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What root-mineral interactions are occurring in the rhizosphere and play a key role in potassium biogeochemistry and plant nutrition?

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The prime function of roots is to take up water and nutrients. Doing so, roots can considerably alter the concentration of nutrients in the soil volume that is influenced by their activity, the so-called rhizosphere (Hinsinger 2004; Hinsinger et al. 2009). For those nutrients exhibiting restricted diffusion capacity such as potassium (K) as well as other major cations, the uptake activity of roots can thereby result in rather steep concentration gradients, with values dropping to the micromolar (μM) range in the immediate vicinity of roots, i.e. two- to three-orders of magnitude less than in the bulk soil. Claassen and Jungk (1982) estimated that soil solution K concentrations were about 2-3 μM close to root surface in the rhizosphere of maize. Such a sharp depletion of K-ions results not only in the diffusion of K-ions over several millimeters from the root surface, but also in a shift of adsorption/desorption equilibria between soil solution K and K-bearing minerals in the rhizosphere. Exchangeable K is thus desorbed in order to replenish soil solution K, ultimately resulting in a depletion of exchangeable K that can extend over several millimeters from root surface (Figure 1).

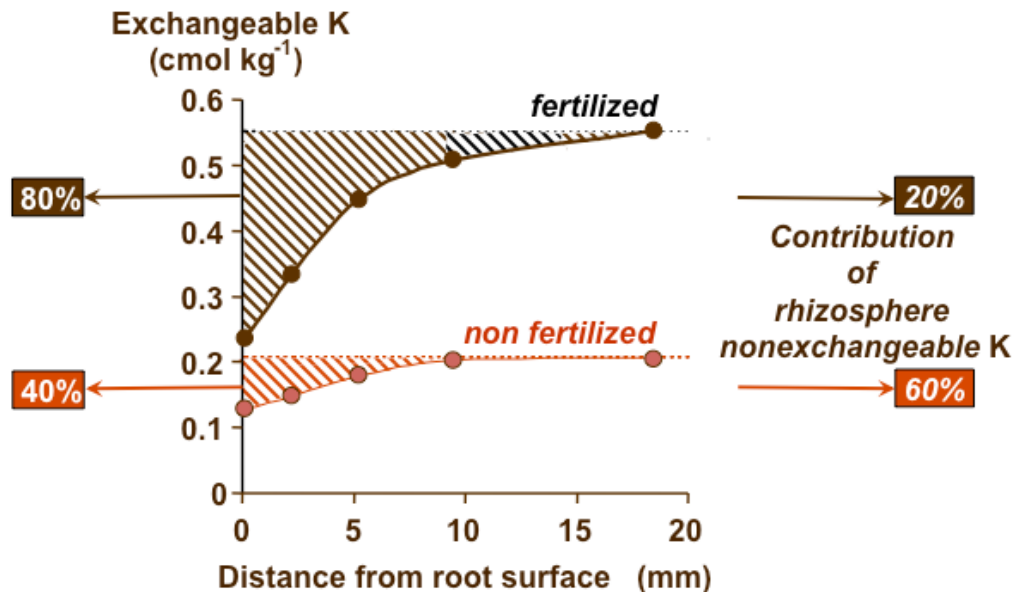


Figure 1. Depletion of exchangeable K in the rhizosphere extends to several millimeters from the root surface within 4 days of plant growth and contributes 40-80% of K uptake by oilseed rape grown in soils of the long-term K fertilizer trial of Gembloux, Belgium (modified from Hinsinger 2004).

Besides a rapid desorption of exchangeable K-ions from the surface adsorption sites of clay minerals, the root-induced depletion of soil solution K can be responsible for a significant release of nonexchangeable K-ions from the interlayers of micaceous clay minerals (illite-like) and primary minerals (micas). Even in the rather short term, this process can contribute a major proportion of K uptake, unless the soil has been heavily fertilized (Figure 1). However, even in such a case, it can contribute a significant percentage of K uptake by plants. Given the high affinity of the interlayer sites of micaceous minerals for K-ions, the release of non-exchangeable K is prevented beyond a critical K concentration of several μM . For instance, Springob and Richter (1998) showed that the rate of release of nonexchangeable K was steeply increasing with decreasing soil solution K concentration below a threshold value of about $3 \mu\text{M}$, i.e. about the level of soil solution K concentration that typically occurs close to root surface as a consequence of root-induced depletion of K-ions in the rhizosphere (Claassen and Jungk 1982; Hinsinger 2002). Hinsinger and Jaillard (1993) showed that such root-induced depletion of soil solution K was the driving force for the rapid release of interlayer K in a phlogopite mica and its concomitant transformation into a clay mineral called vermiculite. They showed that as soon as K concentration in the rhizosphere decreased below a threshold value of about $70\text{-}80 \mu\text{M}$ (Figure 2), the weathering of the phlogopite mica became detectable by X-ray diffraction through the appearance of a typical vermiculite peak forming at the expense of the mica-characteristic peak. This process took only about 2 to 3 days (Hinsinger 2012). In the absence of plants, no significant vermiculite formation was detected. In addition, root-induced acidification and organic ligands (e.g. citrate, oxalate, siderophores) produced by roots or rhizosphere microorganisms can result in proton-promoted or ligand-promoted dissolution of K-bearing minerals such as micas and feldspars (Hinsinger 2012). The contribution of this alternative root-mineral interaction mechanism to plant nutrition is less documented and more difficult to quantitatively assess in the rhizosphere (Hinsinger 2002).

