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Plant functional trait variability and trait syndromes among wheat (*Triticum aestivum*) varieties: the footprint of artificial selection

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HIGHLIGHTS:

A unique quantification of 18 functional traits for 57 wheat varieties showed how modern selection had important, sometimes unintentional, consequences on trait variability among varieties and trait syndromes.

ABSTRACT

Although widely used in ecology, trait-based approaches are seldom applied to study agroecosystems. In particular, how functional trait variability among varieties of a crop species compares to the variability among wild plant species and how variety selection can modify trait syndromes needs to be evaluated. Here, we quantified 18 above- and belowground functional traits for 57 varieties of common wheat, representative of different modern selection histories. We compared trait variability between varieties and between *Pooideae* species and analyzed the effect of selection histories on trait values and trait syndromes. For traits under strong selection, trait variability among varieties was less than 10% of the variability observed between *Pooideae* species. But for traits not directly selected like root N uptake capacities, the variability was up to 75% of the variability among *Pooideae* species. Ammonium absorption capacity by roots was counter-selected for conventional varieties as compared to organic varieties and landraces. Artificial selection also altered some trait syndromes classically reported for *Pooideae*. Identifying traits for which high or low variability is present among varieties and characterizing the hidden effects of selection on trait values and syndromes will benefit the selection of varieties to be used especially for lower N input agroecosystems.

KEYWORDS: above- and belowground functional traits, intraspecific trait variation, root nutrient absorption capacity, wheat variety selection, conventional varieties, organic farming varieties, landraces, MAGIC lines.

INTRODUCTION

Functional diversity is increasingly recognized as a key descriptor of the contribution of biological communities to ecosystem functioning (Villéger et al., 2008; Gagic et al., 2015). Functional diversity can be quantified directly by measuring how different organisms (different individuals from the same species or from different species) perform different functions. Although trait-based approaches are increasingly applied in animal and microbial ecology (Vogt et al., 2013; Krause et al., 2016; Le Roux et al., 2016), they have been more widely used in plant ecology, in particular to analyze how functional diversity influences ecosystem functioning and their responses to perturbations or environmental variations (Diaz and Cabido, 2001; Diaz et al., 2004; Hooper et al., 2005; Cantarel et al., 2012, 2015; Freschet and Roumet, 2017; Pommier et al., 2017). Elucidating the variability of trait values among crop species is critical for predicting and managing agro-ecological processes. Artificial selection of crop varieties by farmers or professional plant breeders, aiming at increased performance based on a small number of traits, may have greatly impacted trait variability, with potential consequences for future breeding. Martin et al. (2018) showed that the variability of values for aboveground traits (*i.e.* specific leaf area (SLA), maximum photosynthetic rates and leaf nitrogen) in wheat (*Triticum aestivum* and *T. durum*) and maize (*Zea mays*) was comparable to that observed among wild plant species. However, the effects of artificial selection on trait variability among crop varieties remain seldom evaluated, particularly for belowground traits.

Comprehensive analyses of multiple above- and belowground traits for a range of plants led to the identification of trait syndromes, *i.e.* consistent associations of plant traits. In particular, plants may be classified according to the well-known ‘leaf economics spectrum’ (LES; Wright et al., 2004; Reich, 2014). The LES highlights a trade-off between resource acquisition and conservation in plants. At one end of the spectrum, plant species with high leaf N concentrations, high specific leaf area (SLA) and low leaf dry matter content (LDMC), are associated with high photosynthesis and respiration rates, and a short life span. The opposite is true at the other end of the spectrum. While leaf trait syndromes and their significance are relatively clear, root trait traits and syndromes are less well understood. A ‘root economics spectrum’ (RES; Roumet et al., 2016) parallel to the LES is still-debated (Kramer-Walter et al., 2016; Ma et al. 2018; Martin-Roblès et al. 2018; Kong et al. 2019). The multiple functions of roots (*i.e* water and nutrients absorption, anchoring, resource storage, interaction interface with soil microorganisms) may not be reduced to a single axis related to resource economics (Laughlin, 2010; Kramer-Walter et al., 2016). However, high root dry matter content (RDMC) values seem to be strongly linked to low soil nutrient availability (Ryser and Lambers 1995) and high LDMC values (Craine et al., 2001; Freschet et al., 2010), suggesting the importance of nutrient storage under nutrient-poor environments. SRL generally showed a positive correlation with relative growth rate (RGR) (Reich et al., 1998; Comas and Eissentat, 2004), suggesting that SRL can be related to whole-plant economics (Kramer-Walter et al. 2016). In contrast, the correlation between RDMC and specific root length (SRL) is more debated in the literature (Craine et al., 2001; Kong et al., 2014). Thanks to all this knowledge and the availability of trait data in databases (*e.g.* TRY database, Kattge et al., 2011), trait-based approaches are increasing applied in agroecology (Garnier and Navas, 2012; Milla et al., 2015; Martin and Isaac, 2015 and 2018), but are still scarcely used in crop sciences.

Wheat represents about 20% of the human food supply (CGIAR Wheat, 2013) and had a long history of artificial selection and intentional breeding. It is thus a relevant crop species for evaluation of artificial selection impact on traits and trait syndromes. Intentional or unintentional human-oriented wheat selection has taken several forms, from variety management across farming practices to modern plant breeding technologies, with potentially contrasting consequences for the co-evolution of wheat traits. Modern wheat varieties have often been selected to produce high seed yield under optimal conditions (high fertilizer and pesticide inputs) and to have higher resistance to diseases and shorter stems to resist lodging (Brancourt-Hulmel et al., 2003), and these varieties can also have excellent performance in production systems with reduced agrochemical inputs (Voss-Fels et al., 2019). Still, selection under optimal conditions can have important consequences for some functional traits. For instance, Aziz et al. (2017) have analyzed the effect of wheat selection (for nine Australian *Triticum aestivum* cultivars) on seven traits and showed that selection for yield reduced total root length and increased N total uptake per unit root length. However, selection might also have had unintentional effects on some non-targeted traits, which remains seldom studied. In addition, up to the early 1900's, farmers applied mass-selection to manage the seeds of landraces often used under low input conditions (Wiebe et al., 2017). More recently, modern wheat varieties have also been specifically selected to perform well under organic farming. Evolutionary breeding is another breeding method, based on the design of composite cross populations (CCPs: obtained by crossing several selected founders, usually varieties and landraces), these CCPs being then re-sown over several generations to adapt to a dedicated cropping system and environment while keeping genetic variability (Finckh and Wolfe, 2015; Döring et al., 2011; Dawson and Goldringer, 2012). Each modern selection history is likely to influence the range of values observed for functional traits among wheat varieties and may alter trait syndromes commonly observed for related plant species (for instance among wild species of the same family).

It is important to characterize the (in particular unintentional) effects of artificial selection on and trait values and variability as on trait syndromes to improve wheat variety screening and selection in the future. Indeed, the development of more sustainable and low-input agriculture will likely need the development and use of suitable varieties and variety mixtures based on their functional traits (Barot et al., 2017). Specifically, the past selection history might have led to trait combinations in elite varieties that are no longer suitable for low-input agriculture. For example, trait values and combinations of traits selected to maximize yield under high nitrogen inputs might be not suitable under low nitrogen inputs. More generally, a better characterization of the impact of different selection schemes on trait variability and trait syndromes could identify plant traits overlooked in conventional agriculture (Lammerts van Buerenet al., 2008; Loueille, et al., 2013) but critical for variety adaptation to low-input conditions.

The three main objectives of our study and associated hypotheses were the following:

(1) To compare the level of intraspecific variability existing for a range of above- and belowground functional traits for common wheat (*Triticum aestivum*) to the variability observed between species belonging to the same subfamily (here *Pooideae* from the *Poaceae* family). We assumed that for traits under strong selection by farmers or plant breeders, trait variability between varieties should be lower than observed between species, except when selection targets differed between modern selection histories (*e.g.* seed mass, height).

(2) To analyze the effect of different modern selection histories on the values of these traits. In particular, conventional varieties are selected to perform well under high soil nitrate concentration (de Boer et al., 1989). We thus hypothesized that the ammonium absorption capacity by roots could have been counter-selected for conventional varieties as compared to organic farming varieties and landraces.

