

## The role of root hairs in rhizosphere acidification and mobilization of P from alkaline soils

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Root morphology strongly affects the ability of crops to maximize the exploitable soil volume. This is of especial relevance for the uptake of essential but immobile nutrients such as phosphorus (P). However, the idea of the key role of root hairs in P uptake is mainly based on the fact that root hairs strongly respond in their growth, abundance, density and elongation to P deficiency in soils. Furthermore, rhizosphere properties related to nutrient uptake such as exuded carboxylate anions, exoenzymatic activity or lowered pH are frequently maximized in the zone of root hairs suggesting their key role in nutrient mobilization. However, besides such indirect hints, direct proof of the role of root hairs for P mobilization is lacking.

We hypothesized that roots hairs improve P mobilization by enhancing rhizosphere acidification and exploited soil volume. Thus, we tested the capability of two varieties of maize and barley with and without root hairs for their potential to mobilize phosphorus of low availability. We applied 33P-orthophosphate (2 MBq per rhizobox) to an alkaline soil (pH 8.3). The soil was dried to ensure a strong sorption and/or precipitation of the P. Alkaline soil was chosen to specifically test for the relevance of rhizosphere acidification as key mechanism for enhanced P mobilization hypothesized to be improved by roots hairs. We used a planar optodes to visualize rhizosphere acidification along the root including the root hair zone at five different growth stages. After harvest, 33P uptake was quantified by combustion of plant and soil material and 33P determination via scintillation counting. Furthermore, we used phosphorimaging to visualize the depletion of 33P in the rhizosphere, it's uptake into roots and its allocation within the root system. N fertilization was applied hypothesizing that an increased N supply provides additional resources to boost P mobilization mechanisms.

After harvest (25 days) the 33P content in the biomass was significantly higher in root hair wildtypes (WT) than in root hairless mutants. N fertilization could be proven to be a key mechanism increasing the exploitation of a larger soil volume and thus the P nutrition of both crops. Maize and barley were able to acidify the rhizosphere from 8.3 to 7.5 in average. The pH change was strongest at the young roots parts, but not directly at the root tips pointing towards the fact that accumulation of organic acids is required for reaching a significant pH decrease in this strongly buffering soil. In maize, specifically crown roots strongly decrease the rhizosphere pH. However, especially at early growth stages spatial correlation between rhizosphere acidification and P uptake as well as the root hair zone and the P depletion zone is rather low suggesting additional mechanisms contributing to the high P uptake.

We conclude that root hairs are a key trait improving P mobilization and uptake from soils with low P availability. However, we observed also P depletion in far distance to the visible roots, root hairs and acidified rhizosphere suggesting additional mechanisms, such as mycorrhization, to contribute to a rather homogenous P depletion.