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Natural variation of the root morphological response to nitrate supply in *Arabidopsis thaliana*

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ABSTRACT

Nitrogen fertilization increases crop yield but excessive nitrate use can be a major environmental problem due to soil leaching or greenhouse gas emission. Root traits have been seldom considered as selection criteria to improve Nitrogen Use Efficiency of crops, due to the difficulty of measuring root traits under field conditions. Nonetheless, learning about mechanisms of lateral root (LR) growth stimulation or repression by nitrate availability could help to redesign root system architecture (RSA), a strategy aimed at developing plants with a dense and profound root system and with higher N uptake efficiency. Here, we explored the genetic diversity provided by natural populations of the model species *Arabidopsis thaliana* to identify potentially adaptive differences in biomass production and root morphology in response to nitrate availability. A core collection of 24 accessions that maximizes the genetic diversity within the species and Col-0 (the reference accession) were grown vertically on agar medium at moderate (N+) nitrate level for 6 days and then transferred to the same condition or to low (N−) nitrate concentration for 7 days. There was a major nutritional effect on the shoot biomass and root to shoot biomass ratio. The variation of the root biomass and RSA traits (primary root length, LRs number, LR mean length, total LRs length and LR densities) was primarily genetically determined. Differences in RSA traits between accessions were somewhat more pronounced at N−. Some accessions produced almost no visible LRs (Pyl-1, N13) at N−, while other produced up to a dozen (Kn-0). Taken together our data illustrate that natural variation exists within *Arabidopsis* for the studied traits. The identification of RSA ideotypes in the N response will facilitate further analysis of quantitative traits for root morphology.

1. Introduction

Nitrogen fertilization has been used for decades to increase crop yield with a relatively low efficiency since a considerable fraction (up to two-thirds) of N input accumulates as runoffs (Frink et al., 1999). The resulting nitrous oxide emissions in the atmosphere and nitrate leaching from soil have detrimental consequences to the environment (Donner

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and Kucharik, 2008). In order to reduce eutrophication and the costly component of crop production, there is an immediate need to reduce N fertilizer inputs. To compensate for that reduction, improved crop genotypes must be sought with higher Nitrogen Use Efficiency (NUE) and particularly its uptake component (Edgerton, 2009; Den Herder et al., 2010; Kant et al., 2011). Currently NUE is defined as the crop yield per unit of available N, estimated as the product of nitrogen uptake efficiency (NupE) and nitrogen utilization efficiency (NutE), which is itself the combination of the efficiencies of assimilation and remobilization (Good et al., 2004; Masclaux-Daubresse et al., 2010). Greater allocation of root biomass along with a branched and dense root system would increase NupE and limit the impact of nitrogen fertilization on the environment. However, the root organ, responsible for nutrient capture, has largely been out of crop breeders' mind due to the difficulty of measuring root traits underground (Robinson, 2004).

Because plants are sessile organisms and cannot migrate towards more prosperous habitats, they have evolved mechanisms to adapt to water and nutrient availability changes. Root organs respond to resource fluctuations by showing developmental plasticity in order to modulate the surface available for the uptake, where the lateral root (LR) branching pattern occupies an important role (Zolla et al., 2010). The formation of LR from pericycle tissue is characterized by several consecutive developmental steps from the initiation of the founder cell division to the meristem elongation out of the parent root; each of those steps being subjected to nutritional influence (López-Bucio et al., 2003; Hermans et al., 2006; Péret et al., 2009; Giehl et al., 2012). A dual effect of external nitrate, which is the main nitrogen mineral form taken up by roots, on LR development has been depicted in the model species *Arabidopsis thaliana*: (i) a systemic inhibition of uniformly high nitrate concentrations at a post-emergence stage of the lateral primordium and (ii) a localized stimulation on N-starved

Table 1 – Definition of biomass and root architecture parameters.

Fresh biomass parameters	
R	Root biomass (5 pooled organs)
S	Shoot biomass (5 pooled organs)
R:S	Root to shoot biomass ratio
Root architecture parameters	
L_{PR}	Length of primary root
N_{LR}	Number of lateral roots visibly emerged (>1 mm) from primary root
ΣL_{LR}	Sum of lateral root length per seedling
L_{LR}	Mean lateral root length
D_{LR}–Z_1	Lateral root density calculated as the number of emerged lateral roots divided by the total primary root length (zone 1)
D_{LR}–Z_2	Lateral root density calculated as the number of emerged lateral roots divided by the length of the primary root portion between the first and last visibly emerged lateral roots (zone 2)

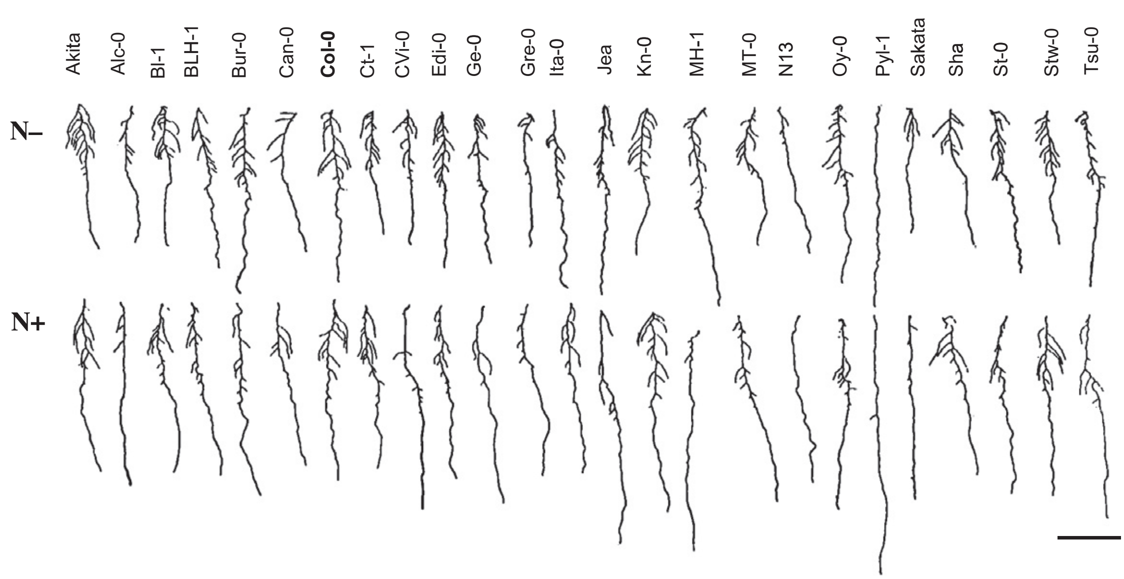

Fig. 1 – Representative root phenotype of 25 *Arabidopsis* accessions in response to the nitrate supply. Seedlings of 24 accessions of the core collection selected by McKhann et al. (2004) and the reference accession Col-0 were grown on medium containing 10 mM NO_3^- and transferred 6 days after germination on a medium of the same concentration (N+) or at 0.01 mM NO_3^- (N−). The photos were taken 7 days after transfer. Scale bar: 5 cm.