



RESEARCH PAPER

# Plant functional trait variability and trait syndromes among wheat varieties: the footprint of artificial selection

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## Abstract

Although widely used in ecology, trait-based approaches are seldom used to study agroecosystems. In particular, there is a need to evaluate 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. Here, we quantified 18 above- and below-ground functional traits for 57 varieties of common wheat representative of different modern selection histories. We compared trait variability among varieties and among *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 among *Pooideae* species. However, for traits not directly selected, such as root N uptake capacity, the variability was up to 75% of the variability among *Pooideae* species. Ammonium absorption capacity by roots was counter-selected for conventional varieties compared with organic varieties and landraces. Artificial selection also altered some trait syndromes classically reported for *Pooideae*. Identifying traits that have high or low variability 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 below-ground functional traits, conventional varieties, intraspecific trait variation, landraces, MAGIC lines, organic farming varieties, root nutrient absorption capacity, wheat variety selection.

## 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 (either 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.*, 2014; Le Roux *et al.*, 2016), they have been more widely used in plant ecology, in particular to analyze how functional diversity influences the functioning of ecosystems 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 to increase 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 the above-ground traits specific leaf area (SLA), maximum photosynthetic rates, and leaf nitrogen (N) in wheat (*Triticum aestivum* and *Triticum 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 are seldom evaluated, particularly for below-ground traits.

Comprehensive analyses of multiple above- and below-ground traits for a range of plants led to the identification of trait syndromes, that is, 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 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 traits and trait syndromes are less well understood. A 'root economics spectrum' (RES; Roumet *et al.*, 2016) parallel to the LES is still being 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. absorption of water and nutrients, anchoring, resource storage, and interaction with soil microorganisms) may not be reduced to a single axis related to resource economics (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. Specific root length (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 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. the TRY plant trait database, <http://www.try-db.org>; Kattge *et al.*, 2011), trait-based approaches are increasing being applied in agroecology (Garnier and Navas, 2012; Milla *et al.*, 2015; Martin and Isaac, 2015, 2018), but are still scarcely used in crop sciences.

Wheat represents ~20% of the human food supply (CGIAR Research Program on Wheat, 2013) and has a long history of artificial selection and intentional breeding. It is thus a relevant crop species for the evaluation of the impact artificial selection 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 (with 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 on seven traits in nine Australian *T. aestivum* cultivars and showed that selection for yield reduced total root length and increased total N uptake per unit root length. However, selection might also have had unintentional effects on some non-targeted traits, which has seldom been studied. In addition, up to the early 1900s, 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 systems. Evolutionary breeding is another breeding method, based on the design of composite cross populations obtained by crossing several selected founders, usually varieties and landraces; these composite cross populations are then re-sown over several generations to adapt to a dedicated cropping system and environment while maintaining genetic variability (Döring *et al.*, 2011; Dawson and Goldringer, 2012; Finckh and Wolfe, 2015). 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 (e.g. among wild species of the same family).

It is important to characterize the effects (in particular, those that are unintentional) of artificial selection on trait values and variability, as well as on trait syndromes, to improve the screening and selection of wheat varieties in the future. Indeed, the development of more sustainable and low-input agriculture will likely require 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 N inputs might be not suitable under low N inputs. More generally, a better characterization of the impact of different selection schemes on trait variability and trait syndromes could identify plant traits that have been overlooked in conventional agriculture (Lammerts van Bueren *et al.*, 2008; Loueille *et al.*, 2013) but are critical for adaptation of varieties to low-input conditions.

The three main objectives of our study and associated hypotheses were as follows. (i) To compare the level of intra-specific variability existing for a range of above- and below-ground functional traits for common wheat (*T. aestivum*) with the variability observed among species belonging to the same subfamily (here, Pooideae from the Poaceae

**Table 1.** Plant traits and yield quantified for the 57 wheat varieties, with details of the plant stage and growth conditions for which they were measured

Trait	Unit	Meaning	Stage/age of the plant	Growth conditions	Comparison with
<i>Below-ground traits</i>					
RDWC	mg g <sup>-1</sup>	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 <sup>-1</sup>	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 <sub>3</sub> <sup>-</sup> uptake	mg g <sup>-1</sup> min <sup>-1</sup>	NO <sub>3</sub> <sup>-</sup> uptake per root unit	8 weeks	Greenhouse conditions in sand and hydroponic solution. Site: Lyon	Grassein et al., 2015 (n=8)
NH <sub>4</sub> <sup>+</sup> uptake	mg g <sup>-1</sup> min <sup>-1</sup>	NH <sub>4</sub> <sup>+</sup> 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 rhizotron. Site: Clermont	–
RootAngle	Degree	Mean root angle	6 days	Hydroponic growth in a 2D rhizotron. Site: Clermont	–
<i>Above-ground traits</i>					
SLA	cm <sup>2</sup> g <sup>-1</sup>	Flag leaf area per flag leaf dry mass	Flowering	Field conditions, 170 plants m <sup>-2</sup> . Site: Grignon	TRY database (n=154)
LNC	%	Flag leaf nitrogen content	Flowering	Field conditions, 170 plants m <sup>-2</sup> . Site: Grignon	TRY database (n=14)
Flowering	days	Flowering date	Flowering	Field conditions, 100 plants m <sup>-2</sup> . Site: Le Moulon	–
Height	cm	Mean height of the main shoot	Grain filling	Field conditions, 100 plants m <sup>-2</sup> . Site: Le Moulon	TRY database (n=289)
Ear/Plant	Ears plant <sup>-1</sup>	Mean number of ears per plant	Harvest	Field conditions, 100 plants m <sup>-2</sup> . Site: Le Moulon	–
SeedMass	g	Thousand-kernel weight/1000	Harvest	Field conditions, 100 plants m <sup>-2</sup> . Site: Le Moulon	TRY database (n=386)
YPresist	%	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 <i>Septoria</i> , percentage of the leaf surface non-attacked	Tillering to flowering	Compilation of data from ARVALIS, and the ECOGER and ECOSYS laboratories	–
<i>Whole-plant traits</i>					
SRR	No dimension	Shoot-to-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 <sup>-2</sup>	Seed yield at harvest	Harvest	Field conditions, 100 plants m <sup>-2</sup> . Site: Le Moulon	–

The last column indicates when it has been possible to compare the variability of a given trait between varieties and between Poideae species using the TRY database or the data set of Grassein et al. (2015). n, number of Poideae species considered.

family). We assumed that for traits under strong selection by farmers or plant breeders, trait variability among varieties should be lower than that observed among species, except when selection targets differed between modern selection histories (e.g. seed mass or height). (ii) 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 ( $\text{NO}_3^-$ ) concentrations (de Boer *et al.*, 1989). We thus hypothesized that the ammonium ( $\text{NH}_4^+$ ) absorption capacity of roots could have been counter-selected for conventional varieties as compared with organic farming varieties and landraces. (iii) To assess how selection has led to particular wheat trait syndromes in comparison to those observed among wild Pooideae species. For instance, we hypothesized that selection would have decreased the total allocation to below-ground compartments relative to above-ground plant compartments, particularly for conventional varieties, which could impact whole-plant economics and lessen or even invert the classical positive relationship between RGR and SRL.