(3) To assess how selection has led to particular wheat trait syndromes in comparison to those observed between wild *Pooideae* species. For instance, we hypothesized that selection would have decreased the total allocation to belowground as compared to aboveground plant compartments, particularly for conventional varieties, which could impact whole-plant economics and lessen or even invert the classical positive relationship between relative growth rate and specific root length.

We quantified 18 plant traits (8 belowground traits, 8 aboveground traits, and 2 whole plant traits) and yield for 57 wheat varieties used in France (especially in the Paris Basin), representing a broad range of modern selection histories, and analyzed trait syndromes among these varieties. We also compared the intraspecific variability of trait values and the trait syndromes observed among wheat varieties to their counterparts observed among *Pooideae* species using the TRY database records (Kattge et al., 2011).

MATERIALS AND METHODS

Wheat varieties studied

The 57 selected bread wheat varieties represent a broad range of modern selection histories (Table S1) commonly used in France. Thirty-two are varieties selected in the French catalogue for conventional agriculture, *i.e.* selected to perform well and have high yield under close-to-optimal conditions (in particular high fertilization). They were chosen for their wide use in the Paris Basin, and are hereafter named conventional varieties, CV. Fourteen are organic farming varieties or landraces cultivated in France in the early 1900es, named OVL. OVL were selected on the basis of their wide use in low input or organic farming systems. Eleven wheat lines have been obtained from INRA MAGIC populations, IM, *i.e.* a highly recombinant and multi-parental population evolved during 15 generations under low input conditions at Le Moulon site (Thepot et al., 2015). This overall set of varieties was used to represent a wide range of modern selection histories and of varieties currently used in France. Assessing a larger collection that would be representative of wheat varieties available worldwide and/or of longer term domestication stages (i.e. geographical and/or temporal coverage) was beyond the scope of the study.

Growth conditions

Each plant trait was measured under the same field (Versailles site and Le Moulon site) or greenhouse conditions for all varieties (see Table 1). In field trials, the 57 wheat varieties were planted in 8 m X 1.75 m plots. When necessary, plots were weeded manually or using herbicide. Crops were treated with fungicides following local agricultural practices. Plots were fertilized with NH_4NO_3 brought in three applications (40, 70 and 40 kg N ha^{-1}). This corresponded to low-input system conditions (Dubs et al. 2018). All the 57 varieties were grown in each of the 2 field sites, which were used to measure 6 aboveground plant traits (Table 1).

In complement, two greenhouse experiments were used to quantify root traits on individual plants grown in standardized conditions. For the first greenhouse experiment, seeds of each of the 57 varieties were sown in tall pots (11.3 × 11.3 × 21.5 cm) containing coarse sand (<4 mm). As suggested by Porter et al. (2012), to minimize pot size effects on plant growth and plant traits, the pot size (2.74 L) was selected to have a total plant biomass:pot volume ratio less than 1 (here 0.85 g.L^{-1} for the highest values in the pot experiment). Three seeds of the same variety were sown per pot, and three replicates (pots) per variety were used. Plants were grown during 8 weeks (16 h light – 8 h night; day and night temperatures of 21 and 18 °C, respectively; and a 350 µmol m^{-2} s^{-1} photosynthetic photon flux) and watered three times per week (twice using 50 mL of deionized water per pot; and once using 25 mL hydroponic nutrient solution with 3.5 mM of nitrate and 3.5 mM of ammonium). After 8 weeks, the N uptake capacities of plants and 4 other root traits were characterized (Table 1). For the second greenhouse experiment, the 57 varieties were sown in 2D rhizotrons containing hydroponic nutrient solution with 3.5 mM of nitrate and 3.5 mM of ammonium. The seminal root number and the seminal root angle were measured after 6 days.

Trait measurements

Yield and 18 functional traits were measured for each of the 57 wheat varieties using either the field trials or greenhouse experiments or literature (Table 1). In these experiments, randomization in plots/pots and samplings were performed to avoid cline/gradient. Values for 2 traits were obtained from a compilation of the *GEVES* (https://www.geves.fr/catalogue) and *ARVALIS* (http://www.fiches.arvalis-infos.fr/) data:

- Sensitivity to *Septoria* (Sresist).
- Sensitivity to yellow rust (YRresist).

For these two traits, adult-plant resistance was scored during registration and commercial cycle of varieties. Resistance was also scored by *BIOGER/ECOSYS* laboratories on MAGIC and Landraces during field trials performed in 2013-2014.

Using the Grignon field trial, 6 plants were collected at least 0.40 m from the border of the plots, and the following traits were measured on each plant (Table 1):

- Specific Leaf Area, SLA (cm².g^{-1}): the 6 flag leaves were placed on a blue board and photographed. The surface of each leaf was calculated by an image analyzer (Image J®) and each leaf was then dried at 80°C during 48 hours. SLA was computed as the leaf surface-to-dry mass ratio.
- Leaf nitrogen content, LNC (%): it was measured for each individual dried flag leaf using the Dumas method with a NA 1500 CN analyzer (Fisons Instruments, France).

Using the Moulon field trial, 10 plants were collected at least 0.40 m from the border of the plots, on which measurements of the following traits were performed (Table 1):

- Height (cm) at the grain filling stage: average stem height was measured.

- Total number of ears per plant: it was counted on 1 m² for each variety at the stem elongation stage, and divided by plant number, previously scored in early spring, at seedling stage, on the same area (after germination and frost damages, i.e. final plant count).
- Seed Mass (g): it was evaluated by weighing (and counting) 500 kernels from each variety at harvest.
- Flowering date (calendar days): during the stem elongation period, a survey of plant phenology every 2 days allowed to score the date where 50% of ears were in flowers (extruding stamens).

In addition, using measurement of plant density and number of kernels per ear, the yield (g m^{-2}) was computed for each variety as ((SeedMass x 1000) x Ear/Plant x Plant density x number of kernels per ear).

Using the pot experiment under greenhouse conditions, the uptake capacities of NO_3^- and NH_4^+ by roots were measured for each variety as described by Florio et al. (2017). After 8 weeks of growth, plant roots were washed carefully with distilled water to remove any remaining sand particles. For each pot, the 3 whole plants were kept intact and their entire root system was immersed in pots containing a nutrient solution with KNO_3 and $(NH_4)_2SO_4$ (300 µM total mineral N concentration, with equal NO_3^- and NH_4^+ amounts). One mL aliquots were sampled after 0, 25, 50, 75 and 100 min of incubation; they were filtered (0.20 µm pore size) and stored at -20°C. The NH_4^+ and NO_3^- concentrations were quantified using an ion chromatograph (ICS 900, Dionex, ThermoElectron, France). Uptake capacities were expressed as mg N-NO_3^- and N-NH_4^+ min^{-1} g^{-1} root dry mass for NO_3^- and NH_4^+ uptake rates, respectively. Immediately following N uptake capacity measurements, the fresh root system was weighed and stored in distilled water a few days at 4°C until fresh root morphology determination by digital scanning. To avoid any bias in term of root order (McCormack et al., 2015), the whole root systems were suspended in 1 cm of water in a 29 cm × 42 cm clear acrylic tray and scanned at 300 dpi with a scanner (Epson Perfection V700 PHOTO, Regent Instruments Inc., Canada). Images were analysed with the WinRHIZO^{TM} software to determine root length and average root diameter. Specific root length (SRL, m g^{-1}) was computed as the root length-to-dry mass ratio. Following root morphology analysis, the sample was weighted and dried for 48 h at 105°C. Root dry matter content (RDMC, mg g^{-1}) was computed as root dry mass divided by water-saturated fresh mass. The foliage of each variety were dried at 105°C for two days to measure above dry masses (DM) and compute the plant Shoot/Root Ratio (SRR). Root aliquots were milled to fine powder in order to determine Root Nitrogen Content (RNC, %) using an elemental analyser (Flash EA 1112 Series CNS analyser, ThermoFisher Scientific, USA).

Strictly speaking, our data were not sufficient to compute the Relative Growth Rate (RGR, g day^{-1}), as RGR often decreases with increasing plant size (Paine et al., 2012). Still, we computed the plant dry matter produced at the end of the 58 days growing period for each wheat variety as DM = DM_{t58} – DM_{t0}; where DM_{t58} is the total plant biomass after 58 days and DM_{t0} is the seed mass. This provides a rough but useful index of the biomass build up during the first weeks after germination, which is highly important for plant carbon economy (Pérez-Harguindeguy et al., 2013).

