from root to soil that is nearly as pronounced (Britto and Kronzucker 2006). This phenomenon was hypothesized to cause toxicity via the cellular energy burden brought about by the maintenance of the active-transport component of the cycle (i.e., the efflux of NH_4^+), and because of the resultant high intracellular accumulation of NH_4^+, which is likely to be, in itself, toxic, due to the displacement of other cations (van Beusichem et al. 1988; Kronzucker et al. 2001; see, however, Zou et al. 2012). Thus, the concept that NH_4^+ toxicity is related to the transport and accumulation of this ion became the first point of examination for our Green Crop Network project. A second point was an investigation of the intriguing possibility that "NH_4^+" fluxes in the toxic range are catalyzed by water channels (aquaporins) that may in fact conduct NH_3 transport at high rates[1] (Jahn et al. 2004). A third point, as yet in the preliminary stage, is the investigation of the poorly understood promotion of growth by provision of mixed inorganic N (e.g., Heberer and Below 1989; Kronzucker et al. 1999).

The elevation of K^+ supply is well known to alleviate NH_4^+/NH_3 toxicity in many plant species (Barker et al. 1967; ten Hoopen et al. 2010). This process is not well understood, but one cause of this might be relief from the potassium deficiency brought about by NH_4^+/NH_3 nutrition in many plants (Britto and Kronzucker 2002). From a different perspective, elevated K^+ might alleviate toxicity by reducing NH_4^+/NH_3 transport and accumulation. We investigated this second idea by examining the effects of altered K^+ provision on fluxes and compartmentation of NH_4^+/NH_3 into, and out of, roots of barley and rice seedlings, by use of the positron emitting radiotracer ^{13}N (Szczerba et al. 2008; Balkos et al. 2010). We found that elevating K^+ supply profoundly reduced the futile cycling components, and accumulation of, NH_4^+/NH_3 in roots of rice and barley, by as much as 76% (Table 1). In addition, the reduction of the futile cycle was very rapid, which suggests that there is a direct effect of K^+ on the transport function. Similarly, ten Hoopen et al. (2010), using extracellular microelectrodes, found

a negative relationship between root K^+ and NH_4^+/NH_3 fluxes in *Arabidopsis* and barley. In our study, net NH_4^+/NH_3 acquisition (the resultant of the inward and outward fluxes) was also reduced in barley, by about 25%, but not in rice, which, surprisingly, showed a slight increase in net NH_4^+/NH_3 flux; in both species, the decline in tissue NH_4^+/NH_3 was nevertheless very substantial (Table 1; also see below). The high root respiration normally seen under high NH_4^+/NH_3 supply was strongly reduced in barley, though not in rice; this is consistent with the demonstration that root respiration increases significantly in barley under NH_4^+/NH_3 stress and cycling, but not in rice (Britto et al. 2001).

In addition, in rice seedlings, elevated K^+ greatly stimulated the activities of glutamine synthetase (GS) and phosphenol pyruvate carboxylase (PEPcase), two key enzymes involved in NH_4^+/NH_3 assimilation:

1. GS: Glutamate $+ NH_3 + ATP \rightarrow$ Glutamine $+ ADP + P_i$
2. PEPcase: Phosphoenolpyruvate $+ HCO_3^- \rightarrow$ Oxaloacetate $+ P_i$

Glutamine synthetase catalyzes the main reaction by which NH_3/NH_4^+ is incorporated into organic N, while PEPcase catalyzes the anapleurotic synthesis of TCA intermediates by incorporating inorganic carbon into organic acids that can be used as C-skeletons for further assimilation of NH_4^+/NH_3 by GS. The upregulation of these two enzymes by high K^+ in our study was not determined in barley. It was, however, confirmed in a study by Roosta and Schjoerring (2008) in cucumber plants. These findings can help explain the observation that internal (and potentially toxic) pools of NH_4^+/NH_3 were substantially reduced in rice (Table 1), even though net acquisition of NH_4^+/NH_3 was slightly increased; they could also potentially explain the much greater decline in

