

Plant trait relationships are maintained within a major crop species: lack of artificial selection signal and potential for improved agronomic performance

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Summary

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- The exploration of phenotypic spaces of large sets of plant species has considerably increased our understanding of diversification processes in the plant kingdom. Nevertheless, such advances have predominantly relied on interspecific comparisons that hold several limitations.
- Here, we grew in the field a unique set of 179 inbred lines of durum wheat, *Triticum turgidum* spp. *durum*, characterized by variable degrees of artificial selection. We measured aboveground and belowground traits as well as agronomic traits to explore the functional and agronomic trait spaces and to investigate trait-to-agronomic performance relationships.
- We showed that the wheat functional trait space shared commonalities with global cross-species spaces previously described, with two main axes of variation: a root foraging axis and a slow–fast trade-off axis. Moreover, we detected a clear signature of artificial selection on the variation of agronomic traits, unlike functional traits. Interestingly, we identified alternative phenotypic combinations that can optimize crop performance.
- Our work brings insightful knowledge about the structure of phenotypic spaces of domesticated plants and the maintenance of phenotypic trade-offs in response to artificial selection, with implications for trade-off-free and multi-criteria selection in plant breeding.

Introduction

Characterizing the constraints shaping the diversification of life has long been debated in ecology and evolution (e.g. Gould *et al.*, 1997; Barton & Partridge, 2000; Grubb, 2016; Garland *et al.*, 2022). For a long time, ecology and evolution, micro- and macroevolution, diverged in the way these constraints can be revealed. Over the last decades, plant comparative ecology has brought interesting insights by exploring the covariations between plant traits from a multivariate perspective (Garnier *et al.*, 2016). Indeed, studies comparing the relative positions of species in a multivariate trait space suggest that natural selection has shaped plant phenotypic diversity within an ‘envelope of constraints’ (Ackerly *et al.*, 2000; Donovan *et al.*, 2011; Reich, 2014). Interspecific comparisons remain limited in their scope though, and the effects of selection cannot be deeply explored. Conversely, intraspecific comparisons are, by nature, better adapted to test the role of selection on phenotypic diversity, but their generalization ability is low. Finding commonalities and peculiarities between intra- and interspecific phenotypic spaces appears as

a promising avenue to test the robustness of ecological diversification laws.

Identifying independent dimensions of variation to document and understand phenotypic diversification across the plant kingdom is pivotal in plant functional ecology (Westoby *et al.*, 2002; Diaz *et al.*, 2004; Díaz *et al.*, 2016). These dimensions – axes of specialization – are traditionally approximated by a set of plant functional traits, defined as any morphological, phenological and physiological feature measurable at the individual scale and that impacts plant survival, growth and reproduction (Grime, 1977; Violle *et al.*, 2007; Garnier *et al.*, 2016). In interspecific comparisons, functional traits have been widely documented as proxies of organismal functions (e.g. light interception, soil nutrient acquisition and use) and of ecological strategies depicting plant adaptation to different environmental constraints (Grime, 1977; Westoby *et al.*, 2002; Diaz *et al.*, 2004) and resources’ use economy (Wright *et al.*, 2004; Garland *et al.*, 2022). Importantly, several traits need to be considered to accurately depict the whole phenotype (Laughlin, 2014; Mouillot *et al.*, 2021). A notable example is the study by Díaz *et al.* (2016) who summarized the

phenotypic variation of vascular plants by a six-dimensional trait space. The authors identified two main axes of variation, one size-related axis, which discriminates small herbaceous plants that produce small diaspores from big trees with large diaspores, and another axis depicting a resource acquisition–conservation trade-off captured at the leaf level (the so-called leaf economics spectrum (LES); Wright *et al.*, 2004). The recent incorporation of roots in these analyses has highlighted novel independent dimensions driven by root traits involved in soil resources' economy (Weemstra *et al.*, 2016; Weigelt *et al.*, 2021), which strengthens the need to integrate the 'hidden' part of plants to grasp the multiple facets of resource foraging strategies (Bergmann & Weigelt, 2020). Overall, global trait-based analyses have been very fruitful in revealing robust trait covariations that together shape and constrain cross-species functional spaces (Walker *et al.*, 2017). However, despite these efforts, the mechanisms driving plant functional spaces are still poorly known, partly because interspecific comparisons are inherently biased by phylogenetic signals (Garnier *et al.*, 2016). Even if recent evidence suggests commonalities when comparing intraspecific LES to interspecific LES (Vasseur *et al.*, 2012; Sartori *et al.*, 2019), the aboveground and belowground space of plant forms and functions still remain to be thoroughly assessed at the intraspecific level.

The fundamental constraints underlying functional trait spaces should delineate a fitness landscape in which certain combinations of traits lead to higher performances than others (Laughlin & Messier, 2015; Laughlin *et al.*, 2020). Even if the functional trait-to-performance linkage is a central tenet of trait-based ecology (Arnold, 1983; Violle *et al.*, 2007; Shipley *et al.*, 2016), interspecific analyses have reported weak and often contradictory findings regarding the functional drivers of plant performances (e.g. Adler *et al.*, 2014; Garnier *et al.*, 2018; Salguero-Gómez *et al.*, 2018; Yang *et al.*, 2018). The first reason is that such a linkage is probably species- and environment-dependent, and thus hardly detectable through interspecific comparisons (but see Rolhauser *et al.*, 2022). A second reason is that plant performance, and plant reproductive performance in particular, is multidimensional. This is well known in crop science where agronomic performance is classically described by several agronomic traits such as grain yield, number of spikes m^{-2} , number of seeds per spike and thousand kernel weight (Bulman & Hunt, 1988; Kozak & Mađry, 2006), whose variation is constrained and structured within an agronomic trait space defined here as a multidimensional space reflecting major trade-offs among agronomic traits. A third reason is that the multidimensional nature of plant performance involves the interaction between several physiological and biomechanical properties of the organism, which can result in redundant mapping of plant performance and the existence of multiple peaks in the fitness landscape (Laughlin & Messier, 2015). In fact, it has long been recognized that numerous phenotypic combinations can yield to similar performance values (Koehl, 1996; Wainwright *et al.*, 2005). Such a 'many-to-one' mapping has already been discussed in the evolutionary biology literature (e.g. Wainwright *et al.*, 2005), but hardly in functional ecology (e.g. Marks & Lechowicz, 2006) despite its putative major role in shaping

patterns of diversification in complex physiological systems (Alfaro *et al.*, 2005).

