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Comparison of N uptake and internal use efficiency in two tobacco varieties

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ABSTRACT

To explain the observation in field experiments that tobacco variety CB-1 was more nitrogen (N)-efficient than K326, the influence of two N levels on growth, N uptake and N flow within plants of the two tobacco varieties was studied. Xylem sap from the upper and lower leaves of both tobacco varieties cultured in quartz sand was collected by application of pressure to the root system. CB-1 took up more N with smaller roots at both high (HN, 10 mmol L^{-1}) and low (LN, 1 mmol L^{-1}) N levels, and built up more new tissues in upper leaves especially at LN level, than K326. Both varieties showed luxury N uptake, and CB-1 accumulated significantly less NO_3^- in new tissues than K326, when grown at the HN level. At both N levels, the amount of xylem-transported N and phloem-cycled N from shoot to root in K326 was greater than those in CB-1, indicating higher N use efficiency in CB-1 shoots than in K326 shoots. The major nitrogenous compound in the xylem sap was NO_3^- irrespective of N level and variety. Low N supply did not cause more NO_3^- reduction in the root. The results indicated that the N-efficient tobacco variety CB-1 was more efficient in both N uptake by smaller roots and N utilization in shoots, especially when grown at the LN level.

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1. Introduction

Chemical nitrogen (N) fertilizer is the main source of nutrients applied to the soil for increasing crop yields in intensive agricultural systems. Chemical N fertilizer is one of the most energy-consuming nutrients, and is likely to cause environmental problems when incorrectly applied [1,2]. Improving nitrogen use efficiency (NUE) is an important task for both sustainable agriculture and global ecosystem stability [3,4]. Variation in N efficiency is known to exist among cereal genotypes, such as wheat (*Triticum aestivum* L.) [5,6], oat (*Avena sativa*) [7,8], rice (*Oryza sativa* L.) [9], and maize (*Zea mays* L.) [10,11]. With sufficient N supply, variation in NUE is due largely to differences in N uptake efficiency, whereas with deficient N supply, such variation is due mainly to differences in utilization of accumulated N [12]. To improve NUE, it is desirable to improve simultaneously both uptake efficiency and utilization efficiency of plants.

Cycling of mineral nutrients and carbon compounds between the root and shoot has been convincingly demonstrated [13–21]. Nitrogen transport and partitioning within plants vary among species, including maize [20], wheat [13,14], tobacco (*Nicotiana tabacum* L.) [22], and castor bean (*Ricinus communis* L.) [23]. Enhanced N cycling between the shoot and root under lower N supply has been reported [13,20,22–24]. Quantification

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of mineral fluxes in the xylem sap can be used for investigating mineral uptake and cycling within plants [25].

The flue-cured tobacco varieties CB-1 and K326 have been widely used in tobacco production in Fujian province in recent years. Regardless of different N application rates (98 kg ha^{-1} for CB-1 and 120 kg ha^{-1} for K326) in local tobacco production, the two varieties had similar leaf N concentrations and yields, indicating that CB-1 is more efficient in N use than K326 [26]. However, differences in N uptake and cycling in the varieties and the extent to which translocation in the xylem and N circulation are altered by different N supplies are not fully understood. The present study was performed to address these questions, with the aim of investigating the influence of N levels on growth, N uptake, and N cycling in the two tobacco varieties, and better understanding the mechanisms underlying the differences in NUE between the two varieties.