Table 1. Effects of elevating K^+ supply on key aspects of NH_4^+ transport, accumulation, and plant performance in seedlings of rice and barley. Adapted from Szczerba et al. (2008) (for barley), and Balkos et al. (2010) (for rice). Percentage increases or decreases are in plants grown at 5 mM K^+, relative to those grown at 0.1 mM K^+ (except where indicated by * – these differences are between 1.5 mM and 0.1 mM K^+-treated plants)

	Rice	Barley
NH_4^+ influx (CATE)	−38%	−63%
NH_4^+ influx (DI)	−49%	−61%
NH_4^+ efflux	−25%	−76%
NH_4^+ net flux	+8%	−25%
Tissue NH_4^+ (root)	−45%	−68%*
Tissue NH_4^+ (shoot)	−68%	−73%*
Rapidity of effect on influx	Immediate	Immediate
Rapidity of effect on efflux	ND[z]	Immediate
Effect on respiration	−28%	−33%
Effect on growth	+120%	+49%
Change in protein content	+25%	ND
Change in PEPcase activity	+331%	ND
Change in GS activity	+61%	ND

[z]ND, not determined.

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[1] For this reason, "NH_4^+" will be referred to as "NH_4^+/NH_3" in the remainder of this paper.

tissue NH_4^+/NH_3 in barley seedlings, as compared with the decline in net NH_4^+/NH_3 flux. These intriguing results, which may lie at the centre of the alleviation from NH_4^+/NH_3 toxicity by K^+, were attributed in the case of rice to the increased assimilation of NH_4^+/NH_3 into organic nitrogen by the increased activities of PEP carboxylase and GS (see Givan 1979). This attribution was substantiated by the greater incorporation of nitrogen into protein in high-K^+ rice plants (Table 1).

Most importantly, from the perspective of the GCN, changes in the nutritional physiology of rice and barley plants brought about by elevated K^+ supply translated into increases in vegetative biomass in the short-term (Table 1, Fig. 1). Importantly, in the case of rice, this increase was greater under NH_4^+/NH_3 provision than that observed with NO_3^- provision, at the same level of external K^+. However, what is even more striking is the effect of long-term supply of NH_4^+/NH_3 and elevated K^+ on the grain yield and water-use efficiency (WUE) of rice plants. Table 2 shows preliminary data which indicate that the number of seeds per panicle, and the seed weight, were both substantially increased in the elevated K^+ condition. As well, we have good indications that more panicles per plant developed under high K^+, resulting in a possible threefold increase in total yield. This staggering gain was accompanied by an apparently much higher agronomic WUE, which may be more than twice as great in high-K^+ plants. We hypothesize that this latter effect is related to aquaporin function and, in turn, its relation to NH_4^+/NH_3 fluxes, to which we shall now turn.

AQUAPORINS AS MEDIATORS OF AMMONIA INFLUX

On the basis of pharmacological data, it was initially proposed that the unusually high, K^+-sensitive, influx of NH_4^+/NH_3 into roots of both barley and rice plants was catalyzed by non-selective cation channels (NSCCs).

Fig. 1. Seven-day-old barley plants grown with 10 mM NH_4^+ and three levels of K^+: (left to right) 0.02, 0.1, and 5 mM.

Table 2. Increases in grain-yield parameters and agronomic water-use efficiency (WUE) in rice plants grown in hydroponic tanks, over 3 mo at two levels of K^+ (percentage increases in 1.5 mM-K^+-grown plants, relative to 0.1 mM controls)

Panicles per tank	+60%
Seeds per panicle	+73%
Weight per 100 seeds	+12%
Seed weight per tank	+208%
Water consumption per tank	+36%
Agronomic WUE	+127%

Recent discoveries that some aquaporins are capable of transporting NH_3, the uncharged conjugate base of NH_4^+, in both plant and animal cells (Jahn et al. 2007), however, have led us to reconsider the means of NH_3/NH_4^+ transport under toxic conditions. The significance of this substrate breadth has not so far been rigorously investigated in intact plants, but in our laboratory we have found substantial preliminary evidence supporting the involvement of aquaporins in the transport of NH_3 into roots of intact plants.