Seminal root morphological characteristics (seminal root number and seminal root mean angle) were measured following the methodology described in Planchamp et al. (2013). Briefly, 10 germinated seeds of each variety were grown for 6 days in individual 2D rhizotron made of pouches lined with wet filter paper supplying water. After 6 days, each rhizotron was opened revealing seedling root system. An image of the whole plant was taken with a digital camera and was analysed using the Smartroot image analysis tool (Lobet et al. 2011) to quantify seminal root number and mean root angle.

Use of existing data sets to retrieve Pooideae *trait values*

The comparison of intra-species variation of trait values for wheat with intra-species variation of traits for other *Pooideae* species was not possible as there is no sufficient data on within-species trait variation in wild species for that many traits. We thus compared the variability of wheat trait values to trait variability between a large panel of grass species, including their wild relatives *sensus largo*, by focusing on the *Pooideae* subfamily from the *Poaceae* family. This subfamily is one of the largest families of *Poaceae*, which contains most of the cereals, including wheat, oats, barley, rye, and contains a large part of grass species from temperate zone and Eurasia (Soreng et al., 2017). The values of the 8 following traits were extracted for *Pooideae* species from the TRY database (Kattge et al., 2011 ; this database contains plant trait data collected worldwide): RDMC, RNC, SRL, average root diameter, SLA, LNC, height and seed mass. Values for RDMC, RNC, SRL, average root diameter, SLA, LNC, height and seed mass were available for 11, 37, 21, 32, 154, 14, 289 and 386 species, respectively. When several values were available for a given species, the mean was considered. For NO_3^- and NH_4^+ uptake capacities, we used the dataset described in Grassein et al. (2015) which includes values of N uptake capacities for 8 *Pooideae* species.

Statistical analyses

All statistical analyses were carried out using JMP Pro17 (SAS Software). To test the level of trait variability for RDMC, RNC, SRL, average root diameter, SLA, LNC, Height, Seed mass and N uptake capacities, among wheat varieties and among *Pooideae* species, the coefficients of variation (*i.e.* standard deviation divided by the mean) were computed and the minimum and maximum trait values for wheat varieties and *Pooideae* species were used. As *Pooideae* traits retrieved from TRY database vary in sample size, from 11 to 368 species and to avoid bias of the sample size in trait variability analyses, we measured the coefficients of variation on data from a random sampling repeated 10 times for each trait studied, in order to have the same number of values for species and varieties. For instance, when values for a given plant trait were available for n species in the TRY database with n<57, random sampling for n varieties was performed on our wheat dataset. When TRY database included more than 57 species for a trait, random sampling of 57 species was performed on the TRY database data. We thus computed coefficient variations with same "n" between wheat varieties and *Pooideae* species (n = 11, 37, 21, 32, 57, 14, 57, 57 and 8, respectively for RDMC, RNC, SRL, average root diameter, SLA, LNC, Height, Seed mass and N uptake capacities). Given that the level of trait variability can strongly differ between traits, we also compared the variability among wheat varieties to that observed among *Pooideae* species for each trait by computing the following log-ratios:

$$LogRatio_{trait} = \log\left(\frac{CVwheat_{trait}}{CVPooideae_{trait}}\right)$$

LogRatio values close to zero thus correspond to similar variability among varieties as compared to the variability among *Pooideae* species, whereas negative LogRatio values correspond to lower variability among varieties than among *Pooideae* species (e.g. -1 corresponds to a variability among varieties equal to 10% of the variability among *Pooideae* species).

To test possible trait differences between the three modern selection histories, a one-way variance analysis (ANOVA) was used. A non-parametric mean analysis (Kruskall-Wallis) was used when data did not conform with assumptions of normality and homogeneity of variances even after Log-transformation of data. We then used HSD Tukey-Kramer test in case of normal data distribution or Kruskall-Wallis multiple mean comparison in case of non-normal data distribution to analyse differences in trait values between selection histories. In addition, a principal component analysis (PCA) was used to explore the distribution of varieties based on their trait values, considering their artificial selection history.

To analyse trait syndromes, correlations between all wheat trait pairs were tested using Pearson test for normally distributed data or Spearman test for non-normally distributed data. Effects with *p-value* < 0.05 are referred to as significant.

RESULTS

Variability of functional traits among wheat varieties and *among* Pooideae *species*

Considering the 11 functional traits for which values for *Pooideae* species were available, trait variability between species was the highest for plant height and seed mass (coefficient of variation of 1.96 ± 0.4 and 1.44 ± 0.38, respectively; Fig. S1). Intermediate values of trait variability between *Pooideae* species were observed for average root diameter, LNC, Ear/Plant, SRL and NO_3^- and NH_4^+ uptake capacities (coefficient of variation between 0.6 and 1.2). RNC, SLA and RDMC had the lowest level of variability between *Pooideae* species (coefficient of variation around 0.4, Fig. S1).

Wheat variety trait range was generally included in the *Pooideae* species trait range (Fig. 1-Top). Only, RDMC lie outside the *Pooideae* species range, with lower values as found for *Pooideae* species. Some wheat traits (i.e. average root diameter and NH_4^+ uptake) were found at extremes of that range, with higher values for root diameter and lower values for NH_4^+ uptake compared to the minimum and maximum data found for *Pooideae* species. The other traits were at the center of *Pooideae* distribution with a very low overlap (<6%) for wheat traits as LNC, seed mass and height and a very high overlap (> 70%) for NO_3^- uptake, on average the overlap for other traits is about 21.7% ± 2.3% (Fig. 1-Top). For all traits, trait variability was significantly lower among wheat varieties than among *Pooideae* species (p < 0.0001) (Fig. 1-Bottom and S1). For 3 of the 10 studied functional traits, the variability observed between wheat varieties was negligible as compared to the variability between *Pooideae* species (Fig. 1). The variability of seed mass, root diameter and leaf nitrogen content (LNC) between varieties was indeed 6.3 %, 6.3 %, and 9.1 % of the variability observed between *Pooideae* species, respectively. The variability between varieties for height, number of ears by plant, specific root length (SRL), specific leaf area (SLA) and root nitrogen content (RNC) represented 13.7 %, 19.4 %, 25.2 %, 25.5 % and 26.5 % of the variability between *Pooideae* species, respectively. Three root functional traits were characterized by a high variability between wheat varieties.

The variability of root dry matter content (RDMC), NO_3^- uptake capacity and NH_4^+ uptake capacity between wheat varieties was indeed 44.2 %, 52.4 % and 75.8 % of the variability observed between *Pooideae* species, respectively (Fig. S1).

Relationships between trait values and selection type for wheat varieties

A PCA was performed for the 57 wheat varieties based on the 16 traits and yield. The first two PCA axes explained in total 43.5 % of the total variance (resp. 22.8% and 20.7%; Fig. 2). Height, SRR, RDMC, yield, SLA, root angle, DM, and NH_4^+ uptake contributed substantially to the first axis (loading values up to 0.45; Table S2). Yield and root angle had negative scores on axis 1, whereas the other traits mentioned above had positive scores. The second axis was mainly based on flowering, RNC, S_{resist}, SRL, height, average root diameter, SLA and Sresist, with negative scores for root diameter (Table S2). NO_3^- and NH_4^+ uptake capacities were the most important traits for PCA axis 3 (10.7% of the total variance; loadings > 0.50; Table S2). Modern selection history was a major factor influencing the trait values of wheat varieties: varieties from the 3 different artificial selection types were significantly discriminated along both PCA axes 1 and 2 (Fig. 2). Along axis 1, conventional varieties (CV) were significantly different from INRA MAGIC (IM) varieties and organic farming varieties and landraces (OVL; Kruskal-Wallis test on variety scores, $\chi^2 = 38.45$, $p < 0.0001$). Along axis 2, all variety types were significantly different from each other (Kruskal-Wallis test, $\chi^2 = 31.1$, $p < 0.0001$).

Trait-by-trait analyses confirmed that most wheat traits studied were significantly influenced by the type of modern selection (Table 2). The 8 aboveground functional traits and the 2 whole-plant traits were all significantly influenced by the modern selection histories. In contrast, 3 of the 8 belowground traits (SRL, root diameter and NO_3^- uptake capacity) were not impacted by the artificial selection type. CV were significantly smaller, more resistant to yellow rust and septoria, and had a higher root angle and ear number per plant, with higher yield (Table 2) than the two other types of varieties. OVL were significantly taller and later, and had higher SLA, SRR and root number than the CV and IM varieties. OVL also had a higher yellow rust resistance than the IM varieties (Table 2) and a higher NH_4^+ uptake capacity and a lower plant dry mass produced (DM)) than CV. Finally, the IM had a low resistance to diseases, a high growth rate, the lowest values of nitrogen content (LNC and RNC) and the highest RDMC values (Table 2).

