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Inhibition of maize root growth by high nitrate supply is correlated with reduced IAA levels in roots

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Summary

The plant root system is highly sensitive to nutrient availability and distribution in the soil. For instance, root elongation is inhibited when grown in high nitrate concentrations. To decipher the mechanism underlying the nitrate-induced inhibition of root elongation, the involvement of the plant hormone auxin in nitrate-dependent root elongation of maize was investigated. Root growth, nitrogen and nitrate concentrations, and indole-3-acetic acid (IAA) concentrations in roots and in phloem exudates of maize grown under varying nitrate concentrations were analyzed. Total N and nitrate concentrations in shoots and roots increased and elongation of primary, seminal and crown roots were inhibited with increasing external nitrate from 0.05 to 5 mM. High nitrate-inhibited root growth resulted primarily from the reduced cell elongation and not from changes in meristem length. IAA concentrations in phloem exudates reduced with higher nitrate supply. Inhibition of root growth by high nitrate was closely related to the reduction of IAA levels in roots, especially in the sections close to root tips. Exogenous NAA and IAA restored primary root growth in high nitrate concentrations. It is concluded that the inhibitory effect of high nitrate concentrations on root growth may be partly attributed to the decrease in auxin concentrations of roots.
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Introduction

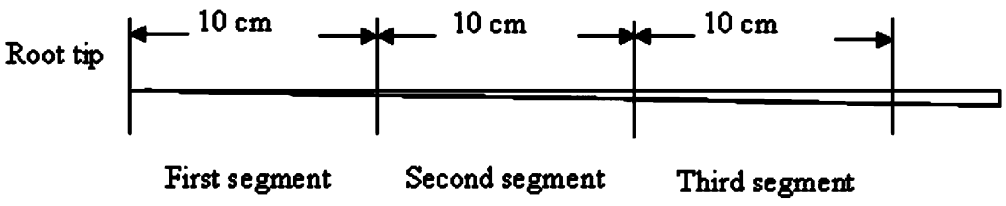
To provide the essential requirements for water, minerals and anchorage, development of the root system must adjust quickly in response to changes in the physical and chemical environment (Stamp et al., 1997). Nutrient supply can affect root development either directly as an external signal or indirectly through changes in the internal nutrient status of the plant (Forde and Lorenzo, 2001). Nitrogen, with its main forms of nitrate and ammonium, is crucial for plant growth and is involved in mediating root development. It has been reported that local supply of nitrate stimulates the rate of lateral root growth (Drew, 1975; Zhang et al., 1999), while uniform application of nitrate greater than 10 mM to roots has a systemic inhibitory effect on both lateral root development (Zhang et al., 1999; Stitt and Feil, 1999; Guo et al., 2005) and primary root growth (Linkohr et al., 2002; Tian et al., 2005). The local stimulatory effect of nitrate on lateral root elongation is likely to result from the nitrate itself acting as a signal rather than being a nutrient (Zhang et al., 1999). The systemic inhibitory effect is mediated by signals from the plant's internal N status (Forde, 2002). Scheible et al. (1997) observed a highly significant negative correlation between leaf nitrate content and total root growth, suggesting that nitrate in leaf may act as a signal, reflecting internal N status and mediating root growth. Nevertheless, the mechanism underlying the dependence of root elongation on the internal N status remains largely unknown.

The phytohormone auxin regulates many cellular responses crucial for plant development. Auxin plays a key role in establishing and elaborating patterns in root meristems (Jiang and Feldman, 2003). Auxin is synthesized predominantly, though not exclusively, in the aerial parts of plants (Bhalerao et al., 2002), and is redistributed within the plant body through a complex transport network. In roots, long-distance auxin transport towards the root tip is conducted via the phloem (Swarup et al., 2001). Unloading of auxin from the phloem and its redistribution in roots are mediated by auxin influx and efflux carriers, respectively (Friml, 2003; Blakeslee et al., 2005). These processes are essential for root cell division and elongation (Blilou et al., 2005) and, thus, for regulating root growth (Casimiro et al., 2001). The auxin transport inhibitor naphthylphthalamic acid suppresses lateral root development in *Arabidopsis* (Reed et al., 1998). Root elongation of *Arabidopsis* is enhanced by exogenous auxin at low concentrations, but is inhibited at high concentrations (Evans et al., 1994). Zhang et al. (1999) found that lateral root elongation of an auxin-insensitive mutant *axr4* is not stimulated by local nitrate supply, suggesting an overlap between the auxin and nitrate signaling pathways. However, Linkohr et al. (2002) found that lateral root elongation of *axr4* does not differ from that of wild-type plants in response to local nitrate supply. Malamy and Ryan (2001) suggested that repression of lateral root initiation by high sucrose and low nitrogen supply may be related to inhibition of auxin transport from shoot to root. It remains unknown how auxin levels in roots are modulated by nitrogen supply. In the present study, we analyzed the changes in auxin levels in maize roots and in the phloem at different N supplies and explored the possible link between auxin and N-mediated root growth.

Materials and methods

Plant culture

Zea mays L. seeds (cv.478) were sterilized in 10% (v/v) H_2O_2 solution for 30 min, and then rinsed three times with de-ionized water. Seeds germinated on filter paper were grown in nutrient solutions containing different concentrations of nitrate (pH 6.0) in a greenhouse under conditions of 14-h-light/10-h-dark cycle and temperatures of 22–28 °C. A photosynthetic photon flux density of 250–300 $\mu mol\, m^{-2}\, s^{-1}$ (at canopy height) was provided during the light phase. Three seedlings were cultured in a 1-L porcelain pot. The nutrient concentrations in the solution were (in mM) 0.75 K_2SO_4, 0.1 KCl, 0.25 KH_2PO_4, 0.65 $MgSO_4$, 0.1 EDTA-Fe, and (in μM) 1.0 $MnSO_4$, 1.0 $ZnSO_4$, 0.1 $CuSO_4$ and 0.005 $(NH_4)_6Mo_7O_{24}$. Nitrogen was supplied in nutrient solution as $Ca(NO_3)_2$ at 0.05, 0.5, 5, 10 or 20 mM. The Ca^{2+} of the low NO_3^- treatments was supplemented with $CaCl_2$ to the same Ca^{2+} concentrations as in 5 mM NO_3^- treatment. The nutrient solution was changed every 2 d. Plants were harvested after 12 d, then dried at 70° for 2 d and weighed. For determination of indole-3-acetic acid (IAA), root samples including the whole roots and the different root segments excised from 10 cm, and 20 cm of primary root tips (such as the following) were frozen in liquid N_2 and stored in a −40° freezer.



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