Euphytica (2025) 221:143
https://doi.org/10.1007/s10681-025-03594-5

RESEARCH

Analyses of phenotypic and genomic based genetic diversity highlight useful trait variation for the improvement of grain and protein yield of pea (*Pisum sativum* L.) grown in Norway

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Received: 3 May 2025 / Accepted: 28 July 2025 / Published online: 15 August 2025
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Abstract Pea (*Pisum sativum* L.) plays a central role for achieving the goal of increased self-sufficiency of plant-based protein for food and feed in Norway. This study characterized 36 pea genotypes of mainly Nordic and eastern European origin grown in a multi-environment field trial in Norway for various agronomic traits including grain and protein yield. The same accessions were also genotyped with a single nucleotide polymorphism (SNP) chip array to investigate the genetic diversity both at the phenotypic and genomic levels. Variance component (VC) analyses found that genotype (G) and genotype by year by location (G × Y × L) interaction VC were the main sources of variation for all the considered traits, with G × Y × L being strongly affected by the different climatic conditions which characterized the two test years. A further dissection of the genotype by environment interactions (GEI) through Additive Main effects and Multiplicative Interaction (AMMI), highlighted pea cultivars which outperformed the reference Norwegian variety Ingrid both in term of yield, protein content and protein yield. Measurements of genetic distance based on phenotypic and genomic data were significantly correlated and distinguished the material in three main clusters which were partially associated with their geographic origin. Overall, this work identified pea genotypes which can be successfully grown in Norway and used as source of genetic diversity for future breeding efforts targeting the Norwegian environment.

Keywords GEI · Breeding · Population structure · Adaptation · Multi-location field trials

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10681-025-03594-5.

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Introduction

Field pea (*Pisum sativum* L.) is a temperate grain legume well adapted to cool temperatures and can be grown also on higher latitudes under long days and short growing seasons. The seed has a high protein content and is well suited both for human foods and animal feed. The pea crop has been cultivated at high latitudes in the Nordic countries since historical times. The production volume has varied, but it has persistently occupied a rather small part of the arable land (in Norway about 1.3% of the total arable area was cultivated with pea and faba bean in

2018, Abrahamsen et al. 2018) that are dominated by cereals. However, renewed interest has been seen during the last decade in the Nordic countries as well as in the EU, driven by demand for high protein crops to replace imported plant protein (EU Farm to Fork strategy as part of the European Green Deal). Increase in the production areas has also been driven by the agronomical and environmental benefits of including grain legumes in a cropping system (Stagnari et al. 2017; van Loon et al. 2023). In Norway pea is grown as a spring crop, due to the severe winters which hinder the use of winter types. The main pea growing region in Norway is located at approximately 60°N, which represents the highest latitude of large-scale cultivation for this crop worldwide.

High-yielding and adapted pea varieties are a prerequisite for successful cultivation and farmer adoption. Specifically, for the pea cultivation regions in southeast of Norway, there is a need for varieties adapted to the prevalent weather conditions characterized by cool spring and then rapidly increasing temperatures together with long days in the first part of the life cycle, and relatively cool and humid weather with decreasing temperatures during the maturation and harvest period. The low spring temperatures can delay emergence and seedling development and thus move maturation and harvest later in the autumn with risk of unfavorable conditions due to decreasing temperatures and increasing precipitation as autumn progresses. On the other hand, the long photoperiod during summer combined with the closer to optimal temperatures in this period can accelerate plant development (Carlson-Nilsson et al. 2021), giving a positive compensating effect. As pea is a facultative long-day plant (Lake et al. 2021), these effects can be strengthened at higher latitudes.

The pea ideotypes for such northern latitudes are not well defined, but the ability to mature early and at decreasing temperatures are likely among the most important. Vanhala et al. (2016) investigated flowering time adaptation in Swedish pea landraces and corresponding diversity in main flowering time genes. The results showed that flowering time adaptation had a complex genetic background. However, strong genetic control of physiological traits related to plant growth and development like days to flowering, days to maturity or flowering duration are reported in many studies, i.e., through high heritability estimates (Ali et al. 2021; P. Annicchiarico et al. 2017a, b; Tolessa 2017; Uhlarik et al. 2022, Sadras et al. 2021).