When considering trait variability between varieties for each modern selection history, variability was similar between selection histories for seed mass, SRL, RNC and SLA (Fig. S2). The variability of NO_3^- uptake capacity and root diameter was lower among OVL than among

IM and CV (Fig. S2). In contrast the variability of RDMC was higher among OVL than among IM or CV. The variability of height was highest among IM (Fig. S2).

Trait syndromes observed between wheat varieties and between plant species

Several syndromes reported in plant ecology for belowground traits were also observed for wheat varieties. For instance, the negative SRL-RDMC and SRL-root diameter correlations were also found for wheat varieties (Fig. 3c and 3d). Similarly, the positive SRL-RNC correlation was also found for wheat varieties (Fig. 3f). In contrast, several syndromes classically reported in plant ecology for aboveground traits were not observed for wheat varieties. In particular, the positive SLA-LNC and SLA-DM correlations were not found for wheat varieties (Fig. 3a and 3b). Moreover, SRL was negatively correlated with DM for wheat varieties ($r = -0.565$ and $p < 0.0001$, Fig. 3e and Table S3). In addition, RNC and LNC were not significantly correlated for wheat varieties, in contrast with the positive correlation generally reported in the literature (Fig. 3g).

Table S3 presents the level of significance and strength of all the relationships between trait pairs. Interestingly, the strongest relationships with yield (the major target of variety selection) were observed not only for height (negative) and Ear/Plant (positive), but also for NH_4^+ uptake capacity (negative). Underlying the latter relationship (Fig. 4), CV had high yield and low NH_4^+ uptake capacity, whereas OVL had low yield and high NH_4^+ uptake capacity (Table 2). In contrast, NO_3^- uptake capacity was not correlated to yield (Table S3, Fig. 4).

DISCUSSION

How does trait variability between varieties of T. aestivum *compare to the variability observed between* Pooideae *species?*

The level of trait variability between wheat varieties as compared to between *Pooideae* species was strongly trait-dependent. Siefert et al. (2015) found that intraspecific variability of trait values represented around 30 % of the interspecific variability observed for different plant communities. In our study, three of the six studied aboveground traits (mass, height and leaf nitrogen content) showed particularly low variability between wheat varieties (less than 10% of the variability found between *Pooideae* species for mass and leaf nitrogen content). The low seed mass variability between varieties of the same species (*Triticum aestivum*) could be explained by the morphologic stature of the observed plants and ecophysiological and biomechanical constraints, *i.e.* small species cannot produce very large seeds (Reich, 2014, Sandel et al., 2016) even under artificial selection. It is also very likely that breeding constrained observed grain size in *T. aestivum*, to facilitate post-harvest technological processing such as milling. In addition, for cultivated species, crop establishment is an important phase of the plant cycle that is improved by relatively large seed size (Gegas et al. 2010). A similar explanation can be used for the small intraspecific variation observed for plant height since this trait has been heavily selected for maximization of harvest efficiency. Leaf chemical traits are known to have high variability in wild species (Kazakou et al., 2014: Siefert et al., 2015). The lower variability of LNC between wheat varieties than between *Pooideae* species could be explained by fertilization which probably leads to a high similarity in term of nutrient availability in cultivated soil relatively to the high variability possibly observed in soils from natural, unmanaged environments. Globally, the two aboveground traits for which intraspecific variability was less than 10% of the total variability observed between *Pooideae* species were (1) seed mass which has been a major target for breeding for centuries (Donald, 1968; Austin et al., 1977), and (2) LNC which was not directly selected but that is a major determinant of grain protein content (i.e. LNC at anthesis stage; Zhao et al., 2005), a trait that itself was a target for breeding. Thus, as stated in our first hypothesis, when traits of a cultivated plant like wheat have been heavily selected, the variability of these traits observed between varieties could be very low as compared to the variability observed between related non-domesticated species. In addition to aboveground traits, low intraspecific variability was also observed for one belowground trait. Average root diameter was also weakly variable between wheat varieties with less than 10% of the variability observed between *Pooideae* species. Average root diameter seems to be a stable functional trait for other crop species (Nakhforoosh et al., 2014). The low variability of average root diameter within wheat varieties could be explained by biomechanical constraints because root diameter contributes, together with root plate size, to the root system ability to resist stem lodging (Crook and Ennos 1993, 1994).

In contrast, all the other measured root traits (*i.e.* root dry matter content, nitrogen uptake capacities) showed a large variability, *i.e.* 44% to 76 % of the variability observed between *Pooideae* species. The variability of nitrate and ammonium uptake capacities between wheat varieties has rarely been studied so far. Our results showing that the nitrate and ammonium uptake capacities are still highly variable between wheat varieties can be useful in an agroecology perspective. Breeding for variety adapted to low input agricultural systems and soils with high ammonium:nitrate ratios might benefit from this trait variability. Indeed this would allow selecting genotypes with high ammonium uptake capacities, a N form that becomes relatively more important under low mineral fertilization regimes More generally, our results suggest that some traits, and especially root traits such as the uptake capacities for different nitrogen forms, display sufficient intraspecific variability to promote functional diversity. This result thus supports previous works that propose to design varietal mixtures that would maximize functional complementarity (Barot et al., 2017).

What are the effects of different modern selection histories on a range of above- and belowground traits?

The modern selection of crop variety characteristics by farmers and plant breeders is known to differ, e.g. when their objective is to obtain varieties suitable for conventional or for organic cropping systems compared to conventional systems (Reid et al., 2011; Mikò et al., 2017). Compared to other modern selection histories, CV were characterized by a higher yield and were also smaller, more resistant to yellow rust and septoria, with higher ear number per plant and higher root angle of seminal roots than for OVL and IM. This is consistent with the fact that yield and traits associated to yield such as the number of ears by plant or the number of grains by ear (Reynolds et al. 2009) along with resistance to diseases, are of major importance for elite genotypes selected for conventional wheat cropping (Smale et al., 1998; Mir et al., 2012). Seminal root angle was also a trait strongly influenced by selection of CV varieties (Smale et al., 1998). Root angle is actually recognized as an index of rooting architecture, with a positive correlation with rooting depth and soil water extraction, hence being related to drought tolerance for crop plants as wheat (Oyanagi et al., 1993; Manschadi et al., 2008), maize (Nakamoto et al., 1991) and sorghum (Singh et al., 2012). The CV varieties with larger seminal root angle are potentially less impacted by drought conditions than OVL varieties. This trait can thus be under indirect selection, as breeding for drought tolerance is an important goal.

In contrast, we found that OVL were significantly taller and later-flowering, with higher specific leaf area, shoot:root ratio and root number than CV and IM varieties. They also had a better yellow rust resistance than the IM varieties and a higher NH_4^+ uptake capacity than CV varieties. Plant height and shoot biomass were already reported to be significantly higher for landraces as compared to modern varieties (Bektas et al., 2016). Although high stems may cause lodging and yield loss (Borlaug, 2007), in organic farming, tall plants are still preferred (i) for their competitiveness against weeds and (ii) for their contribution to straw production (Annicchiarico and Pecetti, 2003). Surprisingly, OVL were characterized by a high number of seminal roots, although the seminal root number is generally positively linked with grain yield for conventional breeding (Lynch et al., 2007; Liu et al., 2013; Xie et al., 2017). However, Xie et al. (2017) reported that a higher number of seminal roots was also associated with a delayed maturity, and OVL were generally less early than other varieties. This suggests co-selection of seminal root number and precocity, or a genetic drift associated to one of the two traits (Smith and Haigh, 1974). OVL were also characterized by a higher capacity to uptake ammonium as compared to CV, whereas CV and OVL did not differ for their capacity for nitrate uptake. This can be explained because CV are selected to perform well under optimal or high nutrient conditions driven by mineral fertilizers application. A large part of ammonium brought to soil by fertilizers is rapidly oxidized and transformed into nitrate in agricultural soils under conventional management (De Boer et al., 1989). For instance, Attard et al. (2016) reported that the ratio of potential nitrification to potential ammonium immobilization was around 3-fold higher for croplands than grasslands. Thus, the ammonium concentrations in soils of conventional wheat-production systems are often much lower than the nitrate concentration (Personne et al., 2015), which can explain the counter-selection of NH_4^+ uptake capacity for CV. In contrast, OVL exhibit trait values that may be beneficial when the major mineral N form in soil is ammonium, which is often the case for soils of organic farming systems (Lammerts van Bueren et al., 2011). Based on our results, it would be of interest to test whether the higher capacity of OVL to uptake NH_4^+ significantly contributes to their good performance in organic farming and more specifically in soils with high ammonium:nitrate ratio.