Exploring the intraspecific space of forms and functions and linking it to an agronomic trait space using model crop species has several advantages. From a theoretical standpoint, analysing the functional trait space of crops allows to investigate evolutionary issues by assessing the impact of artificial selection on trait covariations, their overall flexibility or robustness. Some evidence suggests that intraspecific trait covariations were weakened in crops (Martin & Isaac, 2015; Martin *et al.*, 2017). This may result in fewer correlations between traits at the whole plant scale, especially between root and leaf traits (Milla *et al.*, 2014; Isaac *et al.*, 2017; Roucou *et al.*, 2018), compared with wild species. This could be due to different selection pressures in crops compared with wild species (Milla *et al.*, 2014, 2015; Cantarel *et al.*, 2020), or because crop species have narrower phenotypic variation associated with narrower phylogenetic scales (Messier *et al.*, 2017; McCormack *et al.*, 2020). From an applied perspective, identifying proxies of agronomic performance is a long-standing objective for plant breeders (e.g. McClean *et al.*, 2011). The conceptual thinking of crop ideotypes (Donald, 1968), which seeks combinations of plant traits that contribute to increased yield at high planting densities, has enabled targeted efforts to improve light acquisition and use through aerial ideotype selection (Donald, 1968), and more recently, the development of root ideotypes (Lynch, 2013; York *et al.*, 2013). These approaches demonstrated that different phenotypes, in terms of root anatomy, morphology and architecture, enhance the production in harsh environments (Lynch, 1995; Watt *et al.*, 2006; York *et al.*, 2013). The existence of multiple trait covariations is a well-known obstacle to identifying proxies of crop performance, particularly when biophysical constraints are at play (Annicchiarico & Pecetti, 1998; Yuan *et al.*, 2011; Chairi *et al.*, 2020). Yet, applying functional trait-based approaches, especially when considering the entire phenotype encompassing above- and belowground compartments, holds promise in addressing this issue.

In this study, we investigated intraspecific covariations of above- and belowground traits and agronomic traits measured in the field for 179 genetically and phenotypically diverse inbred lines. These lines represented a highly diversified evolutionary prebreeding population (EPO) founded with wild, primitive and cultivated elite subspecies of durum wheat (David *et al.*, 2014). First, we tested whether the intraspecific functional space of durum wheat is structured by the same trade-offs as those observed at the interspecific level. We hypothesized that the structure of the durum wheat functional space would differ from the well-known interspecific space, as crop species evolution has been strongly driven by artificial selection and by local adaptation to artificial environments. Second, we tested whether and how artificial selection has impacted the structure of functional and agronomic trait space. We hypothesized that artificial selection has led to changes in trait covariations, due to selection pressures that have potentially restricted phenotypic variation and weakened trait–trait relationships. Lastly, we tested whether functional traits (or trait combinations) were related to agronomic

traits. We expected that genotypes' functional trait values, which were used as proxies for functional strategies, would be good predictors of the observed agronomic traits, as suggested by the trait-to-performance mapping framework in trait-based ecology (Arnold, 1983; Violle *et al.*, 2007).

Materials and Methods

Plant material and experimental design

We grew 179 inbred lines of *Triticum turgidum* ssp. *durum* (Desf.) Husn. derived from a highly diversified evolutionary pre-breeding population in the field at Mauguio, southern France (INRAE – UE DIASCOPE – Lat. 43°36'36.7"N, long. 3°58'37"E). The EPO population was developed through crosses between different compartments of durum wheat's domestication history, ranging from wild and primitive *T. turgidum* subspecies to elite genotypes (David *et al.*, 2014). The set of EPO lines is a relevant material to test our questions because it captures a substantial amount of genetic and phenotypic variability of the *T. turgidum* subspecies. We set up the field experiment on 21 November 2017. Each of the 179 inbred lines was cultivated in randomly arranged single-genotype plots. The plots had dimensions of 1.5 m by 1.2 m and consisted of six rows each measuring 1.5 m in length. There was a spacing of 20 cm between rows and 2–3 cm between plants within the same row, resulting in a planting density of 240 plants per square metre. The plots were separated by 30 cm horizontally and 2 m vertically (see fig. 1 in Montazeaud *et al.*, 2020b). The soil at the experimental site was stony loam, with *c.* 1% organic matter and a pH 8.7. Nitrogen fertilization was applied twice during the wheat growth cycle with a rate of 109 and 87 kg ha⁻¹ of Nexen[®]. To protect against biotic damages, one herbicide (Pointer[®] UltraSX[®] (30 g ha⁻¹)), one graminicide (Auzon[®] Duo (1 l ha⁻¹)), one insecticide (Karate[®] Xflow (0.063 l ha⁻¹)) treatments and two fungicides treatments (Priori[®] Xtra (1 l ha⁻¹)) were applied during wheat growth cycle.

Measurement of functional traits

For a comprehensive comparison between intra- and interspecific patterns, we focused on measuring plant functional traits that have been widely studied on global studies (Díaz *et al.*, 2016; Weigelt *et al.*, 2021) and known to describe plant ecological strategies. Plant height (cm) was measured on three plants per plot at plant maturity. The heading date was defined as the date at which spikes become visible in 50% of the plants within a plot. We converted the observed dates into degree days by summing the daily average temperatures since sowing using a 0°C base temperature. One foliar disc with a diameter of 6 mm was collected on four healthy and mature leaves from randomly sampled individuals. The four discs of known area were dried together for a minimum of 48 h at 60°C and then weighted in order to estimate the leaf mass per area (LMA, kg m⁻²). Additionally, the leaf nitrogen content (LNC, %) was estimated using spectral reflectance measurements of the foliar disc obtained with a LabSpec[®] 4 spectrometer (Analytical Spectral Devices Inc. (ASD), Boulder, CO, USA) and in-house calibration

(Earnot *et al.*, 2013; see also supplementary information in Montazeaud *et al.*, 2020b for more details).

