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Shoot growth potential drives N uptake in maize plants and correlates with root growth in the soil

Yunfeng Peng [a], Junfang Niu [b], Zhengping Peng [c], Fusuo Zhang [a], Chunjian Li [a,*]

[a] The Key Laboratory of Plant Nutrition, Ministry of Agriculture, Department of Plant Nutrition, China Agricultural University, Yuanmingyuan West Road 2, Beijing 100193, China
[b] Center for Agricultural Resources Research, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Shijiazhuang 050021, China
[c] College of Resources and Environmental Sciences, Agricultural University of Hebei, Hebei 071001, China

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ABSTRACT

Variation in nitrogen (N) acquisition ability is known to exist among maize genotypes. Field experiments were conducted and the N-efficient maize inbred line 478 and the N-inefficient line Wu312 were employed to illustrate whether the amount of N taken up in maize plants with different N acquisition ability was determined by the shoot growth potential or by the root size. To meet the accelerated growth of the shoot from the jointing stage to the grain-filling stage, the net N gain in whole plants of both genotypes increased dramatically and accounted for 77% and 74% of the total N increment in 478 and Wu312, respectively. Similarly, the 4th to 8th nodal root whorls were initiated predominantly between 35 and 76 d after sowing, which accounted for about 90% of the total root length on 93 d after sowing. The whole plant N content of the N-efficient 478 was significantly higher than that of the N-inefficient Wu312. 478 had also longer root length, including axial and lateral roots, of the embryonic roots and each whorl of shoot-borne roots, and greater root length density (RLD) than Wu312. In spite of the smaller root size, Wu312 had higher shoot N concentration than 478 during the whole growth period, implying that N was not limited for shoot growth in Wu312. It was concluded that maize root growth, especially initiation and development of the shoot-borne roots, as well as the amount of N taken up were coordinated with shoot growth and demand for nutrients. Although a large root system and high RLD in the soil profile were beneficial for efficient N acquisition, amount of N taken up by the two maize genotypes in the presence of sufficient N supply was determined by the shoot growth potential, and not by the root size.

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1. Introduction

Maize is generally considered to have a high soil fertility requirement to attain maximal yields, but variation in nitrogen (N) efficiency is known to exist among maize genotypes (Reed and Hageman, 1980; Rizzi et al., 1996; Paponov and Engels, 2003; Paponov et al., 2005a,b; Uribelarrea et al., 2004, 2007, 2009). With sufficient N supply in the field, variation in N use efficiency (NUE, defined as grain or biomass production per unit of N available in the soil) is due largely to differences in N uptake ability, whereas with deficient N supply, variation in NUE is mainly due to differences in utilization of the accumulated N in plants (Moll et al., 1982). Using maize as a model crop, a lot of works have been done to investigate the changes in metabolite concentration and enzyme activities involved in N metabolism within leaves, stover and cob at different periods of plant development (Seebauer et al., 2004; Hirel et al., 2005a, 2005b; Uribelarrea et al., 2009). Though there are some studies highlight the essential role of root traits in N acquisition (Mackay and Barber, 1986; Sattelmacher et al., 1990; Van Beem and Smith, 1996; Horst et al., 2003; Kondo et al., 2003; Wang et al., 2004), the studies in which the importance of the root system was comprehensively investigated in relation to N supply, biomass production, and yield of maize plants are little reported (Hirel et al., 2007).

Root morphology is an important factor not only for the uptake of immobile nutrients in the soil, such as phosphorus (Marschner, 1998), but also for that of mobile nutrients such as N (Linkohr et al., 2002; Wang et al., 2006). A positive correlation between yield and root size in maize hybrid B73_Mo17 has been reported (Mackay and Barber, 1986). In a field experiment with 10 maize cultivars, nitrate depletion and root length densities in the subsoil layer are closely correlated (Wiesler and Horst, 1994).

* Corresponding author. Tel.: +86 10 6273 3886; fax: +86 10 6273 1016.
E-mail address: lichj@cau.edu.cn (C. Li).

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Effective nutrient acquisition is not only dependent on size of the root system but also on the three-dimensional deployment of roots in the soil, i.e., the root architecture (Lynch, 1995; Linkohr et al., 2002; Dunbabin et al., 2003; Zhu et al., 2005). Maize roots can be classified into an embryonic root system consisting of a single primary root and a variable number of seminal roots, and a post-embryonic root system of several whorls of shoot-borne roots (Hochholdinger et al., 2004). The distribution of axial roots determines root architecture. Root architecture in the soil determines the ability of a crop to catch nutrients and water necessary to sustain plant growth (Li et al., 2006). Root length per unit soil volume is of great importance for the uptake of nitrate from soil (Robinson and Rorison, 1983). Strong relationships have been observed between the amount of fine root biomass present per unit volume of soil and the depletion of soil water and N for grassland plant species (Craine et al., 2003).

Genotypic differences represent a useful tool for the study of mechanisms that determine nutrient acquisition. Two maize inbred lines, 478 and Wu312, show differences in grain yield and N uptake at both high and low N input (Chen, 2001). Genotype 478 is N-efficient with higher yield and N uptake, while Wu312 is N-inefficient with lower yield and N uptake. In solution culture, these genotypes show contrasting N-acquisition abilities in response to N supply. Genotype 478 had a larger root system and absorbed more N than Wu312, especially under low N supply (Wang et al., 2004), and had also larger shoot than Wu312 (Chen, 2001; Wang et al., 2004). On the other hand, Wu312 had always higher N concentration in plants than 478, no matter whether they grew under N-deficient or N-sufficient conditions (calculated according to the results in Wang et al., 2004). These results suggest that Wu312 has not N limitation for growth but had limited shoot growth potential. The question raised is that amount of N taken up in these plants is determined by shoot growth potential or by the root size?