IM lines were characterized by a medium height, a low resistance to diseases, a high growth rate, the lowest leaf and root nitrogen contents and the highest root dry matter content. These lines were derived from a composite cross population evolved under open pollination during 15 generations, under low chemical input. Their evolution was driven by the reproductive success of individuals, while the specific outcrossing regime, based on tagging male sterile plants, has resulted in a selection toward early plants (Thépot et al., 2015). This could explain the marked footprint of selection on relative growth rate for IM lines, because relative growth rate is a key trait impacted by breeding schemes in relation with flowering date. Indeed, grain crops should switch early from vegetative to reproductive phases to avoid environmental stresses like summer drought and achieve a high grain-to-total biomass ratio at harvest. The particularly low values of leaf and root nutrient contents in IM lines may be explained by the difference either in growth stages (more advanced for IM in the field) or in N remobilization efficiency within varieties. In wheat, N remobilization from vegetative tissues can indeed contribute up to 90% of the N incorporated by the grains during anthesis (Kichey et al., 2007; Bogard et al., 2010). The particularly low leaf and root N contents observed at flowering for IM lines could be due to an efficient N-remobilization in favor of grains. Further experiments labelling a range of varieties with ^{15}N during the vegetative stage and comparing the efficiency of N remobilization to fill grains could test this assumption.

Artificial selection can alter trait syndromes typically observed between plant species

Trait-based approaches have provided general insights on plant strategies regarding resource economy, with the idea that plant traits linked to nutrient, water and light resources differ between plants from unproductive ecosystems and those from more productive sites (Craine, 2009). The leaf economics spectrum (LES; Wright et al., 2004) was shown to be also valid at the intraspecific level for wild *Pooideae* species like *Dactylis glomerata*, *Festuca paniculata* and *Sesleria caerulea* (Albert et al., 2010), and for crop species like wheat, maize (Martin et al., 2018), rice (Xiong and Flexas, 2018) or soy (Hayes et al., 2019). In our study, belowground traits syndromes were observed among wheat varieties, e.g., negative correlations between SRL and RDMC, and a positive correlation between SRL and RNC (as seen in Prieto et al., 2015; Roumet et al., 2016; Valverde-Barrantes et al., 2017). Firstly, this could suggest that these root trait syndromes hold for wheat varieties because the root traits would not have been directly selected during domestication and/or by modern selection. Secondly, the traits involved in these root syndromes could have been selected during domestication and/or modern selection but without altering the syndromes due to strong trade-offs related to the underlying genetic architecture or to eco-physiological constraints.

SRL was negatively correlated with DM for wheat varieties. DM was likely positively correlated to RGR of varieties, though it is expected that it underestimated RGR for varieties with the highest biomass (Paine et al., 2012). Still, our results are in opposition to the general positive correlation between SRL and RGR reported when comparing plant species (Reich et al., 1998; Wright and Westoby, 1999; Comas & Eissental, 2004; Kramer-Walter et al., 2016), though there are uncertainties on how root traits covary with aboveground and whole plant traits (Ma et al. 2018; Kong et al 2019). In the literature, high RGR is often a key attribute of exploitative plants that also have a deep root system with high SRL allowing an efficient exploration of the soil volume and acquisition of soil resources (Kramer-Walter et al., 2016; Ravenek et al., 2016). One explanation is that the selection of wheat varieties has been carried out under agronomic conditions that maximize growth and yield under high fertilization, which would have released the selection pressure on the capacity to efficiently acquire soil nutrients. However, the usual positive RGR-SRL (or DM-SRL) relationship was altered for wheat varieties independently of the modern selection histories studied here. This suggests that the shift in this relationship was not related to modern selection, but rather occurred during wheat domestication or early selection. Roucou et al. (2018) suggested that the domestication of *T. turgidum via* changes in management practices (fertilization, crop density…) has uncoupled the above- and belowground traits. These authors found that the wild ancestors of *T. durum* wheat exhibit stronger correlations between above- and belowground traits than the domesticated forms. The domestication and the advent of nitrogen fertilization seem to have accelerated wheat growth and reduced plant investment to roots (Gioia et al., 2015) and may have affected some trait syndromes as suggested by our results.

CONCLUSION

Our results demonstrate that the variability of many traits directly selected by breeders (as seed mass for example) is –as expected– much lower among wheat varieties than among *Pooideae* species, but that the variability of some root traits (RDMC and N uptake capacities) remains remarkably high in wheat varieties. We also demonstrated that modern conventional selection had unintentional and 'hidden' effects on root traits, such as decreasing ammonium uptake capacity by roots. Finally, our results highlight the capacity of artificial selection to alter some plant trait syndromes commonly observed for wild plant species, here the positive relationship between SRL and buildup of biomass during the first weeks following germination turned into a negative relationship for wheat varieties, likely due to selection for high growth and yield in resource-rich or fertilized environments. We believe these results provide interesting prospects in the context of the low-input agriculture. First, the remaining functional diversity existing for some traits, in particular root trait values, makes plausible a breeding effort specifically focused on such low-input systems. Second, this functional diversity existing within wheat varieties can also be a tool used to design variety mixtures with high potential for functional complementarity and thus high yield resilience to fluctuating environmental conditions. In perspective, it remains to be investigated how this variability transpose to field conditions.

DATA ACCESSIBILITY

Data available from the TRY database: Kattge, J., Bönisch, G., Günther, A., Wright, I., Zanne, A., Wirth, C., Reich, P.B. and the TRY Consortium (2011) TRY - Categorical Traits Dataset. Data from: TRY - a global database of plant traits. TRY File Archive https://www.try-db.org/TryWeb/Data.php#3.

SUPPLEMENTARY DATA

Supplementary data are available at JXB online

Table S1: List of the wheat varieties studied, with the variety names and selection type used to obtain each variety.

Table S2: Wheat trait loadings on the three first axes of the principal component analysis.

Table S3: R values retrieved from Pearson or Spearman correlations between each pair of wheat functional traits; and P-values for the same correlations.

Figure S1: Values of the coefficient of variation for 10 traits observed either (white bars) among wheat (*Triticum aestivum*) varieties, (black bars) among *Pooideae* species.

Figure S2: Values of the coefficient of variation for these traits observed either (white bars) among all the 57 wheat varieties or among varieties corresponding to one of the 3 artificial selection types

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AUTHORS’ CONTRIBUTIONS

All authors conceived the ideas and designed methodology; all authors contributed to the data collection; A.A.M. Cantarel analysed the data; A.A.M. Cantarel and X. Le Roux led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Table 1: Plant traits and yield quantified for the 57 wheat varieties, with indication of the plant stage and growth conditions for which they were measured. The last column indicates when it has been possible to compare the variability of a given trait between varieties and between *Pooideae* species using the TRY-database or the Grassein et al. (2015) data set (n = number of *Pooideae* species considered).

