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RESEARCH ARTICLE

Cell Production and Expansion in the Primary Root of Maize in Response to Low-Nitrogen Stress

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Abstract

Maize plants respond to low-nitrogen stress by enhancing root elongation. The underlying physiological mechanism remains unknown. Seedlings of maize (*Zea mays* L., *cv*. Zhengdan 958*)* were grown in hydroponics with the control (4 mmol L^{-1}) or low-nitrogen (40 μmol L^{-1}) for 12 d, supplied as nitrate. Low nitrogen enhanced root elongation rate by 4.1-fold, accompanied by increases in cell production rate by 2.2-fold, maximal elemental elongation rate (by 2.5-fold), the length of elongation zone (by 1.5-fold), and final cell length by 1.8-fold. On low nitrogen, the higher cell production rate resulted from a higher cell division rate and in fact the number of dividing cells was reduced. Consequently, the residence time of a cell in the division zone tended to be shorter under low nitrogen. In addition, low nitrogen increased root diameter, an increase that occurred specifically in the cortex and was accompanied by an increase in cell number. It is concluded that roots elongates in response to low-nitrogen stress by accelerating cell production and expansion.

Key words: cell length, elemental expansion, kinematic analysis, root diameter, root elongation, *Zea mays* L.

INTRODUCTION

In the past 50 years, high crop yield largely depends on the increased use of nitrogen fertilizers (Hirel *et al.* 2007). Unfortunately, the high rate of nitrogen input and low nitrogen use efficiency in soils have had profoundly detrimental effects on the environment, such as the eutrophication of freshwater and marine ecosystems (Beman *et al.* 2005; London 2005). Therefore, agriculture in the future probably requires new varieties that can grow on soils with reduced nitrogen input (Lynch 2007).

The growth and function of roots play a major role in crop production through the acquisition of soil resources. Under phosphorus deficiency, for example, plant roots tend to grow in shallow soil where phosphorus is enriched, more immobile and often more available in surface soil horizons (Lynch 1995). Under low-nitrogen stress, maize root elongation is enhanced (Wang *et al.* 2004; Tian *et al.* 2008; Gaudin *et al.* 2011), which may contribute to acquire nitrogen resource in the deep soil. The rate of root growth depends mainly on the length of the growth zone (i.e., meristem plus elongation zone) and on the underlying rates of expansion. Cell division also has an essential but indirect role in determining root elongation through delivering a steady supply of cells into the elongation zone (Baskin 2013). In the root meristem, new cells are produced and elongate slowly; in the elongation zone, they elongate five to ten times faster than in the meristem; after elongation stops, cells continue to differentiate in the region of maturation.

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Roots might also respond to environmental stress by altering diameter. The radial pattern of a root in the growth zone is made up of two fundamental types of parenchymous tissue, a central stele and a surrounding cortex. Previous studies showed that the water-stressed roots became substantially thinner than well-watered roots (Sharp *et al.* 1988). It is not clear how low-nitrogen stress affects root diameter.

Although a previous study has shown that high-nitrogen supply reduced mature cell length but not the size of meristem (Tian *et al.* 2008), it remains unclear how cell production and expansion process respond to low-nitrogen stress in both longitudinal and radial directions. To understand the adaptive response of maize root to low-nitrogen stress, we analyzed cell production and expansion process in the primary root in both longitudinal and radial directions.

RESULTS

Primary root elongation in response to low-nitrogen stress

Shoot growth was significantly inhibited by low nitrogen stress (Fig. 1). For seedlings grown continuously on 4 mmol L^{-1} nitrate, roots elongated at a steady rate, (1.2±0.1) cm d^{-1}, from 9 to 12 d (Fig. 1 and Table 1). In contrast, for seedlings transferred to 40 μmol L^{-1} nitrogen, root growth was accelerated and the root elongation rate reached a steady rate of (4.9±0.1) cm d^{-1} from 9 to 12 d, approximately 4 times faster than on the controls.