At the end of the tillering stage, a key stage for cereals, explaining a large part of variation in performance traits among plants (e.g. Xie *et al.*, 2016), two soil cores (10 cm diameter and 15 cm depth) with three to five plants, according to their distribution along the row, were collected for each line. Due to the gravitropism of durum wheat, few roots of the central plant of each soil core were cut during the process of soil sampling, allowing us to select well-developed entire roots connected to the plants. Roots connected to the central plant of the soil core were selected for trait measurements. Roots cut by the soil corer were not measured. Then, the roots were separated into seminal roots and adventitious roots. We focused solely on adventitious roots since they were the youngest and well-developed roots with no sign of senescence. In addition, they were produced at the same time as the production of the leaves on which the traits were measured, making it possible to test the covariations between root and leaf traits. By considering a single type of roots instead of a mixed root system, we were able to compare trait values across different genotypes, irrespective of their relative investment in root types (seminal or adventitious in this case). Root angle (RA) was measured at maturity between the two most distant adventitious roots (see also supplementary information of Montazeaud *et al.*, 2020b). The collected roots were stained with methyl violet and scanned at a resolution of 800 dpi (Epson Expression 1680, Los Alamitos, CA, USA). The root scans were analysed using WINRHIZO (pro v.2009; Regent Instrument, Québec, Canada) software to estimate various traits for each sample, including the number of root tips, the distribution of root lengths across different diameter classes, and the total root length and volume. Root subsamples and the remaining roots were then dried separately for at least 48 h at 60°C. Mean root diameter (RD, mm) was calculated as the average of the median root diameters of each diameter class, weighted by the root length of each class. Specific root length (SRL, m g⁻¹) was calculated as the ratio of the total length of the sample divided by its dry mass. We estimated root tissue density (RTD, g cm⁻³) as the ratio of the dry mass divided by the root volume of the subsample and root branching intensity (RBI) as the ratio of the number of root tips in the subsample divided by its length. Root length density (RLD, cm cm⁻³) was computed by dividing the total root length by the soil core volume.

Measurement of agronomic traits

To link functional traits to genotype's agronomic performance, we measured six major agronomic traits at the plot level: vegetative biomass yield, grain yield, total biomass yield, thousand kernel weight, harvest index and seed number per m². At maturity, we harvested the aboveground biomass from the four central rows of each plot, covering a length of 70 cm, while leaving 40 cm on each side of the rows to minimize edge effects. Vegetative (leaves and stems) and reproductive (spikes with grains) biomasses were separated, dried and weighted. The spikes were threshed, and grains were weighted. Grain biomass was used to calculate grain yield (GY, g m⁻²). Vegetative biomass was used to estimate

vegetative biomass yield per unit area (BY, g m^{-2}). We computed the total biomass yield (TBY, g m^{-2}) by summing the biomasses of grains, spikes and vegetative organs. The thousand kernel weight (TKW, g) was estimated by counting and weighting 250 grains per line. We calculated the harvest index as the ratio of the grain biomass divided by the total aboveground biomass (vegetative and reproductive), in order to evaluate whether genotypes with equal biomass invest more in grain or in vegetative biomass. Furthermore, we assessed the number of grains produced per unit area by calculating the ratio of grain biomass to the thousand kernel weight (seed number per m^2 , Seed nb).

Assessing the degree of artificial selection based on genetic distance

Evolutionary prebreeding population lines derived by successive selfing from a prebreeding population originated from crosses between different genetic compartments of durum wheat, including wild and primitive *T. turgidum* subspecies and elite genotypes. Because the elite compartment has been strongly shaped through human selection, we hypothesized that for each EPO line, the lower the genetic distance to the elite compartment, the stronger the artificial selection. We thus used genetic distance as a proxy of the degree of artificial selection for each EPO line. We estimated the genetic distance to elite lines by computing the average genetic distance of each EPO line to a common set of eight durum wheat elite varieties (Supporting Information Table S1) using 50 000 single-nucleotide polymorphisms (SNPs) obtained from the TaBW280K high throughput genotyping array (Rimbert *et al.*, 2018). First, the SNPs matrix was converted into a *genind* object (*df2genind*) function, ADEGENET package), where each column represents a locus and each row a genotype. Next, we estimated the genetic distance as the average allelic differences with the elite compartment (calculated by averaging the allelic differences from the eight elites for each of the 179 genotypes), using the *diss.dist* () function of the POPPR package.

Statistical analyses

All statistical analyses were performed with R v.4.1.0 (R Core Team, 2022).

To assess the structure of the intraspecific functional space of durum wheat, we performed a principal component analysis (PCA) based on aboveground (Height, LMA, LNC, Heading date) and belowground (RA, RBI, RD, RTD, RLD and SRL) traits (functional trait space hereafter), using the *PCA*() function of the FACTOMINER package. A second PCA was performed on agronomic traits (BY, GY, Harvest index, Seed nb, TBY and TKW; agronomic trait space hereafter). To determine the number of dimensions to retain in the PCAs, we employed the approach developed by Mouillot *et al.* (2021) based on the elbow inflexion point for the area under the curve (AUC) criteria and the mean absolute deviation (MAD; Fig. S1). The elbow method is based on the maximization of a given benefit (AUC or MAD gain) while minimizing the cost (number of dimensions). To estimate the occurrence probability of given combinations

of trait values in the multidimensional spaces, we used a two-dimensional kernel density estimation using the *kde*() function from the KS package. Detailed information on kernel density estimation is provided in Díaz *et al.* (2016).

We performed regression models to quantify the relationships between the genetic distance to elite compartment and the principal components of functional trait and agronomic trait spaces using the *lm*() function. We reported the coefficient of determination, R^2 (adjusted R^2) for each model, as well as the 95% confidence level intervals for the model predictions computed as ± 1.96 unconditional sampling standard deviation (Burnham & Anderson, 1998).

To quantify the relationships between major agronomic traits, that is biomass yield, grain yield, harvest index, TKW, total biomass yield and seed number per m^2 , and functional traits, we fitted for each agronomic trait a full model including all the functional traits and their quadratic terms, as explanatory variables (*lm*() function). We used quadratic terms to test whether various trait values could lead to similar agronomic performance (several peaks in agronomic performance; illustrating a ‘many-to-one mapping’ between traits and performance). Both the dependent and independent variables were standardized ($\mu = 0$, $\sigma = 1$). We then performed a backward model selection (*glmulti*() function from the GLMULTI package) to rank the models according to their Akaike information criterion values, corrected for small sample size (Sugiura, 1978; Burnham & Anderson, 1998), and we selected the N best models with Akaike information criterion (AICc) differences from the first model lower than two (Tables S2–S5). We then conducted model-averaging, based on the N best models, using the *coef*() function from GLMULTI package in order to obtain standardized parameter estimates and their 95% unconditional confidence intervals, as well as trait relative importance and adjusted R^2 .

Results

Functional and agronomic trait spaces occupied by durum wheat lines

The four principal components (PC) that structure the functional trait space explained 66% of the variability. The first two principal components, PC1 and PC2, altogether explained 42% of the variability (Figs 1a, S1). PC1 (24.2%) was strongly positively associated with RD and RBI, while negatively correlated with SRL and RLD (Fig. 1a). This component represents a gradient from genotypes that extensively explore the soil with fine, long and sparsely branched roots to genotypes that invest in thicker, more branched roots (left to right in Fig. 1a; Table S6). PC2 explained 17.8% of the variability. It was positively associated with LNC and SRL, while negatively associated with RTD and LMA (Fig. 1a; Table S6). PC2 represents a gradient from genotypes with dense tissues to genotypes with low-density tissues, high nitrogen content and high SRL values. PC3 explained 12.7% of the variability and was positively correlated with RTD, RA and Heading date. PC4, explaining 11.3% of the variability, was positively associated with plant height and RLD and negatively associated with RA (Fig. S2; Table S6).