High and stable yields combined with improved ability to withstand lodging are among the main breeding goals. Today, semi-leafless varieties are dominating, having more tendrils but large stipules (*afaf StSt*) improving the resistance to lodging without sacrificing in leaf area to produce high yield (Tran et al. 2022). Several studies have focused on physiological traits important for yield potential in pea, such as exploring the interrelationships between phenological development, duration of the growth stages, formation of the yield components and yield stability. In many studies, seed yields were positively associated with yield components as thousand seed weight (TSW) and number of pods per plant, but also to plant height, days to flowering and days to maturity (Ali et al. 2021; Carlson-Nilsson et al. 2021; Uhlarik et al. 2022).

Protein content is an important quality trait in pea, both when used for food and feed. Daba and Morris (2022) recently reviewed the variation in protein content in pea and found a general variation from 13 to 38% with the most common variation from 20 to 30%. Many investigations have shown negative correlations between protein and starch content as well as between protein content and seed yield. However, these relationships were not always negative, and positive correlations between protein content and yield were also reported (Červenski et al. 2017; Karjalainen and Kortet 1987). In other studies, the protein content was reported to be independent of the grain yield (Carlson-Nilsson et al. 2021; Ferrari et al. 2016; Mohammed et al. 2018). Heritability estimates for protein content have been shown to be moderately high (reviewed by Daba and Morris 2022). Jha et al. (2013) studied 169 pea accessions and reported that the eastern European accessions were generally higher in protein content compared with western European and Canadian accessions. A similar study by Tzitzikas et al. (2006) reported that brown pea genotypes had higher average protein content than green or yellow (averages of 26.7, 21.5 and 21.8%, respectively). Genotype–environment interactions (GEI) are commonly reported in crops when Multi-Environment Trials (MET) are

performed, including field peas. GEI demonstrate different responses of the genotypes to environmental conditions, giving implications for breeding strategies which are aimed at being managed by selecting for high-performance combined with stability or adaptability to relevant environmental conditions. Statistical models, such as the Additive Main effects and Multiplicative Interaction (AMMI) combined with calculation of stability indexes as the Weighted Average of Absolute Scores (WAAS) developed by Olivito et al. (2019) has been successful to analyze and decompose GEI in several crops. Several recent studies in field pea, across various countries and climatic conditions (Daba et al. 2023; Haile and Tesfaye 2024; Maleki et al. 2024; Sharma et al. 2025), aimed at the dissection of GEI with potential also to provide insight into the factors causing such interactions.

Pea varieties which are high-yielding and adapted to the short growing season are needed to support the increase in grain legume production in Norway. However, there is no pea breeding program in Norway to date, and the available varieties on the market are developed by breeding companies which direct their activities towards regions at latitudes further south. In this study, a set of modern spring pea varieties from breeding companies in northern, central and eastern regions of Europe were collected and tested for agronomic performance in multi-location field trials at northern latitudes of approximately 60° N in Norway. The aims were to analyze the effect of genotype (G), environment (E) and genotype by environment (G X E) on agronomic traits important for the cultivation of peas in Norway, subjected to cool and wet conditions during pod development and maturation. This analysis was complemented by using molecular markers to measure genetic diversity at the genomic level. The aims of this study were to:

(i) identify genotypes that could be recommended for cultivation in Norway.
(ii) assist breeding of pea cultivars adapted to the Norwegian conditions, by pointing at strategies for pre-breeding and selecting genotypes to be used as parents for crossings.

