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Genetic control of nitrogen stress tolerance in winter wheat

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SUMMARY – Breeding wheat adapted to low nitrogen (N) input will be favoured by environmental and economical concerns. Thus, it is worth studying the genetic control of wheat N stress tolerance. We investigated a population of 220 di-haploid (DH) lines derived from the cross between a N stress tolerant and a sensitive cultivar. QTL were detected for sensitivity to N stress and for traits involved in plant functioning under N-limited conditions. The population was evaluated for grain yield and its components in multi-environment field trials under low and high N levels as well as and in growth chamber under N-limited condition. N stress sensitivity was estimated as the slope of a factorial regression where grain yield was regressed on the nitrogen nutrition index (NNI) of cv. 'Récital' measured in each trial. Plant functioning under N-limited conditions was evaluated in growth chamber using a conceptual crop model and a root system characterization. Seven QTL were detected for N stress sensitivity and fourteen were detected for plant functioning. A majority of QTL was detected in the vicinity of the dwarfing gene Rht-B1. Results indicated that N stress sensitivity and plant functioning under N-limited conditions may not be under the same genetic control and that the dwarfing genes may play an important role in the tolerance to N stress.

Introduction

Nowadays, nitrates constitute one major source of water pollution and decisions have been taken for reducing N applied to crops. Moreover, the best margins are no more obtained with high input cropping systems (Rolland *et al.,* 2004). Therefore, future varieties should maintain their yield as well as their protein content at a limited N level. More knowledge is needed about the genetic control of N stress tolerance. Our objective was to identify QTL involved first in sensitivity to N stress and second in plant functioning under N-limited conditions. These QTL were confronted with QTL that represented the global tolerance to N stress identified by confronting QTL detected under N^+ and N^- conditions.

Materials and methods

A population of 220 DH lines, derived from the cross between a N stress tolerant ('Arche'), and a N stress sensitive ('Récital') cultivar, was experimented in the field in seven environments corresponding either to optimal (N^+) or low (N^-) N supplies. Grain yield (GY), its components and grain N content were recorded. A sample of 120 lines was experimented at an early development stage (until 22 days after planting) in growth chamber using the experimental design of rhizotron (Pagès *et al.,* 1992). Plants were grown under hydroponic conditions and were supplied with a N-limited nutrient solution ($[No_3^-]$ = 0.5mM). The genetic map was provided by the French Génoplante program. QTL analyses were performed using QTLcartographer (Basten *et al.,* 2002).

Assessment of N stress sensitivity

In each environment, yield limiting factors were assessed using probe genotypes (Brancourt-Hulmel, 1999) and were best represented by the NNI at flowering of the probe genotype 'Récital' (Laperche *et al*., 2006). NNI is based on the N dilution curve that describes the minimum plant N concentration needed for maximum growth (Justes *et al.*, 1994). To assess N stress sensitivity, a factorial regression (Denis, 1988) was carried out for each line, using the NNI of 'Récital' as a covariate. The slope of the factorial regression was taken as an estimate of the sensibility of the genotype to N stress.

A conceptual model to identify relevant parameters of plant functioning

The conceptual model developed by Laperche *et al.* (in press) was used to explain the plant functioning, and its parameters were considered as genotypic variables for QTL detection. A root architecture description was also carried out. Model parameters and root architecture traits were evaluated using the 120 lines sample evaluated in growth chamber.

Results and discussion

Four GY and Grain Protein Yield (GPY) QTL were detected under both N conditions on linkage groups (LG) 2D1, 3D and 4B. Seven QTL for GY or GPY were specific of a N level and may be involved in the tolerance to N deficiency: LG 1B, 2A1, 2D1, 3D, 4B and 5A1 for GPY, 2A2, 2D1, 3D, 4B, and 5A1 for GY (Fig. 1).

Fourteen QTL were detected for plant functioning traits while seven QTL were detected for N stress sensitivity. A single coincidence was reported between these two QTL sets on LG 4B, in the vicinity of the dwarfing gene Rht-B1. Different genomic regions might be involved in N stress sensitivity control and in plant functioning under stressed conditions.