We quantified 18 plant traits (8 below-ground traits, 8 above-ground 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 with their counterparts observed among Pooideae species using TRY database records (Kattge *et al.*, 2011).

## Materials and methods

### *Wheat varieties studied*

The 57 selected bread wheat varieties (Supplementary Table S1) represent a broad range of modern selection histories commonly used in France. Thirty-two were varieties selected in the French catalogue for conventional agriculture; that is, they were 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 were organic varieties or landraces cultivated in France in the early 1900s (here named OVL). OVL were selected on the basis of their wide use in low-input or organic farming systems. Eleven wheat lines were obtained from INRA MAGIC (IM), a highly recombinant and multi-parental population evolved during 15 generations under low-input conditions at the Le Moulon site (Thepot *et al.*, 2015). The overall set of 57 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 conditions (at the Grignon and Le Moulon sites) or under greenhouse conditions for all varieties (see Table 1). In field trials, the 57 wheat varieties were planted in  $8 \text{ m} \times 1.75 \text{ m}$  plots. When necessary, plots were weeded manually or using herbicide. Crops were treated with fungicides following local agricultural practices. Plots were fertilized with  $\text{NH}_4\text{NO}_3$  supplied in three applications (40, 70, and  $40 \text{ kg N ha}^{-1}$ ). This fertilization strategy corresponded to low-input system conditions (Dubs *et al.*, 2018). All 57

varieties were grown at each of the two field sites, which were used to measure six above-ground plant traits (Table 1).

To complement the field experiments, two greenhouse experiments were used to quantify root traits in individual plants grown in standardized conditions. For the first greenhouse experiment, seeds of each of the 57 varieties were sown in tall pots ( $11.3 \text{ cm} \times 11.3 \text{ cm} \times 21.5 \text{ cm}$ ) containing coarse sand ( $< 4 \text{ mm}$ ). As suggested by Porter *et al.* (2012), to minimize the effects of pot size on plant growth and plant traits, the pot size (2.74 litres) was selected to have a total plant biomass:pot volume ratio less than 1 (here,  $0.85 \text{ g l}^{-1}$  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 for 8 weeks (16 h light/8 h night with a photosynthetic photon flux density of  $350 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , and day and night temperatures of  $21^\circ\text{C}$  and  $18^\circ\text{C}$ , respectively) and were watered three times per week (twice using 50 ml of deionized water per pot, and once using 25 ml hydroponic nutrient solution containing  $3.5 \text{ mM NO}_3^-$  and  $3.5 \text{ mM NH}_4^+$ ). After 8 weeks, the N uptake capacity of plants and four other root traits were characterized (Table 1). For the second greenhouse experiment, seeds of the 57 varieties were sown in two-dimensional (2D) rhizotrons made of pouches lined with wet filter paper supplied with hydroponic nutrient solution containing  $3.5 \text{ mM NO}_3^-$  and  $3.5 \text{ mM NH}_4^+$ . 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) and sensitivity to yellow rust (YRresist). For these two traits, adult plant resistance was scored during the registration and commercial cycle of varieties. Resistance was also scored by BIOGER/ECOSYS laboratories on IM and OVL during field trials performed in 2013–2014.

In the Grignon field trial, six plants were collected at least  $0.40 \text{ m}$  from the border of the plots, and two traits were measured on each plant (Table 1). For specific leaf area ( $\text{SLA}$ ;  $\text{cm}^2 \text{ g}^{-1}$ ), the six flag leaves were placed on a blue board and photographed. The surface of each leaf was calculated by an image analyzer (ImageJ<sup>®</sup>) and each leaf was then dried at  $80^\circ\text{C}$  for 48 hours. SLA was computed as the ratio of leaf surface area to dry mass (DM). Leaf N content (LNC; %) was measured for each individual dried flag leaf using the Dumas method with a NA 1500 CN analyzer (Fisons Instruments, France).

In the Moulon field trial, 10 plants were collected at least  $0.40 \text{ m}$  from the border of the plots, and measurements of four traits were made (Table 1). Height (cm) at the grain filling stage was determined by measuring the average stem height. For calculation of the mean number of ears per plant (Ear/Plant), the total number of ears per plant was counted on plants in an area of  $1 \text{ m}^2$  for each variety at the stem elongation stage and divided by the number of plants, previously scored in early spring at the seedling stage, on the same area (after germination and frost damage, i.e. the final plant count). Seed mass (g) was evaluated by weighing (and counting) 500 kernels from each variety at harvest. For assessment of flowering date (calendar days), a survey of plant phenology conducted every 2 days during the stem elongation period allowed us to score the date when 50% of ears were in flower (extruding stamens). In addition, using measurements of plant density and the number of kernels per ear, the yield ( $\text{g m}^{-2}$ ) was computed for each variety as [(seed mass  $\times 1000$ )  $\times$  Ear/Plant  $\times$  plant density  $\times$  number of kernels per ear].