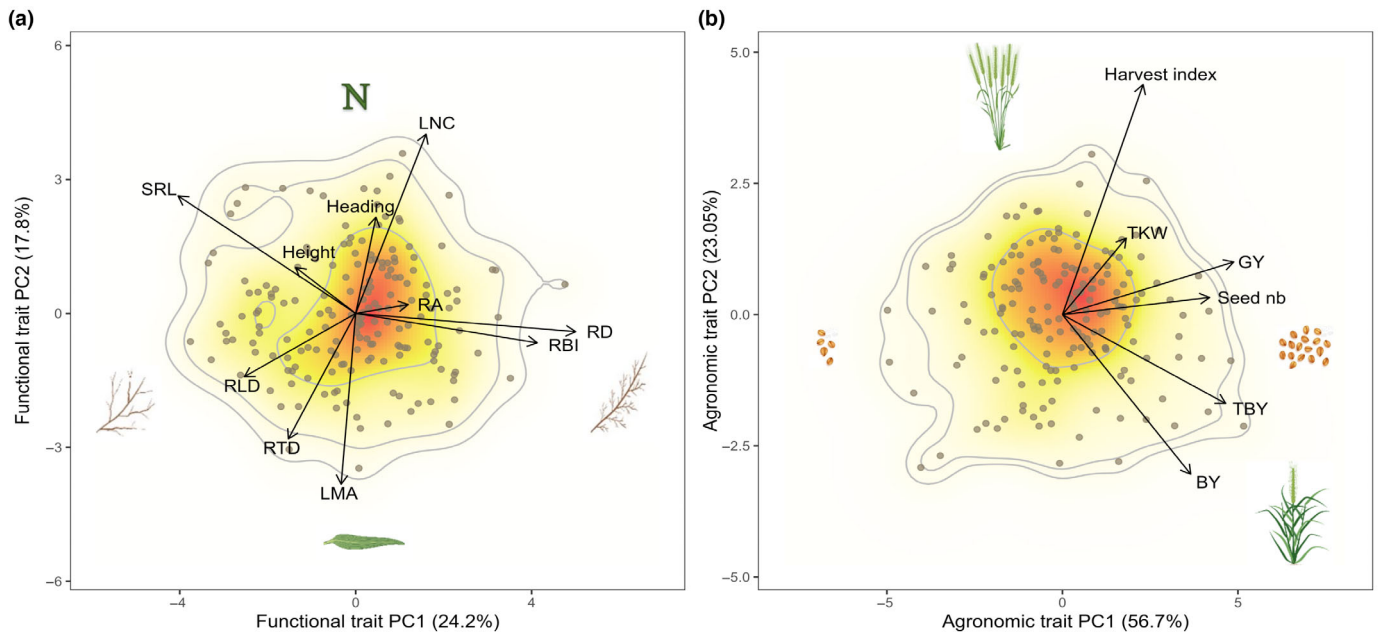


Fig. 1 Projection of the 179 durum wheat lines (*Triticum turgidum* spp. *durum*) on the plane defined by the first two components of a principal component analysis based on: (a) above- and belowground functional traits: Heading (degree days), heading date; Height, maximal plant height (cm); LMA, leaf mass area (kg m^{-2}); LNC, leaf nitrogen content (%); RA, root angle ($^{\circ}$); RBI, root branching intensity (number of tips per length unit); RD, root diameter (mm); RLD, root length density (cm cm^{-3}); RTD, root tissue density (g cm^{-3}); SRL, specific root length (m g^{-1}); (b) agronomic traits related to biomass production and reproduction: BY, biomass yield (g m^{-2}); GY, grain yield (g m^{-2}); Seed nb, seed number m^{-2} ; TBV, total biomass yield (g m^{-2}); TKW, thousand kernel weight (g). The colour gradient and contour lines correspond to the 0.5, 0.95 and 0.99 quantiles of the respective probability distribution, thus highlighting the regions of highest (orange) and lowest (white) trait value combination occurrence probability.

Three principal components characterized the agronomic trait space of the 179 genotypes and accounted for 98% of the variability (Figs 1b, S1; Table S6). PC1 (56.7%) was mainly correlated with grain production, while PC2 (23.05%) was correlated with vegetative biomass. PC1 was positively associated with grain yield and total biomass yield (GY and TBV) as well as seed number per m^2 . PC2 was highly positively associated with harvest index and negatively with biomass yield (BY; Fig. 1b; Table S6). PC3 was positively associated with thousand kernel weight and negatively with the number of seeds per m^2 (Fig. S2; Table S6).

Footprint of artificial selection on the functional and agronomic trait spaces

We detected no significant relationship between PC1 and PC2 of the functional trait space and the genetic distance between EPO lines and the elite durum wheat compartment ($P > 0.05$; Fig. 2a, b). Conversely, the first two PCs of the agronomic trait space were both negatively correlated with the genetic distance ($R^2 = 0.03$, $P = 0.01$; $R^2 = 0.05$, $P = 0.001$, respectively; Fig. 2c, d). Thus, the smaller the genetic distance between an EPO line and the elite compartment, the higher its grain yield, total biomass yield and number of seeds per m^2 (Fig. 2c), the lower its biomass yield, and the greater its harvest index (Fig. 2d). PC3 of the agronomic trait space did not significantly covary with genetic distance ($P > 0.05$; Fig. S3c).