However, these results may be considered with caution. Plant characterization was only performed at 22 days after planting that corresponded to the beginning of tillering. The plant functioning after flowering was not considered, and especially during the nitrogen remobilization phase. Moreover, to be more specific, the experiment under controlled conditions should have been carried out for all plants at the same N stress level. That would imply to modulate individually the nitrogen nutrition to obtain the same NNI for each line. The results we presently obtained under controlled conditions were linked both to different stress levels and to N stress sensitivity differences

Among all detected QTL, nine were on the vicinity of the dwarfing gene rht-B1 (LG 4B). The sensitive parent carried the dwarf allele that corresponded to smaller lateral roots (LRL_LRN), to a higher sensitivity to N stress as well as to a GY and GPY decrease under N^- and to a GY increase and a GPY decrease under N^+. This gene is then important to consider for improving N use efficiency as it has an effect on both root architecture and N stress sensitivity. Its effect on yield under N-limited conditions may be linked to a less efficient soil exploration than tall lines, subsequent to the decrease of individual lateral root length.

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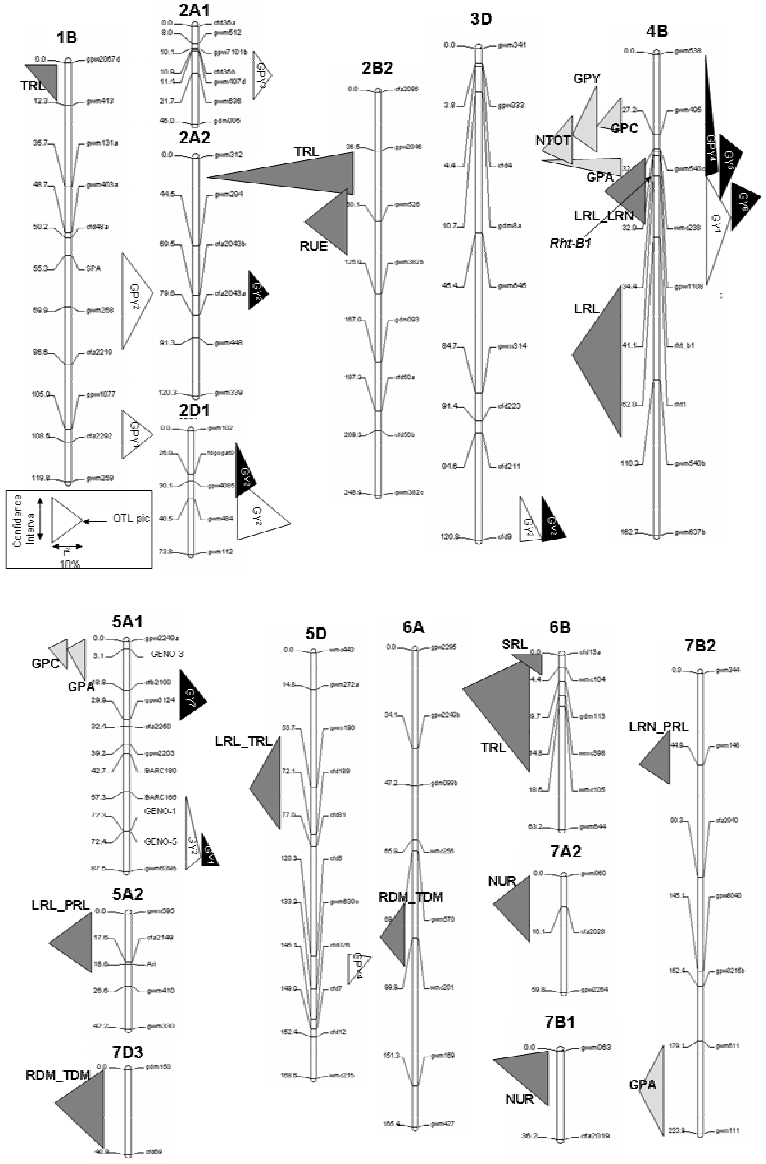

Fig. 1. On the right of the chromosomes are represented QTL detected for GY and GPY either under N^+ (black) or N^- (white). Numbers indicate the environment where the QTL was detected. On the left of the chromosomes are represented QTL either for N stress sensitivity (light grey) or for plant model efficiencies and root architecture traits (dark grey). N stress sensitivity was assessed for grain protein content (GPC), number of grain per m² (GPA), the total N amount at harvest (NTOT), GPY. Plant model efficiencies were the Radiation Use Efficiency (RUE), the ratio between the root dry weight and the plant total dry weight (RDM_TDM), the specific N uptake (NUR) and the Specific Root Length (SRL). The root architecture traits were the total root length (TRL), the lateral root length (LRL), the ratio between lateral root length and primary root length (LRL_PRL), the ratio between lateral root length and total root length (LRL_TRL), the mean individual lateral root length (LRL_LRN) and the branching rate (LRN_PRL) corresponding to the ratio between the lateral root number and the primary root length.