Using the pot experiment under greenhouse conditions, the uptake capacities of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  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 three whole plants were kept intact and their entire root system was immersed in pots containing a nutrient solution containing  $\text{KNO}_3$  and  $(\text{NH}_4)_2\text{SO}_4$  ( $300 \mu\text{M}$  total mineral

N concentration, with equal amounts of  $\text{NO}_3^-$  and  $\text{NH}_4^+$ ). Aliquots of 1 ml were sampled after 0, 25, 50, 75, and 100 min of incubation, filtered (0.20  $\mu\text{m}$  pore size), and stored at  $-20^\circ\text{C}$ . The  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations were quantified using an ion chromatograph (ICS 900, Dionex, ThermoElectron, France). Uptake capacities were expressed as  $\text{mg N-NO}_3^-$  and  $\text{N-NH}_4^+ \text{ min}^{-1} \text{ g}^{-1}$  root DM for  $\text{NO}_3^-$  and  $\text{NH}_4^+$  uptake rates, respectively. Immediately following the  $\text{NO}_3^-$  and  $\text{NH}_4^+$  uptake capacity measurements, the fresh root system was weighed and then stored in distilled water for a few days at  $4^\circ\text{C}$  until determination of the fresh root morphology 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 $\times$ 42 cm clear acrylic tray and scanned at 300 dpi with a scanner (Epson Perfection V700 PHOTO, Regent Instruments Inc., Canada). Images were analyzed with WinRHIZO<sup>TM</sup> software to determine the root length and average root diameter. Following the root morphology analysis, the sample was dried for 48 h at  $105^\circ\text{C}$  and weighed. SRL ( $\text{m g}^{-1}$ ) was computed as the ratio of root length to DM. RDMC ( $\text{mg g}^{-1}$ ) was computed as root DM divided by water-saturated root fresh mass. The foliage of each variety was dried at  $105^\circ\text{C}$  for 2 days for measurement of the above DMs and to compute the plant shoot-to-root ratio (SRR). Root aliquots were milled to a fine powder in order to determine root N content (RNC; %) using an elemental analyzer (Flash EA 1112 Series CNS analyzer, Thermo Fisher Scientific, USA).

Strictly speaking, our data were not sufficient to compute the RGR ( $\text{g day}^{-1}$ ), as RGR often decreases with increasing plant size (Paine *et al.*, 2012). Nevertheless, we computed the plant DM produced at the end of the 58-day growing period for each wheat variety as  $\text{DM} = \text{DM}_{58} - \text{DM}_{t_0}$ , where  $\text{DM}_{58}$  is the total plant biomass after 58 days and  $\text{DM}_{t_0}$  is the seed mass. This calculation provided a rough but useful index of the build-up of biomass during the first weeks after germination, which is highly important for the 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 rhizotrons (as described above) supplying water. After 6 days, each rhizotron was opened to reveal the seedling root system. An image of the whole plant was taken with a digital camera and analyzed using the Smartroot image analysis tool (Lobet *et al.*, 2011) to quantify the seminal root number and mean root angle.

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

It was not possible to compare the intraspecific variation of trait values for wheat with the intraspecific variation of traits for other Pooideae species as there are insufficient data on within-species trait variation in wild species for most traits. We thus compared the variability of the wheat trait values to the trait variability in a large panel of grass species, including their wild relatives *sensu lato*, focusing on the Pooideae subfamily from the Poaceae family. This subfamily is one of the largest subfamilies of the Poaceae, which contains most of the cereals, including wheat, oat, barley, and rye, and contains a large proportion of grass species from temperate zones and Eurasia (Soreng *et al.*, 2017). The values of the following eight traits were extracted for Pooideae species from the TRY database (Kattge *et al.*, 2011), which contains plant trait data collected worldwide: RDMC, RNC, SRL, average root diameter, SLA, LNC, height, and seed mass. Values for each of these traits 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  $\text{NO}_3^-$  and  $\text{NH}_4^+$  uptake capacities, we used the dataset described in Grassein *et al.* (2015), which includes values of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  uptake capacities for eight 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  $\text{NO}_3^-$  and  $\text{NH}_4^+$  uptake

capacities, among wheat varieties and among Pooideae species, the coefficients of variation (i.e. SD divided by the mean) were computed, and the minimum and maximum trait values for the wheat varieties and Pooideae species were used. As Pooideae traits retrieved from the TRY database varied in sample size from 11 to 368 species, and to avoid bias due to 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 the 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 coefficients of variation with same  $n$  for 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  $\text{NO}_3^-$  and  $\text{NH}_4^+$  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-ratio:

$$\text{LogRatio}_{\text{trait}} = \log \left( \frac{CV_{\text{wheat}_{\text{trait}}}}{CV_{\text{Pooideae}_{\text{trait}}}} \right)$$

where  $CV_{\text{wheat}_{\text{trait}}}$  is the coefficient of variation obtained for wheat varieties for a given trait and  $CV_{\text{Pooideae}_{\text{trait}}}$  is the coefficient of variation obtained for Pooideae species for the same trait.

Log-ratio values close to zero correspond to similar variability among varieties of wheat compared with the variability among Pooideae species, whereas negative log-ratio values correspond to lower variability among wheat varieties than among Pooideae species: for example, a value of  $-1$  corresponds to a variability among wheat varieties equal to 10% of the variability among Pooideae species.

To test possible trait differences between the three modern selection histories (i.e. CV, OVL, and IM), a one-way ANOVA was used. A non-parametric mean analysis (Kruskal–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 the Tukey–Kramer HSD test in case of normal data distribution, or Kruskal–Wallis multiple mean comparison in case of non-normal data distribution, to analyze 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.