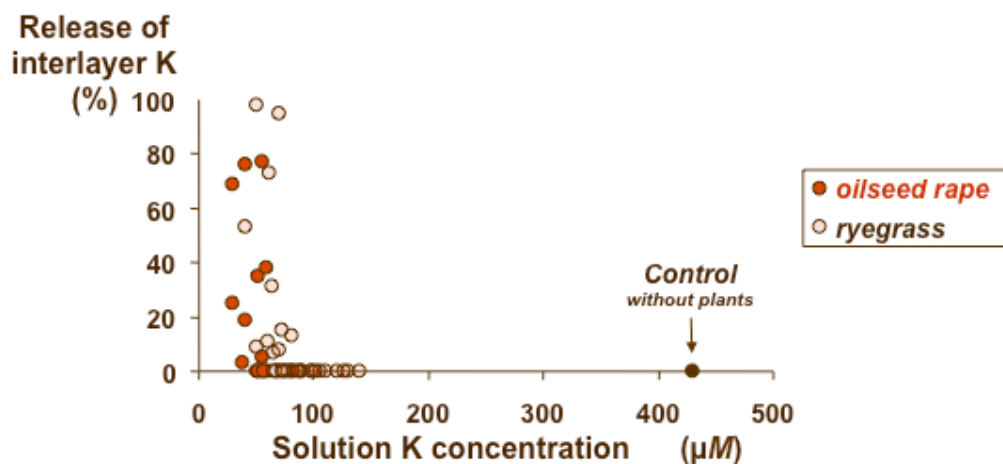


Figure 2. The percentage of release of interlayer K of a phlogopite mica and concurrent weathering to vermiculite in the rhizosphere of oilseed rape and ryegrass sharply increased below a threshold value of about $80 \mu\text{M}$ (modified from Hinsinger and Jaillard 1993 and Hinsinger 2012).

In agroecosystems, accounting for rhizosphere processes has proven essential to understanding the observed K budgets in long-term fertilizer trials (Hinsinger 2002). In

most field trials conducted in Europe, the cumulative K offtake by successive crops in the rotation was much greater than the decrease of exchangeable K in the absence of fertilization (Hinsinger 2002). The rates of release of nonexchangeable K amounted to 11-94 kg K ha⁻¹ yr⁻¹ as an average value computed over the whole duration of these long-term fertilizer trials (Hinsinger 2002 and 2012). The release of nonexchangeable K contributed a major proportion (up to 90%) of K uptake by crops (Hinsinger, 2002), in line with results obtained in short-term pot experiments (Figure 1). Barré et al. (2007) indeed showed that K uptake by ryegrass in a pot experiment was matching the formation of interstratified illite-smectite minerals in the rhizosphere, at the expense of the illite-like clay minerals. Barré et al. (2008) confirmed that K uptake by plants in a long-term K fertilizer trial quantitatively matched the release of nonexchangeable K that was evidenced by the increased amount of interstratified illite-smectite minerals occurring at the expense of illite-like clay minerals. The sink effect of roots and subsequent depletion of soil solution K in the rhizosphere is thus the driving process for the release of interlayer K and concomitant weathering of micaceous minerals in soils (Hinsinger 2002). Plants thereby have a major role in the biogeochemical cycle of K and in the formation and fate of expandable clay minerals (vermiculites or smectites) in topsoils, with illite-like clay minerals playing the role of a large K reservoir in soils. Depending on soil mineralogy, root-induced weathering and release of nonexchangeable K in micaceous minerals can contribute a significant or even prominent proportion of K nutritional requirements of plants, including high-yielding crops.

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