The functional trait-to-agronomic performance mapping

The adjusted mean R^2 of the best full models for each agronomic trait ranged from 0.08 for the seed number per m^2 to 0.31 for biomass yield. Total biomass yield, grain yield, thousand kernel weight and harvest index had intermediate values with R^2 of 0.11, 0.15, 0.22 and 0.25, respectively (Figs 3, S4; Tables S2–S5). We found that functional traits better explained agronomic performance when pooled in the analysis (R^2 ranging from 0.15 to 0.31; Fig. 3) than when analysed individually (R^2 ranging from 0.02 to 0.20; Fig. 4). Several functional traits, both aboveground and belowground traits, had jointly a significant relationship with agronomic traits (Figs 3, 4). Biomass yield was positively related to plant height, leaf nitrogen content and the root angle quadratic term, and negatively to the specific root length quadratic term, that is genotypes with higher vegetative biomass production were tall with high leaf nitrogen content, intermediate SRL values and either very high or very low root angle values (Figs 3a, 4a–d). Grain yield was jointly explained by LMA (quadratic term), heading date, root tissue density and root diameter (Fig. 3b). Additionally, harvest index was positively explained by LMA quadratic term and negatively by root diameter, heading date and height quadratic term (Fig. 3c). Investment in grain biomass was higher for early genotypes, with thinner roots and peaked for low or high LMA values (Figs 3c, 4e–g, i–k). Thousand kernel weight was significantly associated with plant height, RTD (quadratic term) and root diameter (Fig. 3d). Genotypes with high

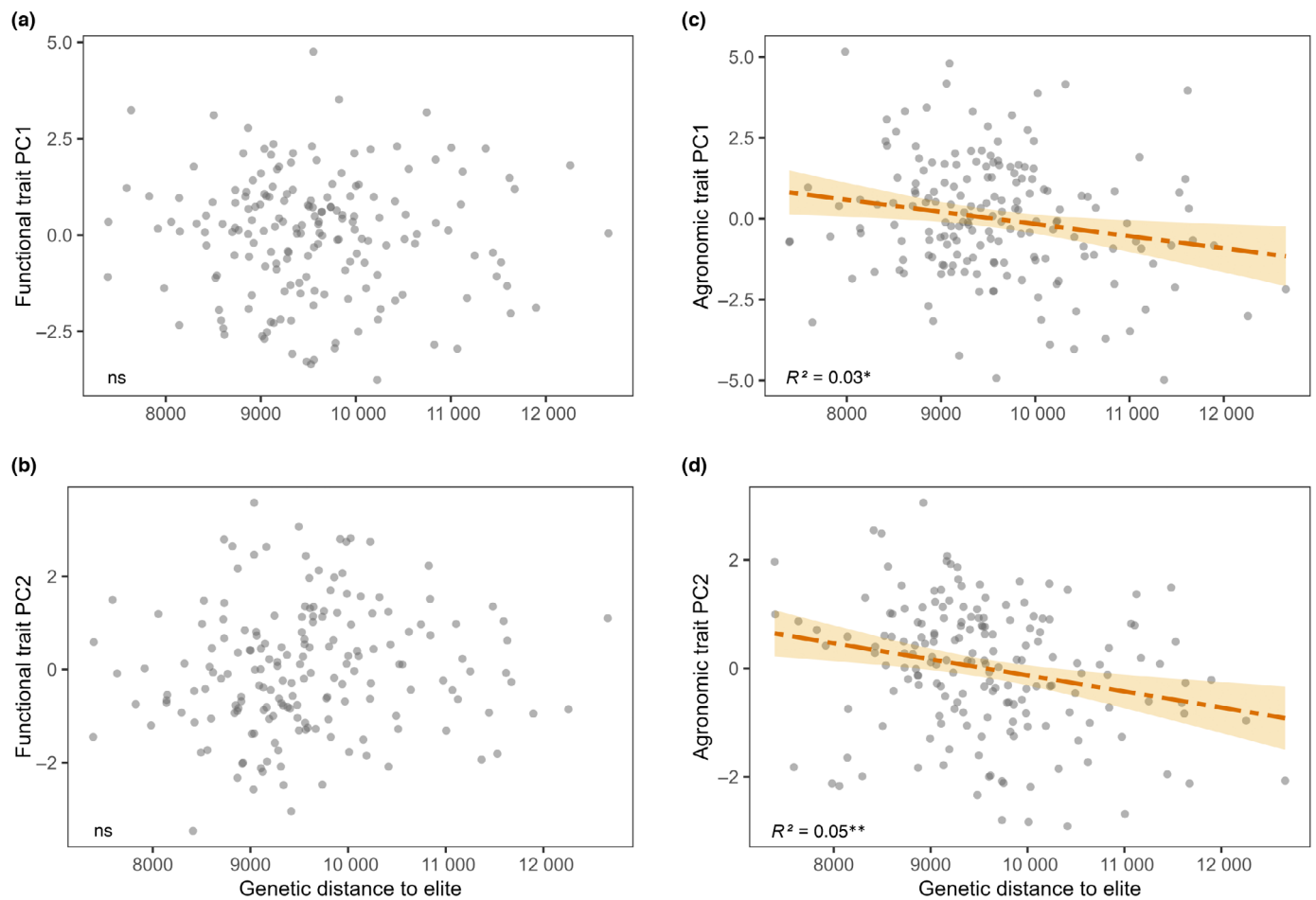


Fig. 2 Relationships between the degree of artificial selection of durum wheat genotypes, *Triticum turgidum* ssp. *durum* (assessed by the genetic distance to elite compartment) and the two first components of the functional trait space (a, b) and agronomic trait space (c, d). For each relationship, the adjusted coefficient of determination R^2 is given. Significance: ns, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The red dotted line shows the predicted relationship by the model with the 95% confidence level interval in orange.

thousand kernel weight values were tall genotypes, with thinner roots, and low or high RTD values (Figs 3d, 4m–o). The functional traits that had the broadest effect on agronomic traits were not always the ones that contributed the most to the functional trait space structure (Fig. 1a); in particular, plant height and heading date (Fig. 4a,e,i,m), which mostly contributed to the third and fourth axes of variation (i.e. PC3 and PC4).

Discussion

In this study, using 179 durum wheat genotypes, we demonstrated that intraspecific trait covariations are structured by the same trade-offs than those previously described at the interspecific level (Westoby *et al.*, 2002; Wright *et al.*, 2004; Reich, 2014; Díaz *et al.*, 2016; Weigelt *et al.*, 2021). We did not detect any effect of artificial selection on the genotype position within this functional space, whereas we found a strong footprint of artificial selection on the agronomic space, confirming the strong impact of human selection on yield-related traits. Our findings also revealed that combinations of above- and belowground traits explained wheat performance at the plot level, which both

enriches our understanding on the relationship between genotype functional traits and their performance outcomes (Wainwright *et al.*, 2005; Violle *et al.*, 2007) and brings insightful information for multi-criteria yield improvement (Arnold, 1983; Annicchiarico & Pecetti, 1998).