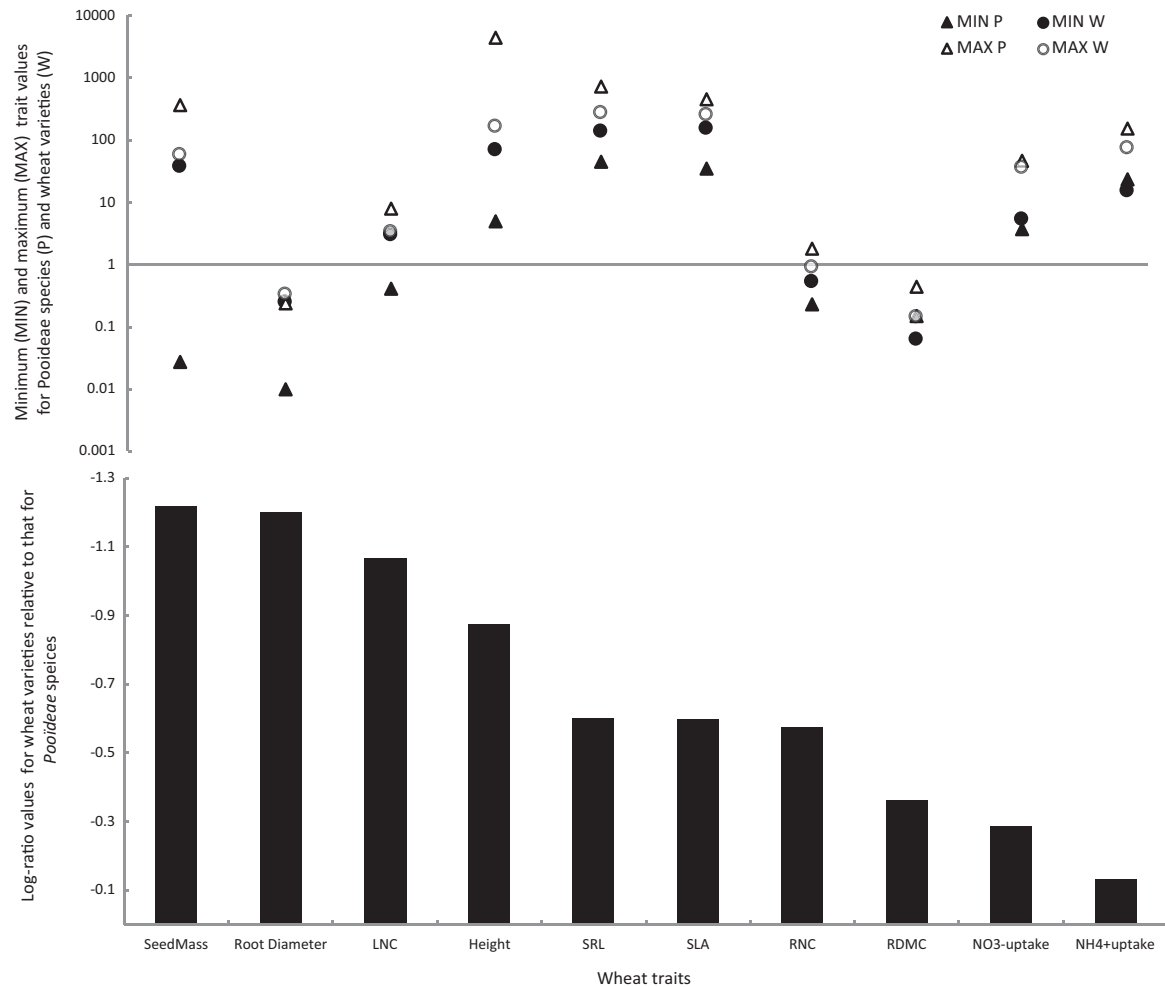
To analyze trait syndromes, correlations between all wheat trait pairs were tested using the Pearson test for normally distributed data or the Spearman test for non-normally distributed data. Effects with  $P < 0.05$  were considered to be significant.

## Results

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

Considering the 11 functional traits for which values were available for Pooideae species, trait variability among species was the highest for plant height and seed mass (coefficients of variation  $1.96 \pm 0.4$  and  $1.44 \pm 0.38$ , respectively; Supplementary Fig. S1). Intermediate values of trait variability among Pooideae species were observed for average root diameter, LNC, Ear/Plant, SRL, and  $\text{NO}_3^-$  and  $\text{NH}_4^+$  uptake capacities (coefficients of variation between 0.6 and 1.2; Supplementary Fig. S1). RNC, SLA, and RDMC had the lowest variability among Pooideae species (coefficients of variation  $\sim 0.4$ ; Supplementary Fig. S1).

The wheat variety trait range was generally included within the Pooideae species trait range (Fig. 1). Only the wheat values



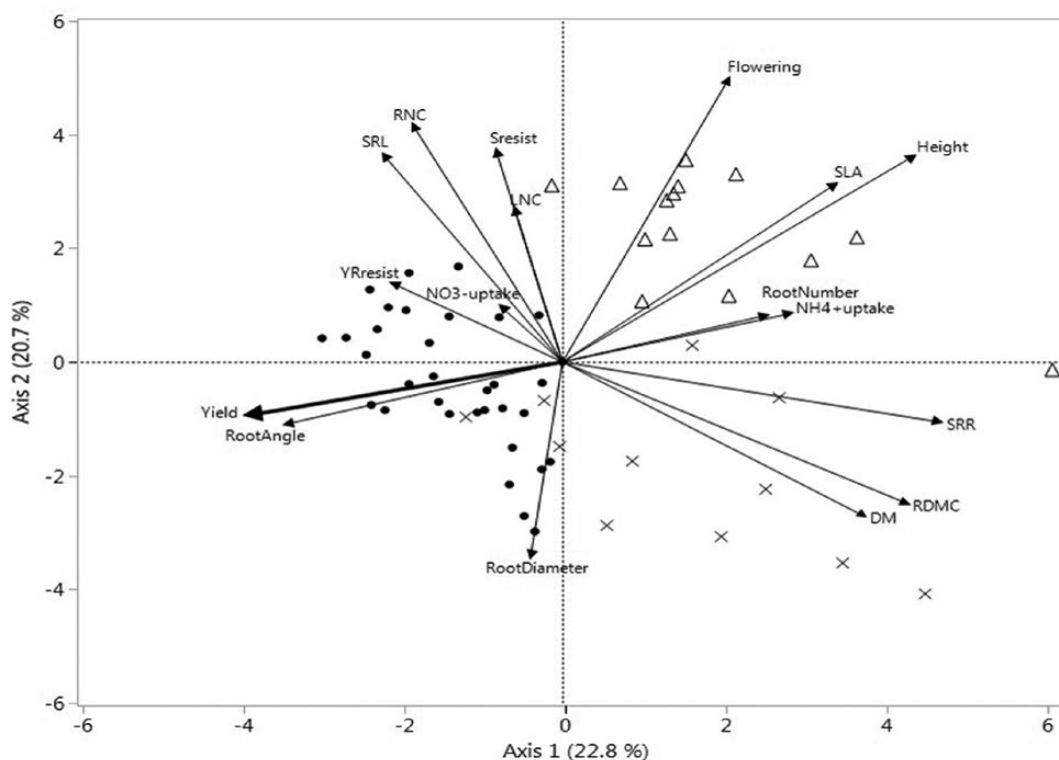
**Fig. 1.** (Upper panel) Comparison of the minimum and maximum values observed for the 10 traits found for wheat (W) varieties and Pooideae (P) species (either in the TRY database or in Grassein et al., 2015; see Table 1). (Lower panel) Variability of trait values observed among wheat varieties compared with 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 compared with the variability among Pooideae species; negative log-ratio values correspond to lower variability among wheat varieties than among Pooideae species (e.g. -1 corresponds to a variability among wheat varieties equal to 10% of the variability among Pooideae species).