Material and methods

Plant material and field trials

Varieties and advanced breeding lines of field peas were collected from European breeders and tested in field trials at three locations in Norway in 2022 and 2023. The selection of varieties was done through contact with breeding companies in northern and central Europe, which provided varieties of spring peas that were assumed to be adapted to Nordic climates. All were of the semi-leafless type (*afafStSt*). The number of varieties tested were 44 and 51 in the seasons 2022 and 2023, respectively. An overview of the varieties tested in the different seasons and of the breeding companies providing the material is given in the supplementary material (S1). A set of 36 genotypes (varieties and breeding lines) common across all test locations and years were considered for the analyses described below. The three locations were Vollebekk (research farm at Norwegian University of Life Science, Ås, $59^{o}39'$ N, $10^{o}45'$ E), Bjørke (research farm of Graminor AS, Hamar, $60^{o}80'$ N, $11^{o}20'$ E), and Apelsvoll (research farm at the Norwegian Institute of Bioeconomy Research, Toten, $60^{o}70'$ N, $10^{o}87'$ E). All locations are within the main grain legumes and cereals producing region in southeast of Norway. Among these, Apelsvoll is representative for growth conditions of slightly cooler temperatures and shorter duration of the growth season while Vollebekk is representative for growth conditions of slightly warmer temperatures, early sowing time and longer growth season. An overview of the daily mean temperature and precipitation at the three locations in the two seasons is provided in the supplementary material (S2). The field trials were laid out as a randomized complete block design with three replicates. Seed rate was set to 100 viable seeds/m^2, and the trials were sown when the soil reached optimal moisture content in the spring. Plot size varied at the different locations, from 9.6 m^2 at Bjørke to 12.8 m^2 at Apelsvoll. Weeds were controlled by using the herbicide Basagran (Bentazon, 870 g/kg). The field trials were carried out on fertile soil of optimal pH. No fertilization nor *Rhizobium* inoculation was applied, but PK fertilized was applied to secure optimal plant growth. An overview of management practices at the different locations is given in the supplementary material (S3).

Phenotyping

Plant development stage was assessed weekly using the BBCH scale (Weber and Bleiholder 1990) on single plots, and the data was used to calculate the number of days from sowing to BBCH60 (first flower open), BBCH70 (end flowering/first pods final length) and BBCH89 (fully ripe). Plant height was recorded in cm from soil surface to top of canopy, using the average of two measurements per plot. Plant height was recorded weekly from the BBCH60 stage to harvest. Maximum height (PLH_max) and height at harvest (PLH_harv) were used in statistical analyses. The field trials were harvested using a plot combine harvester. A seed lot per plot was collected and dried to moisture content below 15% and grain yield was calculated in kg/ha at 15% moisture (YLD). Seed samples taken from single plots was cleaned and the weight of thousand seeds (TSW) was recorded in g. Protein content (PRT) was analysed by Near infrared transmission (NIT) with InfratecTM NOVA instrument (Foss, DK) for the field trials at Apelsvoll and Bjørke. For the field trials conducted at Vollebekk, the seed samples were milled (using Stein Laboratory mill, Fred Stein Laboratories, Inc. Atchison, Kansas) and N content was analysed by the combustion method (Dumas, ISO 16634 (2008)) performed by LABTEK, NMBU, Norway. Protein content was calculated using the conversion factor 6.25 and given as percent of dry weight. Protein yield (PRT_YLD) was calculated from the grain yield and protein content and is given in kg/ha. For all traits phenotyping was done plot-wise for all three replicates per experiment. In some cases, only two full replicates were used. An overview of the phenotyping methods used for each trait and the number of considered replicates per experiment is given in the supplementary material (S4).

Statistical analysis of phenotypic data

A mixed linear model (MLM) with the fixed effects of year, location and their interaction and the random effects of genotype and the various interactions (genotype X year, genotype X location, genotype X year X location and replicate nested within location and year) was fitted for each phenotypic trait by the restricted maximum likelihood (REML) with the breedR package (Muñoz and Sanchez 2020) using the following formula:

$$Y_{sijk} = \mu + \beta_s + u_i + \gamma_{si} + v_j + \alpha_{sj} + w_{ij} + \delta_{isj} + z_{sik} + \epsilon_{sijk} \quad (1)$$