A fundamental question in functional ecology is whether trait covariations are maintained both among species and within species (Shoval *et al.*, 2012; Vasseur *et al.*, 2012; Niinemets, 2015; Isaac *et al.*, 2017; Messier *et al.*, 2017). By considering both above- and belowground traits, we provide evidence that the intraspecific functional space of durum wheat is structured by the same trade-offs than those observed at the interspecific level (Díaz *et al.*, 2016; Weigelt *et al.*, 2021). Root traits played a significant role in shaping the phenotypic space, particularly in supporting the two main axes of trait covariation. The first axis opposed specific root length and root diameter. This axis is commonly described as a gradient of soil exploration strategies, contrasting genotypes that are efficient at exploring the soil and acquiring resources thanks to their ability to develop fine and economical roots, to thick-rooted genotypes that invest more carbon in soil exploration and may rely more on mycorrhizal

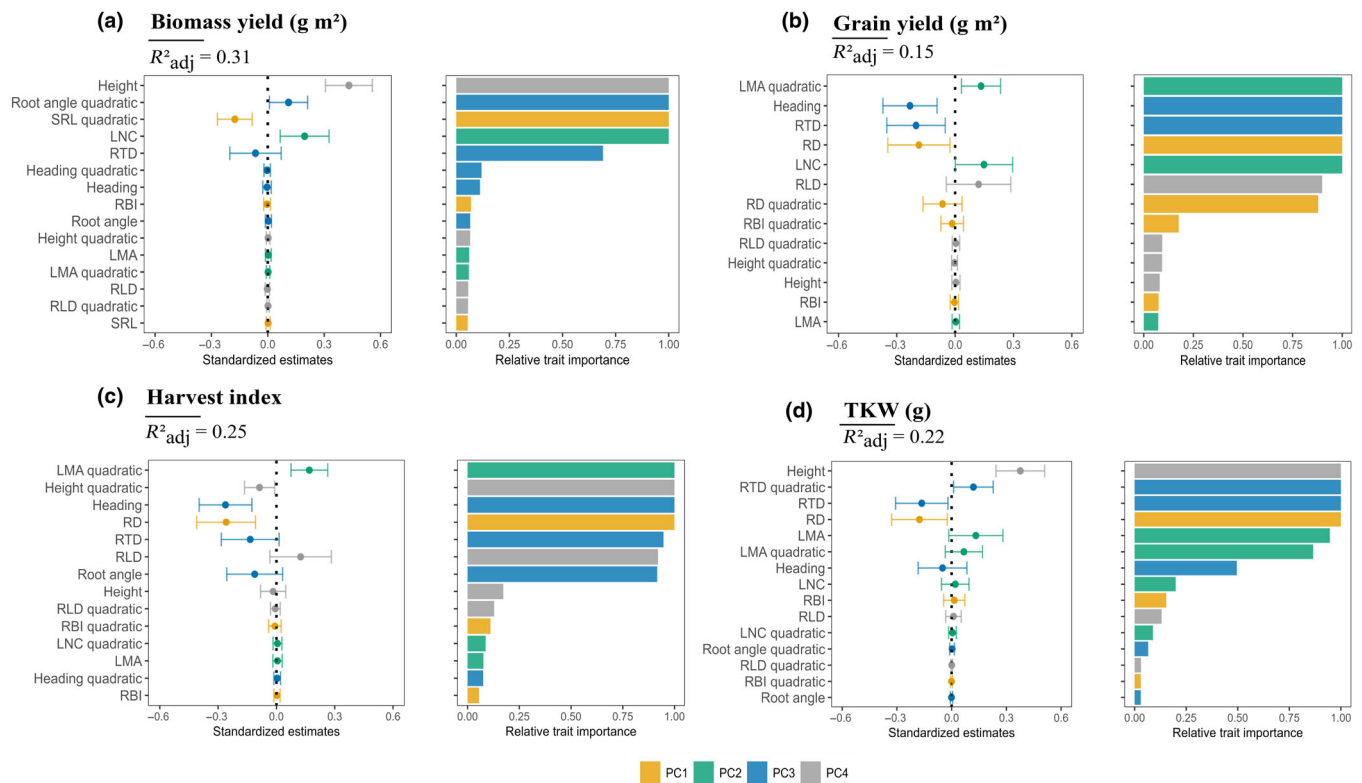


Fig. 3 Standardized effects of functional traits on agronomic traits including biomass yield (g m^{-2} , a), grain yield (g m^{-2} , b), harvest index (c) and thousand kernel weight (TKW, g, d). Above- and belowground functional traits: Heading date in degree days (Heading); maximal plant height in cm (Height); leaf mass area in kg m^{-2} (LMA); leaf nitrogen content in % (LNC); root angle ($^{\circ}$); root branching intensity in number of tips per length unit (RBI); root diameter in mm (RD); root length density in cm cm^{-3} (RLD); root tissue density in g cm^{-3} (RTD) and specific root length in m g^{-1} (SRL). A quadratic term was added in the models to test nonlinear relationships between functional traits and agronomic traits. Backward model selection was performed on a full model with agronomic traits as the response variable and all functional traits as explanatory variables (Supporting Information Tables S2–S5). The N best models based on an Akaike information criterion (AICc) difference < 2 were retained to compute model-averaged estimates reported on the left side of the four panels with their 95% unconditional confidence intervals (error bars). The relative importance of functional traits is reported on the right side of the four panels and can be interpreted as the probability that the trait is in the best model. Although a functional trait is represented on several dimensions, we assigned colours to the dimensions of the functional trait space where the trait contributes the most. Adjusted R^2 averaged across the N best models (R^2_{adj}) are also presented for the four models.

partnerships for resource acquisition (Eissenstat *et al.*, 2015; Kramer-Walter *et al.*, 2016; Bergmann & Weigelt, 2020; Weigelt *et al.*, 2021). In this study, this axis is also associated with the root branching intensity, which positively covaried with root diameter. Thick roots are more densely branched than thin roots; this suggests that genotypes with high specific root length values extensively explore the soil by producing long, thin roots with few ramifications, while thick-rooted genotypes achieve intensive soil exploration through high branching, potentially enhancing their ability to exploit nutrient-rich patches (Hodge, 2004; Kong *et al.*, 2014). This finding contradicts expectations based on tree studies (Eissenstat *et al.*, 2015; Liese *et al.*, 2017) and rice research (Montazeaud *et al.*, 2018), that is thicker roots are usually found to be more sparsely branched. As with many other root traits (e.g. root hairs and exudates), this emphasizes that we lack knowledge about root constraints that shape genotype position within the phenotypic space, despite the acknowledged importance of roots for resource acquisition (York *et al.*, 2013). The second axis of trait covariation can be associated with the well-documented trade-off between ‘fast’ and ‘slow’ return on carbon and nutrient investment (Reich, 2014).