First, evidence that the main permeating species may be NH_3 and not NH_4^+ derives from a pH profile of ^{13}N influx, which shows an alkaline optimum. Second, application of the classic aquaporin blocker Hg^{2+} (Bramley et al. 2009) significantly reduced ^{13}N influx. Third, loading of roots with the membrane-permeating propionic acid resulted in a strong reduction of ^{13}N influx, consistent with the known pH-dependent closure of AQPs via the protonation of a conserved histidine residue on the cytosolic moiety of the protein (Törnroth-Horsefield et al. 2006; Ehlert et al. 2009). Fourth, saturating the root medium with nitrogen gas significantly reduced ^{13}N uptake, which might be explained by an anoxia-induced cytosolic acidification (Törnroth-Horsefield et al. 2006; Ehlert et al. 2009). Finally, we have also found evidence for the possibility that NH_3/NH_4^+ equilibration throughout the plant cell may be very rapid (consistent with intracellular trafficking catalyzed by aquaporins in the tonoplast and other organelle membranes). Taken together, these results suggest that an aquaporin-mediated pathway may be the major one responsible for the influx of NH_3/NH_4^+ (in the form of NH_3) into plant roots in the toxic range (Coskun et al. 2013).

The identification of aquaporins as key mediators of NH_3/NH_4^+ permeation into plants under toxic conditions will open up new possibilities for the alleviation of ammonium toxicity. One intriguing possibility in this regard relates to the downregulation of water flow by increased K^+ that is sometimes observed [e.g., Quintero et al. (2007) and in our own unpublished data on K^+-dependent hydraulic conductivity], an idea that may help explain the increased agronomic WUE of high-K^+ rice plants. If borne out, this finding could tie together effects of K^+ on both water flow and NH_3/NH_4^+ transport, in the context of aquaporin function.

CONCLUSION AND FUTURE DIRECTIONS

Our study shows that there is still much need for "classical" physiological investigation in the quest to solve biological problems and address pressing issues such as climate change and food security. Much work remains to be carried out to determine the changes in growth and yield of crop plants, brought about by elevated K^+ in a background of NH_4^+/NH_3. Long-term growth studies are presently ongoing, with additional intriguing, if preliminary, findings brought about through examination of the effects of combining inorganic N sources in addition to potassium optimization. These studies currently include trials with wheat in addition to barley and rice, and it will be very interesting to extend them to maize, another major Canadian crop, which is used for both food and biofuel production. As a C4 plant, maize has exceptionally high productivity, WUE, and leaf expression of PEP carboxylase (Harpster and Taylor 1986). Moreover, it is known to respond well to balanced N and K nutrition (Belay et al. 2002). It may turn out that the phenomena presented here are broadly applicable to most plant species, particularly in light of similar results from cucumber plants (Roosta and Schjoerring 2008), which are only distantly related to cereals. Thus, we predict that further experimentation with fertilizer poising in biofuel crops, among them both cereals (e.g. switch grass, *Panicum virgatum*) and non-cereals (e.g. *Jatropha curcas*), will likely yield powerful and practical insights.

In addition to exploration of productivity in food and fuel crops, many aspects of the fundamental physiological changes that plants undergo when exposed to high K^+ need to be elucidated. For example, little is known about the role of carbon in this scenario, not just in the context of anapleurotic CO_2 assimilation in roots and its potential role in the alleviation of toxicity, but also that of primary carbon fixation in photosynthesis with nutritional poising. Specific research questions in this area include: How does increased plant K^+ status enhance photosynthesis? Does it occur via improved stomatal control (a central role of K^+), increased N transport to the leaf (with K^+ as a counter-ion in NO_3^- transport; Ben Zioni et al. 1971), upregulation of pivotal enzymes, or, as we have suggested for rice (Britto and Kronzucker 2004), some combination of these? In addition, the patterns of gene expression and metabolic activity that accompany changes in K^+ nutrition are virtually unexplored, as are the effects of changing the expression of aquaporins, glutamine synthetase, and PEP carboxylase on NH_3/NH_4^+ tolerance and toxicity. Thus, a combination of genomic, proteomic, and metabolomic analyses will be essential to unravel the mechanisms underlying plant growth and yield under high-productivity nutritional poising.

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