	Unit	Meaning	Stage/age of the plant	Growth conditions	Comparison with...
a) Below-ground traits					
RDMC	mg g^{-1}	Root Dry Matter content	8 weeks	Greenhouse conditions in sand and hydroponic solution, *Site: Lyon*	TRY database (n= 11)
RNC	%	Root Nitrogen Content	8 weeks	Greenhouse conditions in sand and hydroponic solution, *Site: Lyon*	TRY database (n= 37)
SRL	m g^{-1}	Specific Root Length	8 weeks	Greenhouse conditions in sand and hydroponic solution, *Site: Lyon*	TRY database (n= 21)
RootDiameter	mm	Mean root diameter	8 weeks	Greenhouse conditions in sand and hydroponic solution, *Site: Lyon*	TRY database (n= 32)
NO_3^-uptake	mg g^{-1} min^{-1}	NO_3^- uptake per root unit	8 weeks	Greenhouse conditions in sand and hydroponic solution, *Site: Lyon*	Grassein et al. 2015 (n= 8)
NH_4^+uptake	mg g^{-1} min^{-1}	NH_4^+ uptake per root unit	8 weeks	Greenhouse conditions in sand and hydroponic solution, *Site: Lyon*	Grassein et al. 2015 (n= 8)
RootNumber	No dimension	Mean root number	6 days	Hydroponic growth in a 2D rhyzotron, *Site: Clermont*	-
RootAngle	Degree	Mean root angle	6 days	Hydroponic growth in a 2D rhyzotron, *Site: Clermont*	-
b) Above-ground traits					
SLA	cm².g^{-1}	Flag leaf area per flag leaf dry mass	Flowering	Field conditions, 170 plants m^{-2}, *Site: Grignon*	TRY database (n= 154)
LNC	%	Flag leaf nitrogen content	Flowering	Field conditions, 170 plants m^{-2}, *Site: Grignon*	TRY database (n= 14)
Flowering	days	Flowering date	Flowering	*Field conditions,* 100 plants m^{-2},	-

				Site: Le Moulon	
Height	cm	Mean height of the main shoot	Grain filling	Field conditions, 100 plants m^{-2}, *Site: Le Moulon*	TRY database (n= 289)
Ear/Plant	Ears plant^{-1}	Mean number of ears per plant	Harvest	Field conditions, 100 plants m^{-2}, *Site: Le Moulon*	
SeedMass	g	Thousand Kernels Weight/1000	Harvest	Field conditions, 100 plants m^{-2}, *Site: Le Moulon*	TRY database (n= 386)
YRresist	%	Sensitivity to yellow rust, percentage of the leaf surface non-attacked	Tillering to flowering	Compilation of data from ARVALIS, and the ECOGER and ECOSYS laboratories	-
Sresist	%	Sensitivity to septoria, percentage of the leaf surface non-attacked	Tillering to flowering	Compilation of data from ARVALIS, and the ECOGER and ECOSYS laboratories	-
c) Whole-plant traits					
SRR	No dimension	Shoot root ratio	8 weeks	Greenhouse conditions in sand and hydroponic solution, *Site: Lyon*	-
DM	g	Plant dry matter produced	8 weeks	Greenhouse conditions in sand and hydroponic solution, *Site: Lyon*	-
Yield	g.m^{-2}	Seed yield at harvest	Harvest	Field conditions, 100 plants m^{-2}, *Site: Le Moulon*	-

Table 2: Effect of wheat variety selection type on the 18 plant traits studied and on yield. Trait acronyms are as in Table 1. CV: conventional varieties; IM: INRA MAGIC populations; and OVL: organic varieties and landraces. For each trait, means (presented with standard deviations) are compared between the 3 selection types. P-values in bold indicate significant differences (P<0.05) between selection types for a given trait, and different letters then indicate significant differences. * indicate log-transformed data.

	Wheat Selection Type			**Statistical Analysis**	
Traits	CV	IM	OVL	Tests	p-value
a) Below-ground traits					
SRL	193.35 ±29.73	183.83 ±26.23	204.51 ±29.37	One-Way ANOVA	0.211
RNC	0.72 ±0.05 ^{a}	0.65 ±0.07 ^{b}	0.76 ±0.06 ^{a}	One-Way ANOVA	**<0.001**
RDMC	79.23 ±7.53 ^{a}	92.86 ±14.18 ^{b}	83.97 ±18.03 ^{ab}	Kruskall-Wallis	**0.017**
RootDiameter	0.28 ±0.02	0.29 ±0.03	0.27 ±0.01	One-Way ANOVA*	0.079
NH_4^+uptake	29.47 ±8.81 ^{a}	38.33 ±13.46 ^{ab}	41.32 ±11.39 ^{b}	One-Way ANOVA*	**0.001**
NO_3^-uptake	17.21 ±6.08	13.92 ±4.6	17.55 ±3.54	One-Way ANOVA*	0.095
RootNumber	3.57 ±0.45 ^{a}	3.86 ±0.55 ^{ab}	4.12 ±0.48 ^{b}	Kruskall-Wallis	**0.003**
RootAngle	149.73 ±6.64 ^{a}	144.05 ±4.72 ^{b}	142.93 ±4.93 ^{b}	One-Way ANOVA	**<0.001**
b) Above-ground traits					
SLA	19.14 ±1.45 ^{a}	20.28 ±1.78 ^{a}	22.58 ±1.75 ^{b}	One-Way ANOVA	**<0.001**
LNC	3.63 ±0.32 ^{a}	3.31 ±0.24 ^{b}	3.75 ±0.22 ^{a}	One-Way ANOVA	**0.002**
Flowering	18.36 ±3.63 ^{a}	16 ±4.7 ^{a}	29.25 ±3.91 ^{b}	One-Way ANOVA	**<0.001**
Height	86.75 ±6.17 ^{a}	97.5 ±15.66 ^{b}	145.5 ±10.48 ^{c}	Kruskall-Wallis	**<0.001**
SeedMass	46.19 ±3.27 ^{a}	46.35 ±4.35 ^{ab}	49.42 ±4.3 ^{b}	One-Way ANOVA	**0.027**
Ear/Plant	7.38 ±1.2 ^{a}	6.12 ±1.31 ^{b}	6.12 ±1.14 ^{b}	One-Way ANOVA	**0.001**
YRresist	89.64 ±13.31 ^{a}	56.09 ±23.41 ^{b}	76.07 ±20.24 ^{c}	Kruskall-Wallis	**<0.001**
Sresist	59.37 ±14.55 ^{a}	35.03 ±18.78 ^{b}	68.13 ±16.46 ^{a}	One-Way ANOVA	**<0.001**
c) Whole-plant traits					
SRR	0.83 ±0.13 ^{a}	1.24 ±0.69 ^{ab}	1.20 ±0.59 ^{b}	Kruskall-Wallis	**0.009**
DM	1.69 ±0.04 ^{a}	1.93 ±0.07 ^{b}	1.76 ±0.06 ^{ab}	One-Way ANOVA	**0.020**
Yield	987.8 ±152.4 ^{a}	732.5 ±112.3 ^{b}	659.5 ±126.6 ^{b}	One-Way ANOVA	**<0.001**

Figure legends:

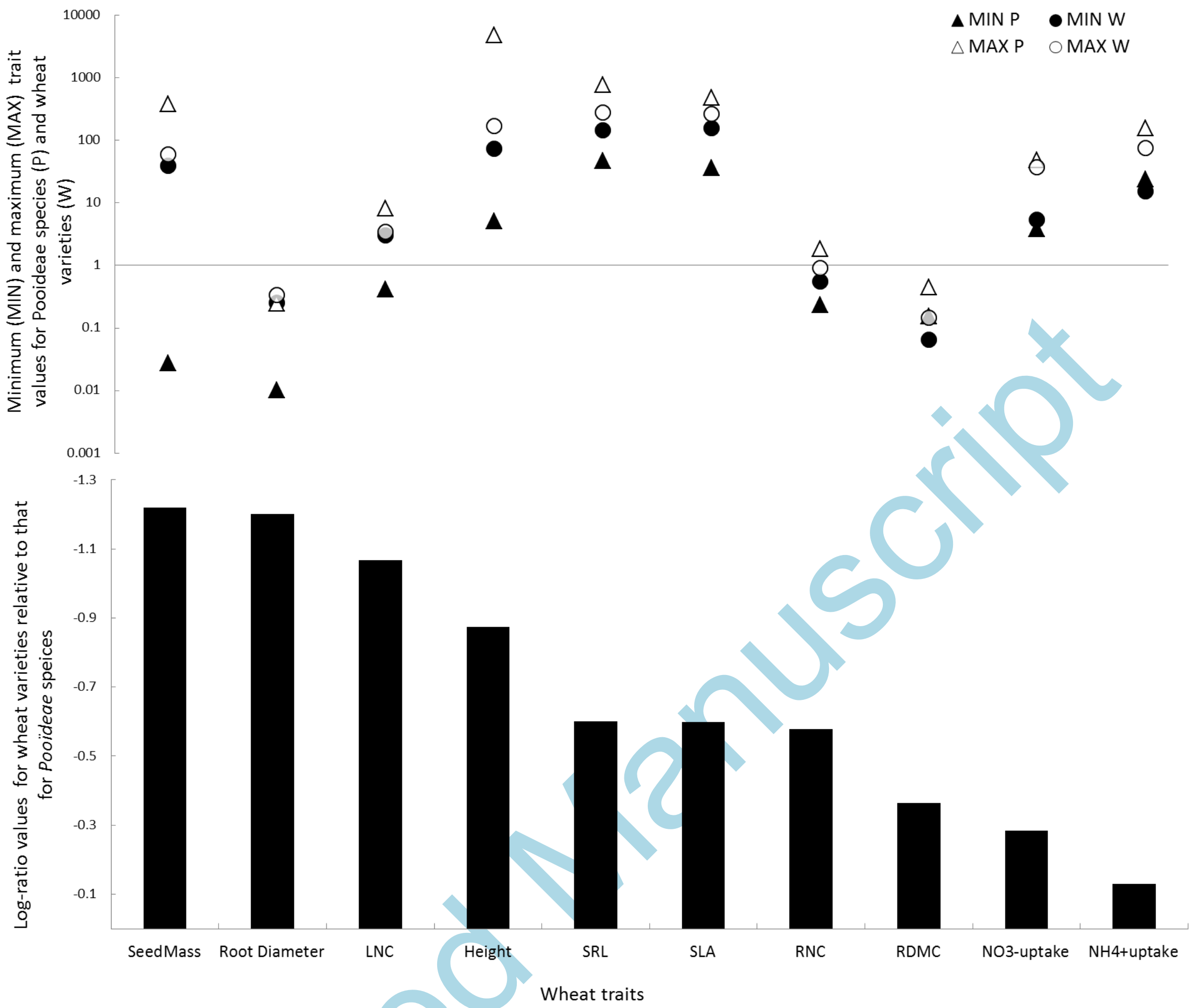
Figure 1: (Top) Comparison of the range of values (minimum and maximum) observed for the 10 traits found for wheat varieties and *Pooideae* species (either in the TRY database or in Grassein et al. 2015 – see Table 1). (Bottom) Variability of trait values observed among wheat varieties as compared to the variability reported between *Pooideae* species, expressed as a log-ratio, for each trait for which a sufficient number of *Pooideae* species were available. Log ratio values close to zero correspond to similar variability among wheat varieties as compared to the variability among *Pooideae* species; negative Log ratio values correspond to lower variability among varieties than among *Pooideae* species (e.g., -1 corresponds to a variability among varieties equal to 10% of the variability among *Pooideae* species).

Figure 2: Biplot resulting from the Principal Component Analysis applied to the 57 wheat varieties and based on the 16 wheat traits studied plus yield (in bold). Acronyms of wheat traits as in Table 1. •: conventional varieties; ×: INRA MAGIC populations ; and Δ: organic varieties and landraces.

Figure 3: Testing the existence, among wheat varieties, of major trait syndromes reported in plant ecology literature. Symbols referring to the 3 selection types used to obtain wheat varieties are as in Figure 2. P-values in bold and plain lines indicate significant correlations. Please not that as RGR could not be modeled from the temporal dynamics of biomass, the build up of biomass after 58 days, DM, was used in this figure.

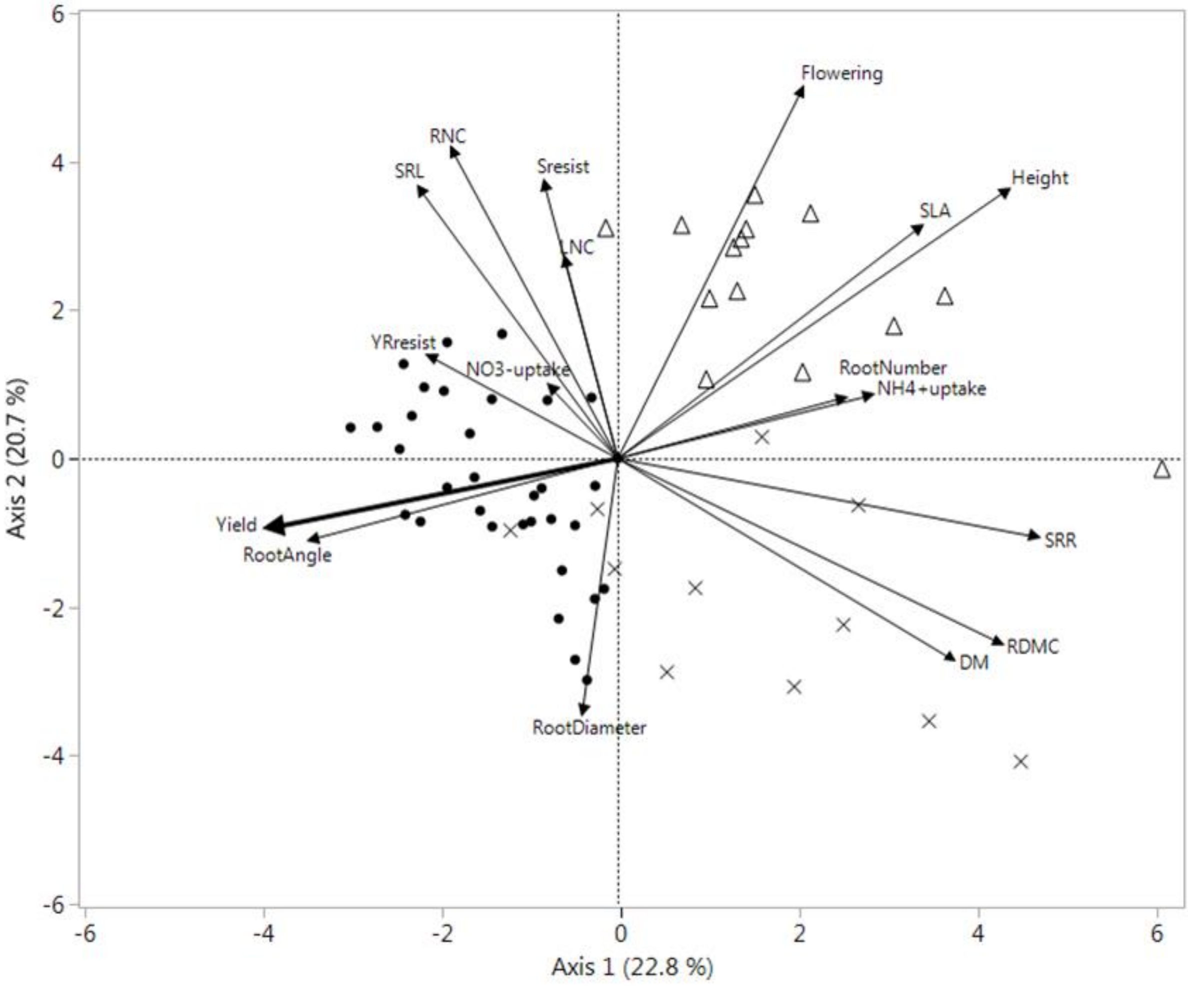
Figure 4: Correlations between root uptake capacity of (Top) NH_4^+ or (Bottom) NO_3^- and yield across the 57 wheat varieties studied. Symbols referring to the 3 selection types are as in Figure 2. P-value in bold and plain line indicates significant correlation.

Figure 1



Minimum (MIN) and maximum (MAX) trait values for Pooïdeae species (P) and wheat varieties (W)
10000
1000
100
10
1
0.1
0.01
0.001
▲ MIN P
● MIN W
△ MAX P
○ MAX W
Log-ratio values for wheat varieties relative to that for *Pooïdeae* speices
-1.3
-1.1
-0.9
-0.7
-0.5
-0.3
-0.1
SeedMass
Root Diameter
LNC
Height
SRL
SLA
RNC
RDMC
NO3-uptake
NH4+uptake
Wheat traits

Figure 2



Flowering
RNC
SRL
Sresist
Height
SLA
LNC
YRresist
NO3-uptake
RootNumber
NH4+uptake
Yield
RootAngle
SRR
RDMC
DM
RootDiameter
Axis 2 (20.7 %)
Axis 1 (22.8 %)
6
4
2
0
-2
-4
-6
-6
-4
-2
0
2
4
6