for RDMC lay outside the Pooideae species range, with lower values found in wheat. Some wheat traits (i.e. average root diameter and  $\text{NH}_4^+$  uptake) were found at the extremes of the respective range in Pooideae, with higher maximum values for root diameter and lower minimum values for  $\text{NH}_4^+$  uptake compared with the minimum and maximum data found for Pooideae species. The other traits were at the center of the distribution of values for Pooideae, with a very small overlap (<6%) for wheat traits such as LNC, seed mass, and height, and a very large overlap (>70%) for  $\text{NO}_3^-$  uptake; for the other traits, the mean  $\pm$ SD overlap was  $21.7 \pm 2.3\%$  (Fig. 1). For all traits, trait variability was significantly lower among wheat varieties than among Pooideae species ( $P < 0.0001$ ) (Fig. 1, Supplementary Fig. S1). For 3 of the 10 studied functional traits, the variability observed among wheat varieties was negligible compared with the variability among Pooideae species (Fig. 1). For example, the variability of seed mass, root diameter, and LNC among wheat varieties was 6.3%, 6.3%, and 9.1% of the variability observed among Pooideae species. The variability among wheat varieties for height, SRL, SLA, and RNC was 13.7%, 19.4%, 25.2%, 25.5%, and 26.5% of the

variability among the Pooideae species. Three root functional traits were characterized by a high variability among wheat varieties: the variability of RDMC,  $\text{NO}_3^-$  uptake capacity, and  $\text{NH}_4^+$  uptake capacity among the wheat varieties was 44.2%, 52.4%, and 75.8% of the variability among Pooideae species (Supplementary 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 (22.8% and 20.7%, respectively; Fig. 2). Height, SRR, RDMC, yield, SLA, root angle, DM, and  $\text{NH}_4^+$  uptake contributed substantially to the first axis (loading values up to 0.45; Supplementary Table S2); yield and root angle had negative scores on axis 1, whereas the other traits had positive scores. The second axis was mainly based on flowering, RNC, Sresist, SRL, height, average root diameter, SLA and Sresist, with a negative score for root diameter (Supplementary Table S2).  $\text{NO}_3^-$  and  $\text{NH}_4^+$  uptake capacities were the most



**Fig. 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). See Table 1 for definitions of the wheat traits. Dots represent conventional varieties (CV); crosses represent INRA MAGIC populations (IM); triangles represent organic varieties and landraces (OVL).

important traits for PCA axis 3 (10.7% of the total variance; loadings  $>0.50$ ; [Supplementary Table S2](#)). Modern selection history was a major factor influencing the trait values of wheat varieties: varieties from the three different artificial selection types were significantly discriminated along both PCA axes 1 and 2 ([Fig. 2](#)). Along axis 1, CV were significantly different from IM varieties and 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 eight above-ground functional traits and the two whole-plant traits were all significantly influenced by the modern selection histories. In contrast, three of the eight below-ground traits (SRL, root diameter, and  $\text{NO}_3^-$  uptake capacity) were not affected by the type of artificial selection. CV were significantly shorter, more resistant to yellow rust and had a larger root angle and number of ears per plant, and a higher yield ([Table 2](#)) than the two other types of varieties. CV were more resistant to *Septoria* than IM varieties, OVL were significantly taller and later flowering, and had a higher SLA, SRR, and root number than the CV and IM varieties. OVL also had higher resistance to yellow rust than the IM varieties ([Table 2](#)) and a higher  $\text{NH}_4^+$  uptake capacity. Finally, IM had a lower plant DM than CV. The IM varieties had a relatively low resistance to both diseases, a high growth rate, the lowest values of N content (LNC and RNC), and the highest RDMC values ([Table 2](#)).

When considering trait variability among varieties for each modern selection history, variability was similar among selection histories for seed mass, SRL, RNC, and SLA ([Supplementary Fig. S2](#)). The variability of  $\text{NO}_3^-$  uptake capacity and root diameter was lower among OVL than among IM and CV ([Supplementary Fig. S2](#)). In contrast, the variability of RDMC was higher among OVL than among IM or CV. The variability of height was greatest among IM ([Supplementary Fig. S2](#)).

#### *Trait syndromes observed between wheat varieties and between plant species*

Several syndromes reported in plant ecology for below-ground traits were also observed for the wheat varieties. For instance, the previously reported negative SRL–RDMC and SRL–root diameter correlations were also found for the wheat varieties ([Fig. 3C, D](#)). Similarly, the positive SRL–RNC correlation was also found for the wheat varieties ([Fig. 3F](#)). In contrast, several syndromes that have been classically reported in plant ecology for above-ground traits were not observed for the wheat varieties. In particular, the positive SLA–LNC and SLA–DM correlations were not found for the wheat varieties ([Fig. 3A, B](#)). Moreover, SRL was negatively correlated with DM for the wheat varieties ( $r=-0.565$ ,  $P<0.0001$ ; [Fig. 3E](#), [Supplementary Table S3](#)). In addition, RNC and LNC were not significantly correlated for the wheat varieties, in contrast to the positive correlation between these traits generally reported in the literature ([Fig. 3G](#)).

Table 2. Effect of wheat variety selection type on the 18 plant traits studied and on yield

