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Physiological aspects of N nutrition in saline and waterlogged soils.

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Summary

The present work highlights a few physiological aspects of NO_3^- nutrition and closely related issues in Magnoliopsidae growing in saline and waterlogged soils. The main interest was to study the effect of high NaCl concentrations in the root zone on NO_3^- uptake. Soil salinity is a major agricultural problem in many semiarid and arid regions of the world and NaCl induced reduction in NO_3^- uptake has occasionally been assumed to contribute to the negative effect on growth and development in crops.

In Chapter 1 it has been demonstrated that relatively salt sensitive plant species such as *Festuca rubra* (even though this sensitivity might be restricted to the seedling stage), are not suitable tools to study the effects of NaCl on NO_3^- uptake. It has therefore been decided to use the highly salt tolerant halophyte *Plantago maritima* as a model species. In contrast to earlier studies performed with relatively salt sensitive crop species, the use of a highly salt tolerant plant allowed easier comparison between NaCl treatments. First, relative growth rate of the plant was not reduced by exposure to external NaCl concentrations of up to 100 mol m^{-3} . Second, biomass partitioning between shoot and root did not change at all NaCl treatments applied in this study. Since the root is not only directly involved in NO_3^- uptake but is also used to express NO_3^- fluxes, equal partitioning of biomass between root and shoot makes it easier to compare uptake fluxes between treatments. Third, *Plantago maritima* does not accumulate N containing osmotic solutes, which might increase the N demand of the plant at high external NaCl concentrations (see also Chapter 2).

Exposure of *Plantago maritima* to elevated NaCl concentrations (50, 100 and 200 mol m^{-3}) in the root zone led to a reduction in NO_3^- net uptake rate at all salinity levels applied but decreased the relative growth rate only at 200 mol m^{-3} NaCl (Chapter 2). Net uptake rates of SO_4^{2-} and H_2PO_4^- were unaffected at all external NaCl concentrations applied. Assessment of net assimilation rate and C partitioning and allocation showed that a reduced C availability to supply energy and building blocks for NO_3^- uptake, reduction and translocation within the plant did not occur. Elevated supply of Ca^{2+} (5 mol m^{-3}) in the nutrient solution increased both relative growth rate and NO_3^- net uptake rate in plants raised at 200 mol m^{-3} NaCl but had no effect at 100 mol m^{-3} , a NaCl concentration at which growth was unaffected. From data in literature and measurement of N partitioning towards NO_3^- and reduced N compounds it became obvious that the reduced rate of NO_3^- net uptake was not due to an inhibition of processes involved in the assimilation of NO_3^- . It was, therefore, concluded that the interaction between NaCl and NO_3^- uptake was due to a direct and specific effect on processes involved in the regulation of NO_3^- uptake at the root plasma membrane.

Assessment of the effect of salinity on root morphology of *Plantago maritima* revealed significant changes at external NaCl concentrations as low as 50 mol m⁻³ (Chapter 3). The presence of NaCl in the nutrient solution inhibited or delayed the initiation, expansion or emergence of lateral root primordia or the subsequent activation of the apical meristem, while length growth of individual roots appeared to be unaffected or even stimulated. This effect might be related to changes in the hormonal balance. The taproot of plants exposed to NaCl became longer and thinner, leading to significant changes in the specific root length. It was, however, concluded that the observed morphological changes had a minor effect on NO₃⁻ fluxes when expressed on a root fresh weight basis (Chapter 4).

Using ¹⁵NO₃⁻ as a tracer, the effect of NaCl on NO₃⁻ influx, efflux and N net translocation to the shoot was then measured in a steady state system (Chapter 4). The results show that the reduced rate of NO₃⁻ net uptake was almost entirely due to a reduced NO₃⁻ influx. Expressed as a proportion of influx, NO₃⁻ efflux remained unchanged and was even lower at 200 mol m⁻³ NaCl. Another important finding was that the rate of ¹⁵N net translocation to the shoot decreased relative to the rate of NO₃⁻ net uptake. Based on these results it was concluded that, at least at non-growth-limiting salinity levels, the negative effect of NaCl on NO₃⁻ uptake was due to interference between Na⁺ and/or Cl⁻ and the NO₃⁻ transport system at the root plasma membrane, or inhibition of N translocation to the shoot.

In some earlier studies the negative effect of NaCl on the uptake of NO₃⁻ by the root has been interpreted in terms of a competitive inhibition between Cl⁻ and NO₃⁻ at the level of the NO₃⁻ transport systems at the root plasma membrane. This possibility has been assessed in a labelling experiment involving measurement of ¹⁵NO₃⁻ influx after transfer to elevated NaCl concentrations in the nutrient solution and after transfer from high NaCl concentrations on which the plants had been raised on to iso-osmotic solutions lacking Cl⁻ (Chapter 5). Based on these results it was concluded that the observed reduction of NO₃⁻ influx in plants raised on elevated NaCl concentrations was not due to a competitive inhibition by external Cl⁻.

There are a few other possibilities remaining that could have been responsible for the observed reduction in NO₃⁻ influx, such as a non-competitive inhibition of NO₃⁻ influx, a lower translocation of NO₃⁻ or reduced N compounds to the shoot or decreased accumulation of NO₃⁻ in the shoot vacuole. Unfortunately, the present work was not successful in localising the precise point(s), which are affected by the presence of NaCl and eventually led to a reduced rate of NO₃⁻ influx. Preliminary results, however, suggest that the NaCl induced reduction in NO₃⁻ uptake might have been the cause for the observed reduction of the relative growth rate (General Discussion). Further research would be needed to assess the validity of this hypothesis.

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Finally, a short excursion to the effect of waterlogging on NO_3^- uptake in *Oryza sativa* has been made (Chapter 6). Soil waterlogging leads to anoxic conditions in the rhizosphere. Plants react by enhanced formation of aerenchyma providing a low resistance pathway for movement of gases such as O_2 from the shoot to the root. In the root O_2 is consumed by respiration for maintenance, growth and ion uptake or diffuses into the rhizosphere via radial O_2 loss. It has been shown that radial O_2 loss from roots of plants raised in anoxic solution decreased with distance behind the root tip. This effect has been interpreted in terms of induction of a high resistance barrier to diffusion between the aerenchyma and the external medium. The biological basis for the decline in radial O_2 loss is unclear, but is generally assumed to be, at least partly, due to anatomical changes in the apoplast of cell layers exterior to the aerenchyma. A possible drawback associated with this adaptation is a reduced capacity for nutrient uptake. In the present study we tested whether there is a relationship between the induction of a barrier to radial O_2 loss and the capacity of the root to take up NO_3^- . Radial O_2 loss from the root surface of plants raised under anoxic conditions, measured at 3 to 5 cm behind the root tip, was more than 90% lower than in plants which had developed no barrier to radial O_2 loss. In contrast, NO_3^- net flux towards the root surface in an aerated solution containing 0.1 mol m^{-3} NO_3^- was the same in plants without or with a barrier to radial O_2 loss. It is therefore concluded that the assumed induction of a high resistance barrier to radial O_2 loss had no effect on the uptake of NO_3^- if present at low external concentrations.