2. Materials and methods

2.1. Plant culture and growth conditions

Tobacco seeds (*N. tabacum* var. CB-1 and K326) were germinated in a mixture of 60% (v/v) peat culture substrate, 20% (v/v) vermiculite, and 20% (v/v) perlite, and grown in a seedbed in a naturally lit glasshouse for 40 days. Before they were transferred to 2.0 L pots (one plant per pot) containing quartz sand (0.25–0.50 mm in diameter), the tobacco seedlings were washed with tap water to remove all substrate from the roots. The plants were watered initially with a half-strength nutrient solution. After 1 week a full-strength nutrient solution was substituted, consisting of the following compounds (mmol L^{-1}): 2 NH_4NO_3, 1 KH_2PO_4, 2.5 K_2SO_4, 2 $MgSO_4 \cdot 7H_2O$, 5 $CaCl_2 \cdot 2H_2O$, 3.7×10^{-2} Fe-EDTA, 4.6×10^{-2} H_3BO_3, 7.65×10^{-4} $ZnSO_4 \cdot 7H_2O$, 3.2×10^{-4} $CuSO_4 \cdot 5H_2O$, 1.6×10^{-5} $(NH_4)_6Mo_7O_{24}$, and 9×10^{-3} $MnCl \cdot 4H_2O$. The initial pH of the nutrient solution was adjusted to 6.0 ± 0.1. The plants were watered every 3 days before the beginning of the treatments and daily thereafter during the treatments in the morning with an excess of the nutrient solution. Small holes at the bottom of the pot allowed drainage. The drainage solution was discarded. The plants were grown under controlled conditions with a 14 h photoperiod. The photosynthetically active radiation at the surface of the pots was 210–250 μmol m^{-2} s^{-1} provided by reflector sunlight metal halide lamps (250 W, Philip Hipplus, Belgium).

2.2. Treatments and harvest procedures

The first harvest was performed 65 days after germination or 25 days after transfer to the controlled conditions, and the second harvest was performed 9 days later. For harvesting, the six plants of the two tobacco varieties each were divided into three groups of similar size and developmental stage. One group of each variety was used for the first harvest and the remaining two groups for the second harvest. On the day of the first harvest, the remaining two groups of plants were treated with either 1 mmol L^{-1} N (LN) or 10 mmol L^{-1} N(HN) as NH_4NO_3. The other components of the nutrient solution were as described above.

Leaves were numbered in ascending order, starting from the lowest mature leaf, which was designated as leaf 1. Smaller leaves that had already senesced were removed. The youngest unfolded leaf was leaf 8 at the first harvest; leaf 10 for the LN-treated plants and leaf 12 for the HN-treated plants at the second harvest, respectively. At harvest, plants were separated into roots, stem, lower leaves (1–6) and upper leaves (leaves 7–8 for the first harvest and 7–12 for the second harvest). Roots were washed free of sand with tap water. The two strata of leaves were divided into two lateral symmetrical parts: one was kept at −20 °C until analysis of tissue NO_3^- contents, and the other with roots and stem was treated at 105 °C for 30 min, dried at 70 °C to constant weight, weighed, and ground into powder.

Appropriate amounts of the ground plant tissues were used to determine total N content by a modified Kjeldahl digestion method that included reduced nitrate [27]. Calcium in the tissue was analyzed using a flame spectrophotometer (Cole-Parmer 2655-00, Cola-Paymqv Company, USA). To measure tissue NO_3^- content, the frozen leaves were homogenized with distilled water and centrifuged. The extracts of the leaf samples were subjected to NO_3^- determination by a modified salicylic acid method [28].

2.3. Collection of xylem sap

For collection of xylem sap, plants were grown in special pots in order to apply pressure to the root system [29], but treated in the same way as the plants for harvest. The procedure for collection of xylem sap was described by Jeschke and Pate [15]. Briefly, xylem sap was collected by compressing the moist quartz sand substrate and the root system in a pressure vessel. At approximately midway along the length of leaves an incision was made into the midrib. The cut surface was carefully washed and a Teflon tube was attached. After slow application of pressure, xylem sap started to exude from the midribs after a balancing pressure was reached [29], and the sap was collected 50 kPa above this pressure. The first exudate was discarded to avoid contamination from cut cells. Xylem sap was kept on ice during collection and stored at −20 °C before analysis. Samples were taken from leaves 5 and 7. Xylem sap collection was repeated three times 2, 5, and 8 days after commencement of the treatments. Calcium in the xylem sap was analyzed directly after appropriate dilution using ICP (Perkin Elmer 3300 DV, USA). Nitrate and ammonium in the xylem sap were analyzed following dilution by a TRAACS-2000 auto-analyzer (Bran + Luebee, Germany). Amino acids in the xylem sap were determined using an amino acid autoanalyzer (Hitachi, 8800, Japan). The total N in the xylem sap was the sum of measured NO_3^- N, NH_4^+ N, and amino acid N.

2.4. Estimation of net N flow through the xylem and phloem in the whole plant

Net N flow in plants was estimated using the method described by Armstrong and Kirkby [30] and Jiang et al. [18]. The assumption of the model is that nutrients were transported solely through xylem and phloem, while Ca^{2+} can be transported only apically through xylem and has no mobility in phloem.

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