where: Y_{sijk} is the raw phenotype, μ is the overall mean; β_s is the fixed effect of the s-th year; u_i represents the fixed effect of the i-th location; γ_{si} is the fixed effect of the interaction between the s-th year and the i-th location; $v_j \sim N(0, \sigma_v^2)$ represents the random effect of the j-th genotype; $\alpha_{sj} \sim N(0, \sigma_\alpha^2)$ represents the random effect of the interaction between the the s-th year and the j-th genotype; $w_{ij} \sim N(0, \sigma_w^2)$ represents the random effect of the interaction between the i-th location and the j-th genotype; $\delta_{isj} \sim N(0, \sigma_\delta^2)$ represents the random effect of the interaction between the s-th year, the i-th location and the j-th genotype, $z_{sik} \sim N(0, \sigma_z^2)$ represents the random effect of k-th replicate nested within the s-th year and the i-th location and $\epsilon_{sijk} \sim N(0, \sigma_\epsilon^2)$ is the residual error term.

Variance component (VC) analyses of each phenotypic trait were conducted with the restricted maximum likelihood (REML) procedure using the model described in Eq. 1. The standard error of each variance component was calculated with the confint() function of the R package stats. Also, the significance of each variance component was assessed as the p-value of the Likelihood Ratio Test (LRT) by dropping the associated single term in the model. As an example, to assess the significance of the genotypic variance component, the genotype term was dropped from the original model and the ANOVA test was performed with the anova() function of the R package stats between the reduced and original models. The absolute values for each VC were then used to calculate the percentage of the total phenotypic variance explained by each VC for each phenotypic trait, as well as the broad sense heritability (h^2) using the following equation:

$$h^2 = \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_{GxL}^2}{nL} + \frac{\sigma_{GxY}^2}{nY} + \frac{\sigma_{GxYxL}^2}{nYxnL} + \frac{\sigma_{Rep}^2}{nR} + \sigma_\epsilon^2/nLxnR} \quad (2)$$

whereσ_G^2, σ_{GxL}^2, σ_{GxY}^2, σ_{GxYxL}^2 σ_{Rep}^2 and σ_ϵ^2 are the genotype, genotype by location, genotype by year, genotype by year by location, replicate and residual error variance components and *nL, nY* and *nR* are the

number of locations, years and replicates per location, respectively.

The environmental individual effects (at plot level) due to year, location and the various interactions were subtracted from the observed phenotype to obtain adjusted phenotypes which were then used (as genotypic means) to conduct the multivariate analyses described below.

The choice of assigning year and location as fixed effect in model 1 was justified by the facts that: (1) the three test locations represent three climatically distinguished micro environments within the major pea cultivation area in Norway; (2) the two test years 2022 and 2023 were characterized by two distinguished climatic trends that were representative of the climate which characterizes the current (2022) and predicted (2023) growing seasons in Norway, the latter characterized by a dry spring and early summer and exceptionally wet and cool late summer.

All the data was checked for normality of the residuals' distribution and the homogeneity of the variance through the Shapiro Wilk and Levene's tests using the shapiro.test() and leveneTest() functions of the R packages stats and car (R Core Team 2025), respectively.

Analysis of genotype by environment interaction (GEIs) and genotype stability

To further analyze the GEI effects an AMMI analysis was conducted to partition GEIs into different principal components. For these analyses the combination of location and year were considered as single environments (environment specifications is provided in the supplementary material, S4). The analyses were performed in R software 4.0.3 (R Core Team 2025) using the package "metan" (Olivoto and Lúcio 2020). The AMMI ANOVA was performed using a linear model with genotype, environment and their interaction as fixed effects. To identify the most stable genotypes the WAAS, Weighted Average of Absolute Scores, (Olivoto et al. 2019) were calculated considering all AMMI principal component axes that were significant ($p < 0.05$). Likewise, WAASY, the weighted average of absolute scores and response variable were calculated to identify the most stable and high performing genotypes considering equal weights for response and WAAS values. The analyses described above were performed for the three traits of major agronomic interest: yield (YLD), protein content (PRT) and protein yield (PRT_YLD).