Traits	Wheat selection type			Statistical analysis	
	CV	IM	OVL	Test	P-value
<i>Below-ground traits</i>					
SRL	193.35±29.73	183.83±26.23	204.51±29.37	One-way ANOVA	0.211
RNC	0.72±0.05 <sup>a</sup>	0.65±0.07 <sup>b</sup>	0.76±0.06 <sup>a</sup>	One-way ANOVA	<b>&lt;0.001</b>
RDMC	79.23±7.53 <sup>a</sup>	92.86±14.18 <sup>b</sup>	83.97±18.03 <sup>ab</sup>	Kruskal–Wallis	<b>0.017</b>
RootDiameter	0.28±0.02	0.29±0.03	0.27±0.01	One-way ANOVA*	0.079
NH <sub>4</sub> <sup>+</sup> uptake	29.47±8.81 <sup>a</sup>	38.33±13.46 <sup>ab</sup>	41.32±11.39 <sup>b</sup>	One-way ANOVA*	<b>0.001</b>
NO <sub>3</sub> <sup>-</sup> uptake	17.21±6.08	13.92±4.6	17.55±3.54	One-way ANOVA*	0.095
RootNumber	3.57±0.45 <sup>a</sup>	3.86±0.55 <sup>ab</sup>	4.12±0.48 <sup>b</sup>	Kruskal–Wallis	<b>0.003</b>
RootAngle	149.73±6.64 <sup>a</sup>	144.05±4.72 <sup>b</sup>	142.93±4.93 <sup>b</sup>	One-way ANOVA	<b>&lt;0.001</b>
<i>Above-ground traits</i>					
SLA	19.14±1.45 <sup>a</sup>	20.28±1.78 <sup>a</sup>	22.58±1.75 <sup>b</sup>	One-way ANOVA	<b>&lt;0.001</b>
LNC	3.63±0.32 <sup>a</sup>	3.31±0.24 <sup>b</sup>	3.75±0.22 <sup>a</sup>	One-way ANOVA	<b>0.002</b>
Flowering	18.36±3.63 <sup>a</sup>	16±4.7 <sup>a</sup>	29.25±3.91 <sup>b</sup>	One-way ANOVA	<b>&lt;0.001</b>
Height	86.75±6.17 <sup>a</sup>	97.5±15.66 <sup>b</sup>	145.5±10.48 <sup>c</sup>	Kruskal–Wallis	<b>&lt;0.001</b>
SeedMass	46.19±3.27 <sup>a</sup>	46.35±4.35 <sup>ab</sup>	49.42±4.3 <sup>b</sup>	One-way ANOVA	<b>0.027</b>
Ear/Plant	7.38±1.2 <sup>a</sup>	6.12±1.31 <sup>b</sup>	6.12±1.14 <sup>b</sup>	One-way ANOVA	<b>0.001</b>
YRresist	89.64±13.31 <sup>a</sup>	56.09±23.41 <sup>b</sup>	76.07±20.24 <sup>c</sup>	Kruskal–Wallis	<b>&lt;0.001</b>
Sresist	59.37±14.55 <sup>a</sup>	35.03±18.78 <sup>b</sup>	68.13±16.46 <sup>a</sup>	One-way ANOVA	<b>&lt;0.001</b>
<i>Whole-plant traits</i>					
SRR	0.83±0.13 <sup>a</sup>	1.24±0.69 <sup>ab</sup>	1.20±0.59 <sup>b</sup>	Kruskal–Wallis	<b>0.009</b>
DM	1.69±0.04 <sup>a</sup>	1.93±0.07 <sup>b</sup>	1.76±0.06 <sup>ab</sup>	One-way ANOVA	<b>0.020</b>
Yield	987.8±152.4 <sup>a</sup>	732.5±112.3 <sup>b</sup>	659.5±126.6 <sup>b</sup>	One-way ANOVA	<b>&lt;0.001</b>

Trait acronyms are as in Table 1. CV, conventional varieties; IM, INRA MAGIC populations; OVL, organic varieties and landraces. For each trait, means (presented with SDs) are compared between the three selection types. *P*-values in bold indicate significant differences (*P*<0.05) between selection types for a given trait, and different letters indicate significant differences among the three selection types (*P*<0.05) based on Tukey–Kramer HSD tests. Asterisks indicate log-transformed data.

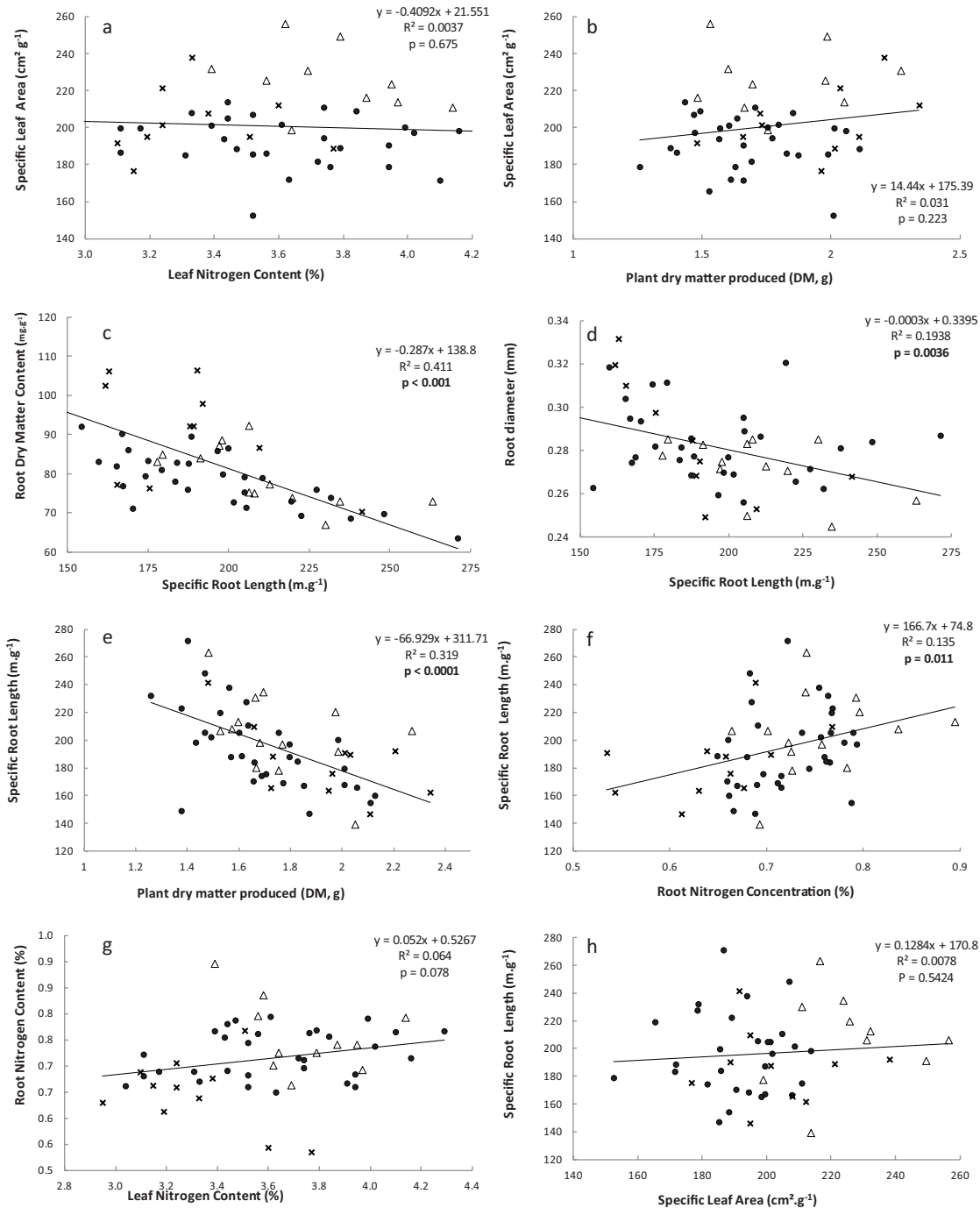
Supplementary Table S3 presents the level of significance and strength of all the relationships between trait pairs. Interestingly, the strongest relationships with yield, the major target of variety selection, were observed not only for height (negative) and Ear/Plant (positive), but also for NH<sub>4</sub><sup>+</sup> uptake capacity (negative). Underlying the latter relationship (Fig. 4), CV had high yield and low NH<sub>4</sub><sup>+</sup> uptake capacity, whereas OVL had low yield and high NH<sub>4</sub><sup>+</sup> uptake capacity (Table 2). In contrast, NO<sub>3</sub><sup>-</sup> uptake capacity was not correlated to yield (Supplementary Table S3, Fig. 4).