Figure 3

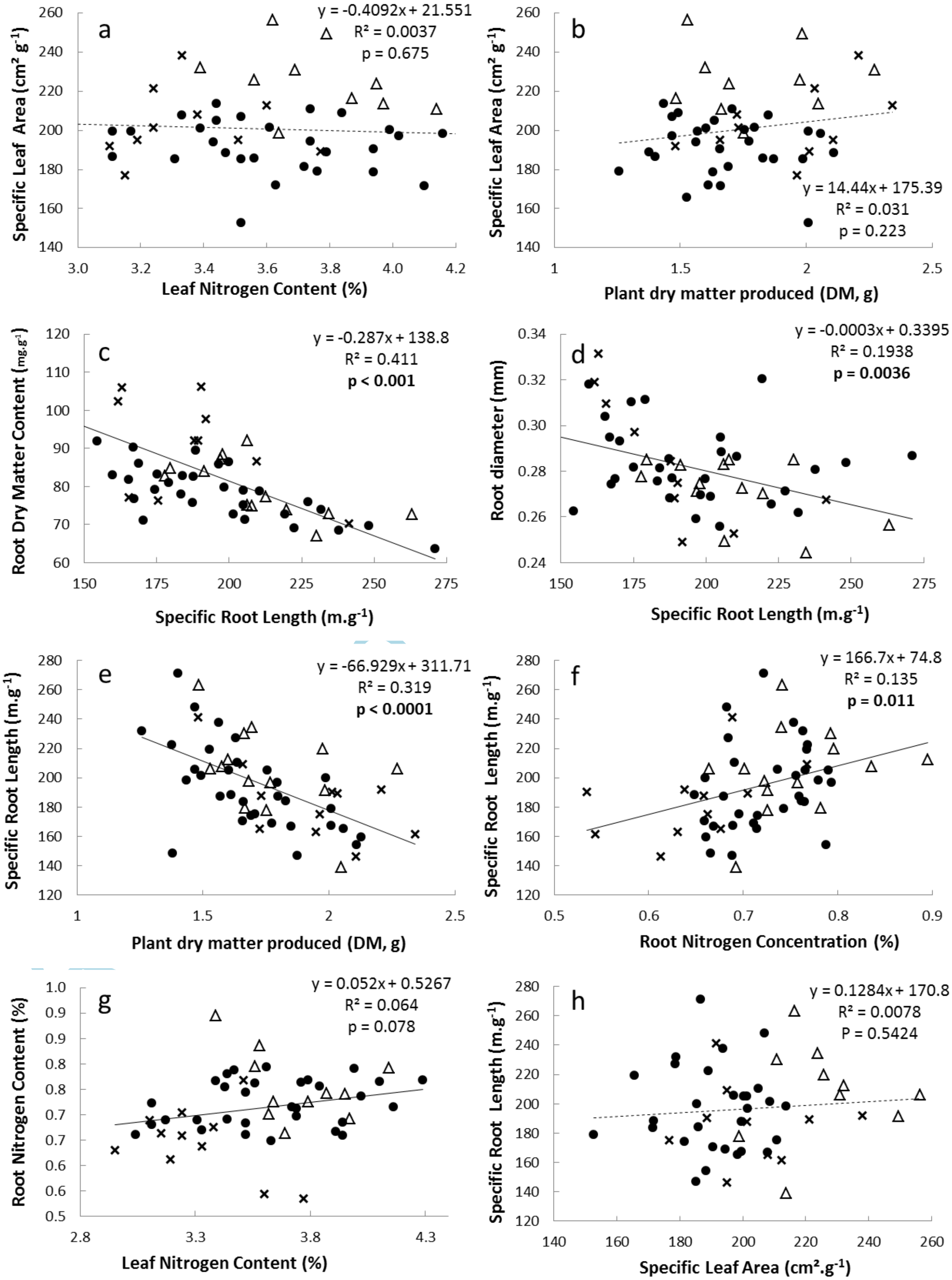
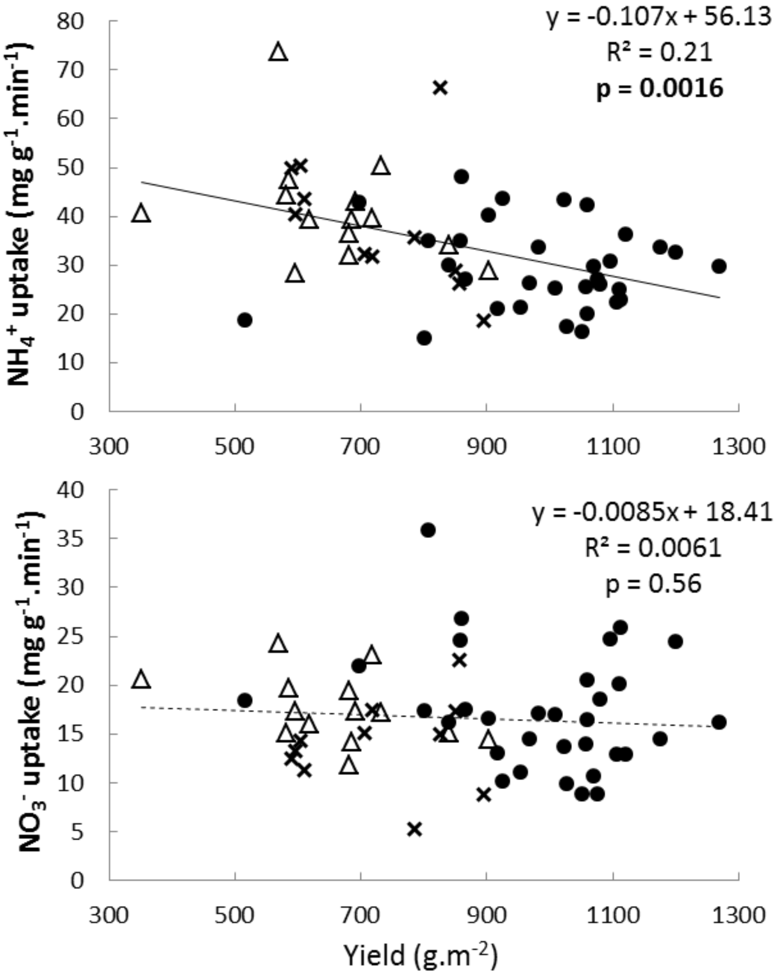

a
y = -0.4092x + 21.551
R² = 0.0037
p = 0.675
Specific Leaf Area (cm² g⁻¹)
260
240
220
200
180
160
140
3.0
3.2
3.4
3.6
3.8
4.0
4.2
Leaf Nitrogen Content (%)
b
y = 14.44x + 175.39
R² = 0.031
p = 0.223
Specific Leaf Area (cm² g⁻¹)
1
1.5
2
2.5
Plant dry matter produced (DM, g)
c
y = -0.287x + 138.8
R² = 0.411
p < 0.001
Root Dry Matter Content (mg.g⁻¹)
120
110
100
90
80
70
60
150
175
200
225
250
275
Specific Root Length (m.g⁻¹)
d
y = -0.0003x + 0.3395
R² = 0.1938
p = 0.0036
Root diameter (mm)
0.34
0.32
0.30
0.28
0.26
0.24
150
175
200
225
250
275
Specific Root Length (m.g⁻¹)
e
y = -66.929x + 311.71
R² = 0.319
p < 0.0001
Specific Root Length (m.g⁻¹)
280
260
240
220
200
180
160
140
120
1
1.5
2
2.5
Plant dry matter produced (DM, g)
f
y = 166.7x + 74.8
R² = 0.135
p = 0.011
Specific Root Length (m.g⁻¹)
0.5
0.6
0.7
0.8
0.9
Root Nitrogen Concentration (%)
g
y = 0.052x + 0.5267
R² = 0.064
p = 0.078
Root Nitrogen Content (%)
1.0
0.9
0.9
0.8
0.8
0.7
0.7
0.6
0.6
0.5
2.8
3.3
3.8
4.3
Leaf Nitrogen Content (%)
h
y = 0.1284x + 170.8
R² = 0.0078
P = 0.5424
Specific Root Length (m.g⁻¹)
280
260
240
220
200
180
160
140
120
140
160
180
200
220
240
260
Specific Leaf Area (cm².g⁻¹)

Figure 4


y = -0.107x + 56.13
R² = 0.21
p = 0.0016
NH4+ uptake (mg g-1.min-1)
0
10
20
30
40
50
60
70
80
300
500
700
900
1100
1300
y = -0.0085x + 18.41
R² = 0.0061
p = 0.56
NO3- uptake (mg g-1.min-1)
0
5
10
15
20
25
30
35
40
Yield (g.m-2)