Relationships among phenotypic traits

The relationship between the phenotypic traits was investigated as phenotypic and genetic correlations. Phenotypic correlations were calculated with the Pearson method for all traits across locations and years. The genetic correlation was assessed using a multi-trait model as explained in (Gutierrez et al. 2024). Briefly, for each random effect a full covariance matrix is estimated. The cov2cor() function in the R package stats was used to compute the genetic correlation between traits from the additive genetic variance–covariance matrix. The genetic correlation among traits was extracted and compared with the phenotypic correlation. Descriptive analysis and correlations of the phenotypic data were conducted with the R 4.3.3 software (R Core Team 2025).

Multivariate analyses of adjusted phenotypes

The matrix of genotypic means for the adjusted phenotypes was scaled and centered before performing multivariate analyses. Centering ensures that each variable has a mean of zero, and scaling standardizes the variance of each variable to 1. Principal component analysis (PCA) and hierarchical clustering analysis (HCA) were performed with PCA() and hclust() function of the factormineR (Husson et al. 2008) and the stats package function in R, respectively.

For HCA the distance matrix was calculated using Euclidean distance with the dist() function of the stats package, and the clustering algorithm used was ward.D2. Dendrograms were created with the fviz_dend() function from the factoextra package (Kassambara and Mundt 2020) in R. The NbClust() function from the NbClust package (Charrad et al. 2014) was used to identify the best number of clusters, employing various statistical indexes for this purpose. The results were complemented by the visual assessment of the dendrograms to choose the optimal number of clusters.

Genotyping and SNP filtering

A total of 43 genotypes, (phenotyped in the field during the 2022 test year, S1) were genotyped with the

GenoPea 13.2 K SNP Array chip (Tayeh et al. 2015) by the company SGS Trait Genetics, Gatersleben, Germany. DNA was extracted from pooled leaves of 10 young seedlings for each accession. A total of 11,634 SNPs with known map position were identified for this plant material, SNPs with unknown genome position were initially discarded. Then, SNPs with more than 20% missing values or overall minor allele frequency (MAF) < 0.01 were removed. This resulted in a set of 8859 SNPs of which 8558 (96.6%) were located on chromosomes and 301 on unanchored scaffolds. The number of missing values per marker and per individual, as well as the allele frequency distribution, after filtering, is shown in supplementary material (S5 and S6). Missing data after filtering (0.65% of all sample and SNP genotype calls) were imputed by replacing each missing data point with the mean allele frequency across all accessions per SNP. The distribution of the filtered SNPs along the genome is displayed in the supplementary material (S7).

Linkage disequilibrium

The linkage disequilibrium (LD) for each single chromosome was calculated using only the SNP markers with known chromosomal position. LD was estimated as the squared allele frequency correlations (r^2) for each pairwise combination of markers distanced within 1 Mbp with the pcor.shrink () function of the package corpcor (Schafer et al. 2021) in R studio. LD was then plotted against the genomic distance between marker pairs and the LD decay was visualized with the LOESS regression model. The LD decay was estimated as the point where the fitted curve reached half of its maximum value (Gutierrez et al. 2024).

Analysis of population genetic structure

The population structure was analyzed with the snmf() and Q() functions of the R package LEA (Frichot and Francois 2015) which output the results in a similar way as the STRUCTURE software although it employs different algorithms and was indicated as being more accurate for self-pollinating species (Crosta et al. 2023). Filtered SNP data, as described in the section above, were used as input in the analyses. The optimal number of genetic clusters was selected after visual assessment of the cross-entropy parameter plot estimated through cross-validation. In addition, a discriminant analysis of principal component (DAPC) was performed with the R package adegenet (Jombart and Ahmed 2011) on the same dataset (matrix of filtered and imputed SNPs) to visualize pattern of structural variation in the genomic data in the bidimensional space. DAPC analysis first identifies the best number of clusters in the data and then maximize the differences between clusters. The find.clusters() function first performs a PCA on the data, then performs a clustering algorithm (k-means) that considers a range of potential K values to group the data. The goodness of fit of each K value is indicated by a BIC score, where the lowest BIC indicates the best fit. The dapc() function performs a discriminant analysis with the chosen K value, finding the axis of variation that best discriminates among the groups. The results are then visualized similarly to a PCA plot, however, DAPC analysis typically results in a stronger grouping than that shown by PCA.