Discussion

Comparison of trait variability among varieties of *T. aestivum* and among Pooideae species

The level of trait variability among wheat varieties compared with the variability among Pooideae species was strongly trait-dependent (Fig. 1, Supplementary Fig. S1). Siefert et al. (2015) found that intraspecific variability of trait values represented ~30% of the interspecific variability observed for different plant communities. In our study, three of the six above-ground traits studied (mass, height, and LNC) showed particularly low variability among wheat varieties (<10% of the variability found among Pooideae species for mass and LNC) (Fig. 1). The low variability of seed mass among varieties of the same species (i.e. *T. aestivum*) could be explained by the morphological stature of the observed plants and by ecophysiological and biomechanical constraints—that is, 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 the 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 in order to maximize 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 among the wheat varieties than among the Pooideae species could be explained by fertilization, which probably leads to a high similarity in terms of nutrient availability in cultivated soils relative to the high variability likely to exist in soils from natural, unmanaged environments. Globally, the two above-ground traits for which intraspecific variability was less than 10% of the total variability observed among Pooideae species were seed mass, which has been a major target for breeding for centuries (Donald, 1968; Austin et al., 1977), and LNC, which was not directly selected but is a major determinant of grain protein content (i.e. LNC at the 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 such as wheat have been heavily selected, the variability of these traits among varieties could be very low compared with the variability among related non-domesticated species. In addition to these above-ground traits, low intraspecific variability was also

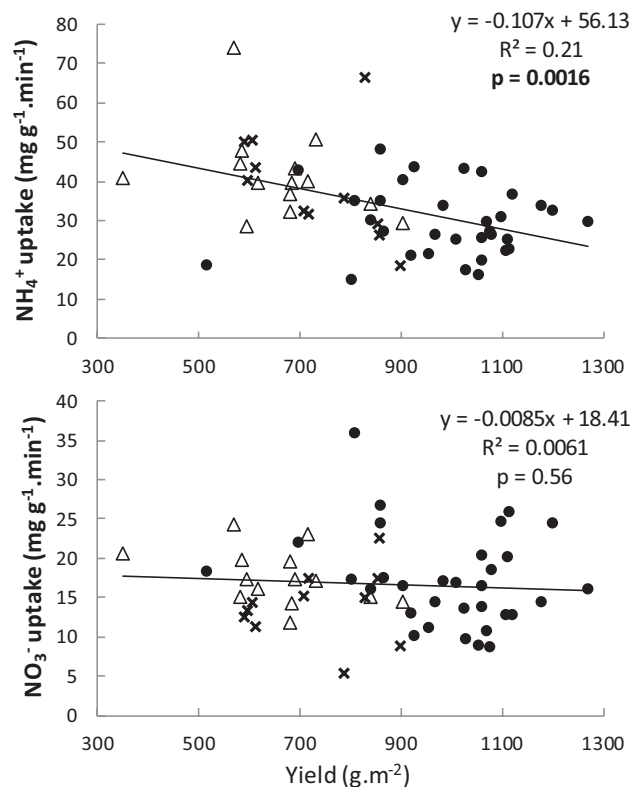


**Fig. 3.** Testing the existence, among wheat varieties, of major trait syndromes reported in plant ecology literature. (A) The SLA/LNC relationship; (B) the SLA/DM relationship; (C) the RDMC/SRL relationship; (D) the root diameter/SRL relationship; (E) the SRL/DM relationship; (F) the SRL/RNC relationship; (G) the RNC/LNC relationship; (H) the SRL/SLA relationship. Dots represent conventional varieties (CV); crosses represent INRA MAGIC populations (IM); triangles represent organic varieties and landraces (OVL). *P*-values in bold and solid lines indicate significant correlations. 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.

observed for one below-ground trait. Average root diameter was only weakly variable among the wheat varieties, with less than 10% of the variability observed among 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 among the wheat varieties could be explained by biomechanical constraints because root diameter, together with root plate size, contributes to the

ability of the root system to resist stem lodging (Crook and Ennos 1993, 1994).

In contrast, the other measured root traits (i.e. root dry matter content,  $\text{NO}_3^-$  and  $\text{NH}_4^+$  uptake capacities) showed a large variability, with 44–76% of the variability observed among Pooideae species (Fig. 1, Supplementary Fig. S1). The variability of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  uptake capacities among wheat varieties has rarely been studied to date. Our results showing that



**Fig. 4.** Correlations between root uptake capacity of (upper panel)  $\text{NH}_4^+$  or (lower panel)  $\text{NO}_3^-$  and yield across the 57 wheat varieties studied. Dots represent conventional varieties (CV); crosses represent INRA MAGIC populations (IM); triangles represent organic varieties and landraces (OVL). *P*-values in bold and solid lines indicates significant correlations.

the  $\text{NO}_3^-$  and  $\text{NH}_4^+$  uptake capacities are still highly variable among wheat varieties could be useful from an agroecology perspective. Breeding for varieties adapted to low-input agricultural systems and soils with high  $\text{NH}_4^+:\text{NO}_3^-$  ratios might benefit from this trait variability. Indeed, this would allow the selection of genotypes with high  $\text{NH}_4^+$  uptake capacity;  $\text{NH}_4^+$  is a form of N that becomes relatively more important under low mineral fertilization regimes. More generally, our results suggest that some traits, especially root traits such as the capacities to take up different forms of N, display sufficient intraspecific variability to promote functional diversity. This result thus supports previous studies that propose to design varietal mixtures that would maximize functional complementarity (Barot et al., 2017).

