Title

Sugar transport and nitrate reductase activity rate in roots affect plant adaptation to cold and warm climate plants

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Discussion

Plants assimilate in the root virtually all of the NH_4^+ and from 5 to 95% of the NO_3^- absorbed by the roots (Andrews 1986, Oaks and Hirel (1985). Nitrogen assimilation is an energy-intensive process in plants (Bloom et al. 1992), with shoots expending up to 25% of their respiratory energy on nitrogen assimilation (Bloom et al. 1989).

Nitrogen metabolism in a root cell is controlled by 2 fluxes:
1) Nitrate uptake rate from the external solution.
2) Transport rate of sugar from the leaves down to the finest root cells.

Ammonium in the cell forms α-amino glutamic acid according to the schematic equation:
$NH_4^+ + HCO_3^- + 1^1/_3\ C_6H_{12}O_6 + 3^1/_3 O_2 = C_5H_9O_4N + 4CO_2 + 6H_2O$.

Nitrate in the root have two alternative pathways:
1) Convert to α-amino glutamic acid in the root and consume the root sugar.
2) Transport to the leaves, where it is reduces to ammonia.

Sugar is used for cell respiration and nitrate reduction. When sugar transport to root cells is slower than its consumption for respiration and ammonium metabolism, the root cells will die immediately from ammonia toxicity as showed by Ganemore-Neumann and Kafkafi (1985).

The rate of sugar supply to the root is species dependent. The rate of sugar respiration is a function of root temperature. Moritsugu et al. (1983), demonstrated that at constant concentration of 5 mM ammonium in the nutrient solution the monocots grew well in the presence of either ammonium or nitrate sources, while Chinese cabbage and spinach plants died. Moritsugu and Kawasaki (1983) showed that when grown in 0.05 mol m^{-3} the plant produced equivalent growth to plants grown in 5 mM nitrate nutrition. The fact that at high ammonium concentration plant roots died but at low ammonium concentration the plant died suggests that the rate of sugar supply did not match the rate of ammonia accumulation in the root cells. For natural ecosystems, Andrews (1986) defined four general groups of plants with regard to the activity of their root nitrate reductase:
1) Temperate, perennial species growing at low soil nitrate concentrations (about 1 mol m^{-1}) - their nitrate assimilation is in the root.
2) Temperate, annual legume species growing at low soil nitrate - their nitrate assimilation is mostly in the root.
3) Temperate, annual non-legume species vary greatly in their partitioning of nitrate assimilation between root and shoot when growing in low external nitrate concentrations.
4) Tropical and subtropical species, annual and perennial. The partitioning of nitrate assimilation between root and shoot remains constant as external nitrate concentration increases.

All temperate legume species studied carry out most of their nitrate assimilation in the root at low external nitrate concentrations, but as external nitrate concentration is increased, shoot assimilation becomes increasingly important. In contrast, tropical legume species tend to carry out a substantial and constant proportion of their nitrate assimilation in the shoot regardless of external nitrate concentration (Andrews, 1986).

In tomato, low root temperatures result in nitrate accumulation in the roots, and a shortage of N transport to the leaves (Kafkafi, 1990). Both water and nitrate transports are inhibited by low root temperatures (Ali et al. 1994). The fraction of total nitrate reduction in plant roots is responsible for the natural distribution of plants between temperate and hot climates.

Nitrate reductase activity (NRA) in legume roots is relatively higher than that of the summer crop sunflower (van Beusichem 1989). Of the total 1175 $mmol_c$ of nitrate taken up by the roots of the pea plant, only 648 $mmol_c$ of nitrate (55% of all nitrate uptake) moved upward in the xylem flow, while in sunflower 86% of the nitrate uptake is transported to the leaves for reduction. Moritsugu et al. (1983) showed at 5 mol m^{-1} of N in the nutrient solution that at identical root temperature and at constant pH in the root zone, rice, barley, corn and sorghum, bean and cucumber grew very well on both nitrate and ammonium. However, tomato, lettuce, cabbage, carrot and radish grew better in the presence of nitrate. Chinese cabbage and spinach died when grown in a 5 mol m^{-1} ammonium solution. However these sensitive plants grew very well in the presence of ammonium that was kept constant at 0.05 mol m^{-1} in a nutrient solution (Moritsugu and Kawasaki 1983).

The results by Moritsugu et al. (1983) suggest that plants that transfer high sugar levels to the root can stand high root temperature and ammonium concentration in the soil or nutrient solution. The fact that the same plants grew very well at low ammonium concentration in the root zone but died at high ammonium in the solution stress the role of the rate of sugar supply to the roots in plant adaptation to changes in nitrogen form in the root zone. Based on the observations of Andrews (1986) on the distribution of nitrate reductase activity in natural vegetation, the pioneering works of Moritsugu's group and our own observations on the responses of agricultural plants to root temperatures, a general plant survival mechanism seems to emerge as follows:

In cold soils in nature, and in cold root conditions in hydroponic conditions, the rate of sugar accumulation in the root is greater than the demand for cell respiration and for simultaneous nitrate and ammonium metabolism in the roots. NRA is slowed down at low root temperature. Summer crops or natural vegetation in hot climates respond to high root zone temperatures by slowing down nitrate reductase activity, reserving available sugar for root respiration, while most of the nitrate is transported to the leaves, where NRA is carried out close to the site of sugar production by photosynthesis.

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