To evaluate the effect of the nitrogen treatment on the performance of the meristem, we calculated cell production rate from the ratio of root elongation rate in the period from 9 to 12 d and mature cortex cell length on the 12th d (Silk 1992). Low nitrogen increased the mature length of cortical cells and the rate of cell production (Table 1). These results imply that 40 μmol L^{-1} nitrogen treatment accelerated both division and elongation processes.

The profile of cell length, velocity and elemental expansion rate

Cell length at root apex region (0-1 mm from root tip) remained unaffected by nitrogen status (Fig. 2). Thereafter, low nitrogen significantly increased cell length. The final cell length of the low-nitrogen plants in the mature zone was 1.8-fold larger than that of the control plants (Fig. 2 and Table 1). Cell length profiles *vs.* position were converted to velocity profiles by means

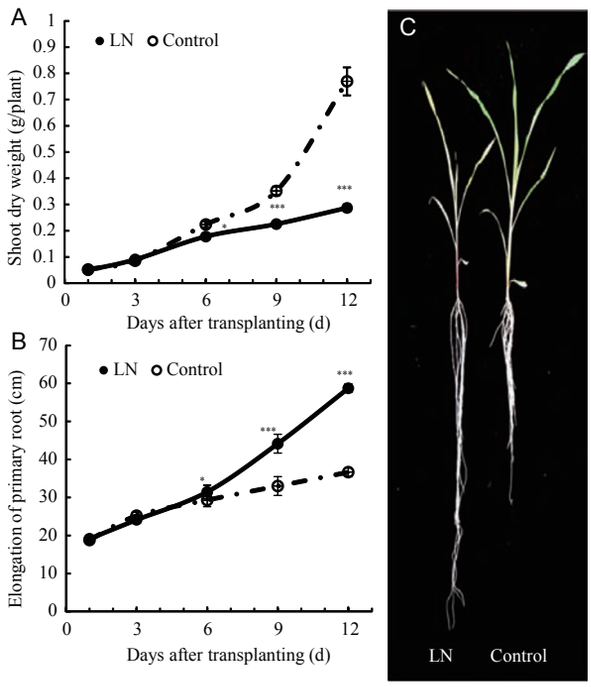

Fig. 1 Effect of nitrogen supply on shoot growth and the pimary root length. A, shoot dry weight. B, primary root length. Maize plants were grown on the control (4 mmol L^{-1}) and low-nitrogen (40 μmol L^{-1}) condistions. Data were evaluated from maize seedlings after 1-, 3-, 6-, 9- and 12-d nitrogen treatments. C, 12-d-old maize seedlings were sampled under the controls and low nitrogen. Data are means±SE of 9 primary roots. *, ** and *** indicate significant differences between nitrogen treatments at P=0.05, P=0.01 and P=0.001, respectively. The same as below.

Table 1 Parameters characterizing cell division and expansion in the root growth under two nitrogen treatments[1)]

Parameter	Control	Low nitrogen
Root elongation rate (cm d^{-1})	1.2±0.1	4.9±0.1***
Final cell length (μm)	217±11	393±8***
Maximal elemental expansion rate (% h^{-1})	9.24±0.01	22.8±0.02***
Number of cells in the elongation zone	21.4±1.5	44.7±2.6***
Average elongation duration (h)	9.22±0.76	8.56±0.43
Cell production rate (cell h^{-1})	2.37±0.14	5.21±0.10***
Cell division rate (cell per cell h^{-1})	0.026±0.003	0.069±0.005***
Cell cycle duration (h)	28.4±2.7	10.5±0.9**
Number of cells per meristematic cell file	94.4±6.0	78.6±5.8**
Division zone length (mm)	1.50±0.05	1.15±0.04***
Elongation zone length (mm)	6.53±0.41	9.44±0.25**

[1)] Seedlings were grown for 12 d at the control and low nitrogen supply. **, P<0.01; ***, P<0.001. Data are means±SE of 9 primary roots. The same as below.