This axis opposes genotypes with dense root tissue and high leaf mass per area values to those with high leaf nitrogen content. This result supports the idea that the ‘fast–slow’ trade-off is common for both above- and belowground organs (Weigelt *et al.*, 2021) and that similar trade-offs shape plant phenotypic space at both inter- and intraspecific level, even within a crop species. These findings emphasize the importance of further investigating intraspecific variation in root traits, considering their crucial role in determining key physiological and ecological plant strategies across different environments (Borden *et al.*, 2020; Freschet *et al.*, 2021; Weemstra *et al.*, 2021).

In addition to the commonalities observed between the wheat functional space and interspecific spaces described in functional ecology, we highlighted peculiarities that can be attributed to the life history of durum wheat, notably the breeding history of EPO lines. Unlike the study of Díaz *et al.* (2016), in which the first axes of variation depict a size gradient, here variation in plant height was not well described by the two major axes of the functional space. This discrepancy between patterns of variation in natural populations and those observed in our study could be

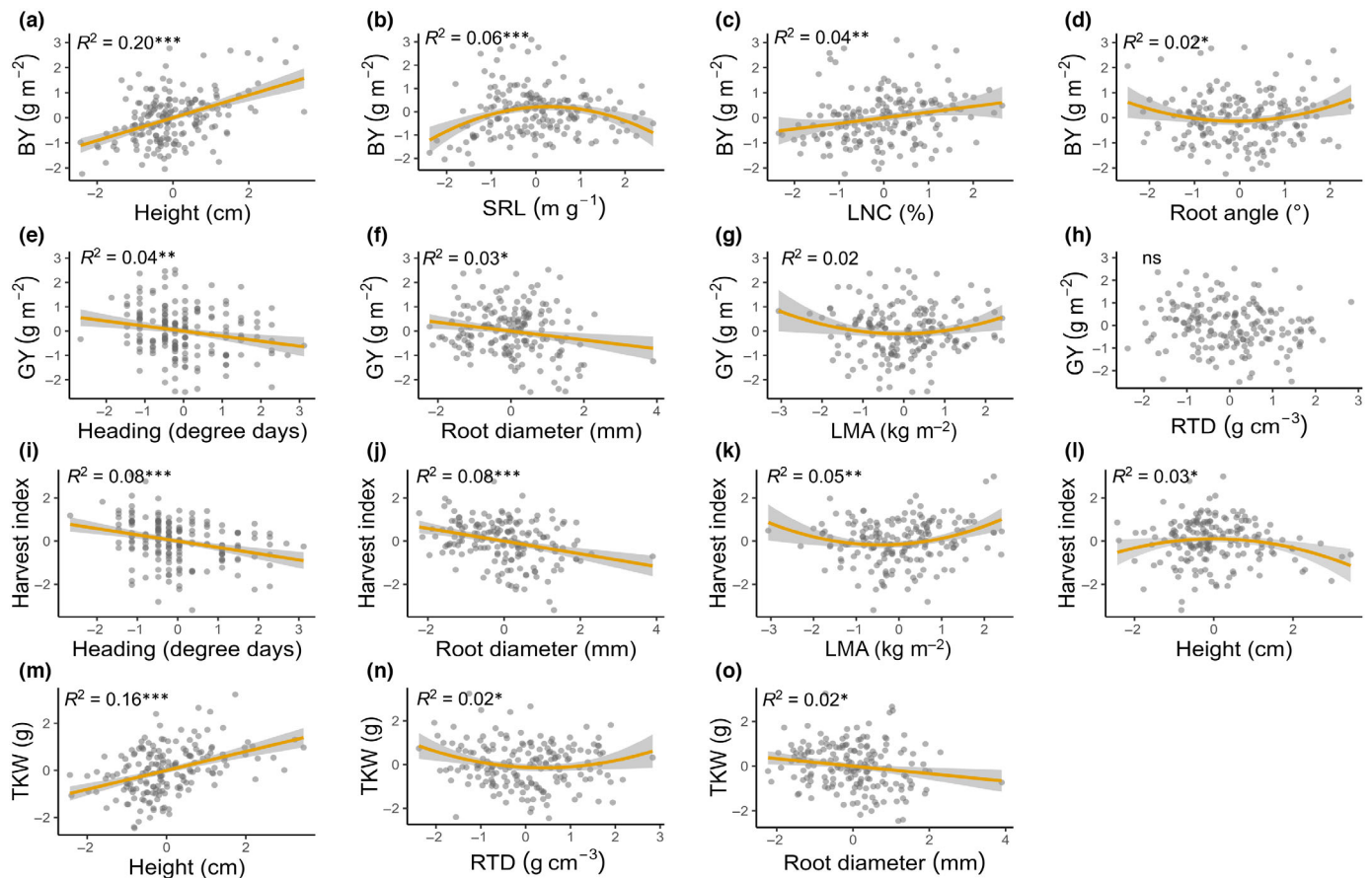


Fig. 4 Univariate relationships between the four agronomic traits and functional traits. Agronomic traits related to biomass production and reproduction: BY, biomass yield (g m^{-2}) (a to d); GY, grain yield (g m^{-2}) (e to h); Harvest index (i to l); TKW, thousand kernel weight (g) (m to o). Above- and below-ground functional traits: Heading (degree days), heading date (e, i); Height, maximal plant height (cm) (a, l, m); LMA, leaf mass area (kg m^{-2}) (g, k); LNC, leaf nitrogen content (%) (c); root angle ($^{\circ}$) (d); root diameter (mm) (f, j, o); RTD, root tissue density (g cm^{-3}) (h, n); and SRL, specific root length (m g^{-1}) (b). Functional traits shown had the highest relative importance (i.e. they were selected by all the N best models; Fig. 3) and had standardized estimates with 95% unconditional confidence intervals that did not cross 0. For each relationship, the adjusted coefficient of determination R^2 is given. Significance: ns, not significant; ., $P < 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The orange solid line shows the predicted relationship by the model with the 95% confidence level interval in grey.

explained by the fact that plant height variability has been reduced through the selection of durum wheat. Reduced stature has been strongly favoured since the Green Revolution to prevent lodging in nitrogen-rich conditions and to limit plant competition for light (Donald, 1968; Peng *et al.*, 2011; Montazeaud *et al.*, 2020a). Because of its breeding history (David *et al.*, 2014; Montazeaud *et al.*, 2020b), height variability in EPO remains higher than in modern durum wheat and we expected this height variability to further shape the phenotypic space of this species, but our findings did not support this expectation. The third variation axis was phenology-driven, where late heading was associated with high carbon-based construction costs, as indicated by high root tissue density, highlighting the existence of another component that may be related to the ‘fast–slow’ continuum. This finding underscores the significant role of phenology in crop physiology and justifies its long history of selection in agronomy (e.g. Jung & Müller, 2009). Conversely, phenology has been poorly integrated in interspecific functional spaces so far (but see Segrestin *et al.*, 2018). Beyond the well-known key role of

phenology in annual plants (see e.g. Sartori *et al.*, 2019), a more systematic integration of phenological traits in large-scale inter-specific analyses is a priority for the research field.