In the present study, a field experiment with sufficient N supply was conducted, and both maize inbred lines 478 and Wu312 were employed to investigate the initiation, growth and changes in lengths of different whorls of shoot-borne roots (including axial and lateral roots), amount of N taken up and their relations to shoot development during the whole growth period. Root distribution in the soil profile expressed as root length density (RLD) at the grain-filling stage was studied using a monolith method. The aim of the study was to clarify whether the amount of N taken up in maize plants was determined by the shoot growth potential or by the root size.

2. Materials and methods

2.1. Experimental design

The field experiment was carried out at the Dongbeiwang Experimental Station of the China Agriculture University in Beijing, China. The soil type at the study site is a calcareous alluvial fluvo-aquic soil with a loamy and silt texture (FAO) typical of the region. The soil was analyzed before sowing. The chemical properties of the 0–30 cm soil layer were as follows: extracted mineral N (N_{min}) 39 kg ha^{-1}, pH (H_2O) 8.0, soil density 1.33 g cm^{-3}, Olsen-P 17.5 mg kg^{-1}, NH_4OAc-extracted K 157.5 mg kg^{-1}, and organic matter 21 g kg^{-1}. Seeds of the N-efficient maize inbred line 478 and N-inefficient genotype Wu312, provided by the maize breeding group of the Department of Plant Nutrition, China Agricultural University, were sown on April 28, 2005. Maize was over-seeded with hand planters and the plots were thinned at the seedling stage to a stand of 60,000 plants ha^{-1}. Urea was used as fertilizer at a rate of 150 kg N ha^{-1}, of which 30% was applied before sowing as base fertilizer and the rest was applied 52 d after sowing (DAS) as a top dressing. At planting, 120 kg P_2O_5 ha^{-1} (superphosphate) and 67.5 kg K ha^{-1} (potassium chloride) were banded. The experiment was a randomized block design with four replicates each of 230 plants. The distance between rows and plants was 50 and 33 cm, respectively. Border plots were included on the sides of the experimental field. Weed growth on plots was controlled by pre-emergence herbicides and cultivation.

2.2. Plant harvest

Both genotypes had about the same phonological stages during the whole growth period: jointing stage 45 DAS, tasselling 76 DAS and physiological maturity 128 DAS. The total green leaf areas of both genotypes were measured from the jointing stage until the maturity. There were 14 measurements with the same 5 plants in each plot. SPAD values of the ear leaf of both genotypes were read by using chlorophyll meter (SPAD-502, Konika Minolta Sensing Inc., Japan). There were 4 measurements from the end of silking (84 DAS) until the maturity with the same 10 plants in each plot. Dry weight, N contents and concentrations of shoots and roots, as well as length of embryonic and different whorls of shoot-borne roots of the both genotypes, were examined. There were 10 harvests during the growing period, from the seedling stage to maturity (for details see figures). On each sampling date, two whole plants were taken from each plot; two shoots and one root were dried immediately and used to assess dry weight and N content, and the other root was washed free of soil with tap water and kept at −20 °C until measuring of root length. At each harvest, each single plant was excavated with a soil volume of 50 cm × 33 cm and a depth of 40 cm. For dry weight and N determination, the plant was separated into the shoot and roots. The whole root system was obtained from the soil and washed free of soil. All samples were killed at 105 °C for 30 min, dried at 70 °C until constant weight, weighed (dry weight) and ground into powder. Appropriate amounts of the ground plant material were used to determine the total N content using a modified Kjeldahl digestion method (Nelson and Somers, 1973).

In order to comprehensively study the root spatial distribution in soil, a monolith method (Böhm, 1979) was used to harvest roots on 93 DAS, on which date the maize plants were at the grain-filling stage and had the largest root system as shown in our preliminary experiment. Soil cubes with 5 cm sides (125 cm^3) were dug one by one in a soil volume of 60 cm × 50 cm and a depth of 55 cm (two plants, with a distance of 33 cm between plants). The total number of the monoliths for the two plants was 2640. Each soil block was placed in a separate plastic bag and marked with the spatial coordinates.

2.3. Length analysis of the whole root system

Roots harvested as whole root systems in the 10 harvests were divided into embryonic roots and different whorls of nodal roots. The node in the coleoptile was defined as the first node. Roots were scanned with a scanner (Epson 1680, Indonesia). For scanning, the root sample was placed in a glass rectangular dish (200 mm × 150 mm) with a layer of water about 4–5 mm deep to untangle the roots and minimize root overlap. When necessary, a root was separated into subsamples until they could be placed into the rectangular dish. Because the root of the plants harvested after silking was very large, in the last 4 harvests, besides scanning the embryonic root and all of the nodal roots from the 1st to 3rd nodal root whorls, 2 representative nodal roots from the 4th to 8th nodal root whorls were selected for scanning. After multiplying by the actual numbers of the nodal roots in the 4th to 8th nodal root whorls, the total length of each whorl of node roots could be obtained. The images were analyzed using the software WinRHIZO

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