#### *Effects of different modern selection histories on a range of above- and below-ground traits*

The modern selection of crop variety characteristics by farmers and plant breeders is known to differ, for example, when their objective is to obtain varieties suitable for conventional rather than organic cropping systems (Reid et al., 2011; Mikò et al., 2017). Compared with the other modern selection histories, the CV included in this work were characterized by a higher yield and were also smaller, more resistant to yellow rust and *Septoria*, and had a larger number of ears per plant and a greater root angle of seminal roots than the OVL and IM varieties

(Table 2, Fig. 2). This observation is consistent with the fact that yield and traits associated with yield, such as the number of ears per plant or the number of grains per 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 and has a positive correlation with rooting depth and soil water extraction, and hence is related to drought tolerance for crop plants such as wheat (Oyanagi et al., 1993; Manschadi et al., 2008), maize (Nakamoto et al., 1991), and sorghum (Singh et al., 2012). The CV with larger seminal root angles are potentially less impacted by drought conditions than the OVL. 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 SLA, SRR, and root number than the CV and IM varieties (Table 2). They also had better resistance to yellow rust than the IM varieties, and a higher  $\text{NH}_4^+$  uptake capacity than the CV. Plant height and shoot biomass have previously been reported to be significantly greater for landraces compared with modern varieties (Bektas et al., 2016). Although tall stems may cause lodging and yield loss (Borlaug, 2007), in organic farming, tall plants are still preferred both for their competitiveness against weeds and 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 delayed maturity, and OVL were generally later flowering than other varieties (Table 2). This suggests co-selection of seminal root number and precocity, or a genetic drift associated with one of the two traits (Smith and Haigh, 1974). OVL were also characterized by a greater capacity to take up  $\text{NH}_4^+$  compared with CV, whereas CV and OVL did not differ in their capacity for  $\text{NO}_3^-$  uptake (Table 2, Fig. 2). This can be explained by the fact that CV are selected to perform well under optimal or high nutrient conditions driven by the application of mineral fertilizers. A large proportion of the  $\text{NH}_4^+$  added to soil in fertilizers is rapidly oxidized and transformed into  $\text{NO}_3^-$  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  $\text{NH}_4^+$  immobilization was around 3-fold higher for croplands than grasslands. Thus, the  $\text{NH}_4^+$  concentrations in soils of conventional wheat-production systems are often much lower than the  $\text{NO}_3^-$  concentrations (Personne et al., 2015), which could explain the counter-selection of  $\text{NH}_4^+$  uptake capacity for CV. In contrast, OVL exhibit trait values that may be beneficial when the major mineral N form in soil is  $\text{NH}_4^+$ , 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 take up  $\text{NH}_4^+$  significantly contributes to their good performance in organic farming and more specifically in soils with a high  $\text{NH}_4^+:\text{NO}_3^-$  ratio.

IM lines were characterized by a medium height, low resistance to diseases, a high growth rate, the lowest LNC and RNC, and the highest RDMC (Table 2, Fig. 2). 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-flowering plants (Thépot *et al.*, 2015). This could explain the marked footprint of selection on RGR for IM lines, because RGR is a key trait impacted by breeding schemes, in relation with flowering date. Indeed, grain crops should switch from the vegetative to the reproductive phase early to avoid environmental stresses such as summer drought and to achieve a high grain-to-total biomass ratio at harvest. The particularly low values of LNC and RNC 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 contribute up to 90% of the N incorporated by the grains during anthesis (Kichey *et al.*, 2007; Bogard *et al.*, 2010). The particularly low LNC and RNC observed at flowering for IM lines could be due to an efficient remobilization of N from the leaf and root in favor of the grains. Further experiments labelling a range of varieties with  $^{15}\text{N}$  during the vegetative stage and comparing the efficiency of N remobilization to fill the 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 LES (Wright *et al.*, 2004) was shown to be also valid at the intraspecific level for wild Pooideae species such as *Dactylis glomerata*, *Festuca paniculata*, and *Sesleria caerulea* (Albert *et al.*, 2010), and for crop species such as wheat, maize (Martin *et al.*, 2018), rice (Xiong and Flexas, 2018), and soybean (Hayes *et al.*, 2019). In our study, below-ground trait syndromes were observed among wheat varieties (Fig. 3), for example, a negative correlation between SRL and RDMC, and a positive correlation between SRL and RNC (as also reported in Prieto *et al.*, 2015; Roumet *et al.*, 2016; Valverde-Barrantes *et al.*, 2017). First, 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. Second, the traits involved in these root trait 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 ecophysiological constraints.

SRL was negatively correlated with DM for the wheat varieties (Fig. 3E). DM was likely positively correlated to the RGR of the wheat varieties, although it is expected that DM underestimated RGR for varieties with the highest biomass (Paine

*et al.*, 2012). Still, our results are in opposition to the positive correlation between SRL and RGR generally reported when comparing plant species (Reich *et al.*, 1998; Wright and Westoby, 1999; Comas and Eissental, 2004; Kramer-Walter *et al.*, 2016), although there are uncertainties about how root traits co-vary with above-ground and whole-plant traits (Ma *et al.*, 2018; Kong *et al.*, 2019). In the literature, high RGR is often reported as a key attribute of exploitative plants that also have a deep root system with high SRL, allowing the 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 acquire soil nutrients efficiently. 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 *Triticum turgidum* via changes in management practices (e.g., fertilization, crop density) has uncoupled the above- and below-ground traits. These authors found that the wild ancestors of *T. durum* exhibited stronger correlations between above- and below-ground traits than the domesticated forms. Domestication and the advent of N fertilization seem to have accelerated wheat growth and reduced plant investment in the 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 (e.g. seed mass) 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 among wheat varieties. We also demonstrated that modern conventional selection had unintentional and ‘hidden’ effects on root traits, such as decreasing  $\text{NH}_4^+$  uptake capacity by roots (Fig. 4). 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 the wheat varieties, likely due to selection for high growth and yield in resource-rich or fertilized environments. We believe that these results provide interesting prospects in the context of low-input agriculture. First, the remaining functional diversity that exists for some traits, in particular root trait values, makes plausible a breeding effort specifically focused on low-input systems. Second, the functional diversity existing within wheat varieties can also be used to design variety mixtures with high potential for functional complementarity and thus high yield resilience to fluctuating environmental conditions. It remains to be investigated how this variability will transpose to field conditions.

## Supplementary data

The following 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.

Fig. S1. Values of the coefficient of variation for 10 traits observed either among wheat (*Triticum aestivum*) varieties or among Pooideae species.

Fig. S2. Values of the coefficient of variation for 10 traits observed either among all the 57 wheat varieties or among varieties corresponding to one of the three artificial selection types.

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## Author contributions

All authors conceived the study and designed the methodology; all authors contributed to the data collection; AAMC analyzed the data; AAMC and XLR led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Data availability

Data are available from the TRY database: Kattge J, Bönisch G, Günther A, Wright I, Zanne A, Wirth C, Reich PB, 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>. The other (non-TRY) data that support the findings of this study are available from the corresponding author, Amélie A.M. Cantarel, upon reasonable request.

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