Several studies have shown that domesticated species tend to have faster growth and more ‘fast’ resource-use strategies than their wild relatives (Hancock, 2012; Milla *et al.*, 2015; Milla & Mate-sanz, 2017; Roucou *et al.*, 2018; Isaac *et al.*, 2021), which is interpreted as an adaptation to nutrient-rich habitats (Chapin, 1980; Pujol *et al.*, 2008; Milla *et al.*, 2014; Roucou *et al.*, 2018). Here, variation in functional traits was not explained by the genetic distance of EPO genotypes to modern varieties, which can be interpreted as a lack of effect of artificial selection on the positioning of genotypes within the phenotypic space, suggesting that trade-offs between traits are difficult to overcome. However, we cannot ignore a potential bias in our quantification of the degree of artificial selection that has been inferred on the whole-genome level while only a reduced number of genes probably capture human-driven selection (Doebley *et al.*, 2006). On the contrary, we found significant relationships between the different

facets of wheat's agronomic performance and the degree of artificial selection. As expected, genotypes that shared more genetic similarities with modern varieties displayed higher values of harvest index, total biomass and grain production, and lower values of vegetative biomass. This could be explained by the fact that artificial selection has deliberately acted on yield components in the evolutionary history of crops (Harlan *et al.*, 1973; Hay, 1995; Peleg *et al.*, 2011; Peng *et al.*, 2011). Due to the absence of a significant effect of genetic distance to modern varieties on durum wheat functional traits that are indirectly linked to agronomic performance, we hypothesize that these traits could serve as promising candidates for future breeding programmes aimed at better-adapting varieties to constraints of new environments.

According to Arnold's (1983) paradigm, later adapted in functional ecology (Violle *et al.*, 2007), functional traits are expected to influence directly and indirectly plant fitness. The multifaceted nature of resource-use strategies and plant performance has long impeded a comprehensive evaluation of the functional traits-to-performance mapping in both wild and crop species (Phillips & Arnold, 1989; Laughlin & Messier, 2015). The complexity of trait–performance relationships stems from the multivariate nature of plant phenotypes, where traits are interrelated throughout the plant. For example, if trait A has a positive effect on genotype performance, this effect can, in fact, be due to the effect of a trait B that interacted with A (Phillips & Arnold, 1989). Here, we identified above- and belowground traits combinations that were related to agronomic performance, thus confirming that trait–performance mapping is multidimensional. Although these combinations of functional traits explain a limited part of the variation for some agronomic traits, it is noteworthy that functional traits from the fourth PC axis of the durum wheat phenotypic space are involved in these relationships, which underlines the fact that agronomic performances are dependent on the whole plant phenotype. Despite not being well described by the first two axes of the phenotypic space, plant height and heading date were strongly associated with agronomic performance. Tall genotypes produced higher amounts of vegetative biomass and heavier grains, but did not necessarily produce the greatest amount of grains, in part because of the quadratic relationship between plant height and harvest index. In parallel, heading date was negatively related to harvest index and grain yield. As a result, early heading genotypes with an intermediate plant height had higher harvest index and grain yield. Plant height and crop phenology jointly strongly influence the yield of crops, as previously described in rice crops (Li *et al.*, 2012), in wheat (Hyles *et al.*, 2020) and oat (Rosielle & Frey, 1975), in particular, because these traits are strongly involved in plant responses to abiotic and biotic factors and therefore influence allocation patterns within the plant (Donald & Hamblin, 1976; Hill & Li, 2016). Simultaneously, traits associated with the 'fast–slow' economic spectrum also played a significant role in explaining agronomic performances: mid-spectrum genotypes (displaying intermediate LNC, LMA and RTD) produced less vegetative biomass and grain biomass than 'fast' genotypes, which produced higher vegetative biomass and heavier seeds. Moreover, root systems characterized by high specific root length, high root length density and low root

diameter can facilitate belowground resource foraging (e.g. Campbell *et al.*, 1991; Freschet *et al.*, 2021), which could in turn increase the allocation of resources to the growth and reproductive function. We found in particular a maximization of biomass yield at intermediate values of specific root length. These findings support the links between root traits, resource acquisition strategies and yield components and underpin the importance of an underground ideotype for crop improvement (Richardson *et al.*, 2011; Lynch, 2013; York *et al.*, 2013).

Our findings call for mobilizing breeding approaches that consider multidimensional phenotypic space to take into account plant trade-offs and potentially even override them (Denison, 2015; Isaac & Martin, 2019; Rolhauser *et al.*, 2022). The existence of multiple phenotypic pathways to plot-level performances opens new avenues for plant breeding programmes since several traits should be targeted simultaneously. Multi-criteria crop breeding has made a lot of progress in recent years though (Cabrera-Bosquet *et al.*, 2012; Moeinizada *et al.*, 2020), and we are confident that future fruitful interactions between ecology and agronomy will lead to better identification of breeding targets and to the removal of still largely unknown phenotypic and genetic constraints.

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Competing interests

None declared.

Author contributions

CV, FF and HF planned and designed the research. GM, AR, FF and HF performed the experiment. TL analysed the data. TL, CV and FF wrote the first version of the manuscript, with inputs from GM, HF and MEI. All authors read and approved the final manuscript.

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Data availability

The data to reproduce all analyses of this paper can be accessed at <https://osf.io/23vfe/>.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Influence of the number of dimensions used to build the functional trait and the agronomic trait spaces, on the space quality assessed by the area under the curve criteria and the mean absolute deviation.

Fig. S2 Projection of the 179 durum wheat lines (*Triticum turgidum* ssp. *durum*) on the plane defined by the last two components of a principal component analysis based on above- and belowground functional traits and then by the first and the third principal components based on agronomic traits.

Fig. S3 Relationships between the genetic distance to the elite compartment and the last components of the functional trait space and the agronomic trait space.

Fig. S4 Standardized effects of functional traits on agronomic traits including total biomass yield (g m^{-2}) and seed number per m^2 .

Table S1 Name and date of registration in the catalogue of the eight elite wheat varieties (*Triticum turgidum* ssp. *durum*) used to calculate the average genetic distances with the 179 genotypes.

Table S2 Model selection for biomass yield.

Table S3 Model selection for grain yield.

Table S4 Model selection for harvest index.

Table S5 Model selection for thousand kernel weight.

Table S6 Correlation coefficients between traits and principal component axes for the functional trait space and the agronomic trait space.

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