Relationship between phenotypic and genetic diversity

A reduced SNP matrix containing only the data for the 36 genotypes phenotyped in both the 2022 and 2023 field trials (S1) was used for further analyses of genetic structure through both ordination (PCA) and classification (HCA). The method used for HCA was the same as that described for the phenotypic dataset. Finally, the consistency between estimates of dissimilarity provided by the morphophysiological traits measured in the field and molecular markers for the 1296 possible pairs of distances (36 distances based on genotypes by 36 distances based on phenotypes) was assessed by simple correlation analysis as well as through visual comparison of the dendrograms and biplot conducted on (adjusted) phenotypic, and genotypic data respectively.

Results

Trait variation and interrelationship

The results of the analysis of variance across years (Eq. 1) found that year had a significant effect for all the phenotypic traits (Table 1). The first testing year

Table 1 F values for the fixed effects variance components (±SE) for the random effects estimated with the model in *Eq.* 1 and line mean broad-sense heritability (±SE) for the phenotypic traits registered for 36 pea genotypes across 2 years and three locations

	YLD	TSW	PRT	PRT_YLD	PLH_max	PLH_har	BBCH60	BBCH70	BBCH79
Fixed Effect									
L‡	45.31***	6.78***	16.402**	34.62***	ns†	21.58***	23.59***	2.60*	11.80***
Y	182.88***	146.64***	4.155*	143.55***	102.31***	197.12***	638.48***	616.77***	51.85***
L X Y	31.41***	42.27**	4.547*	8.65**	ns	91.40***	7.85**	61.88***	21.94***
Variance Component									
G	620.05 (474.50)	536.89 (136.90)***	0.96 (0.30)***	30.40 (20.61)	38.38 (13.83)***	36.037 (14.66)***	0.73 (0.35)**	3.87 (1.29)***	5.79 (1.45)***
L X G	ns	ns	0.45 (0.16)***	ns	ns	18.26 (11.09)*	ns	3.06 (0.70)***	ns
Y X G	746.40 (536.39)*	27.73 (24.78)	ns	ns	24.47 (8.67)***	ns	ns	0.38 (0.27)*	ns
Y X L X G	3511.48 (509.05)***	126.93 (25.74)***	0.25 (0.11)***	169.01 (26.52)***	13.03 (3.87)***	38.61 (12.19)***	1.52 (0.34)***	0.63 (0.36)**	6.97 (1.34)***
Rep	265.09 (109.07)***	20.12 (8.97)***	0.48 (0.16)***	30.54 (11.03)***	11.74 (4.66)***	9.47 (3.91)***	0.43 (0.17)***	1.27 (0.42)***	4.04(1.31)***
Res	2330.62 (161.37)	226.32 (17.07)	0.50 (0.04)	68.27 (5.44)	26.37 (2.34)	86.77 (6.472)	3.21 (0.25)	3.25 (0.26)	9.05 (0.72)
h^2	0.37(0.21)	0.91 (0.02)	0.71 (0.07)	0.38 (0.21)	0.65 (0.35)	0.58 (0.17)	0.49 (0.13)	0.66 (0.27)	0.62 (0.16)

*, **, *** significance at the 0.1,0.05 and 0.01 levels, respectively

†ns, not significant

‡ L = Location; Y = Year; L X Y = Location X Year interaction; G = Genotype; L X G = Location X Genotype interaction; Y X G = Year X Genotype interaction; Y X L X G = Year X Location X Genotype interaction; Rep = Replicate; Res = Residuals

(2022) had more favorable growth and harvesting conditions which resulted in higher grain yield, protein content and protein yield across all testing locations. The maximal plant height was also higher in 2022 compared to 2023. Plant height at harvest was higher in 2022 at Vollebekk and Apelsvoll than at Bjørke, while in 2023 plants were affected by heavy lodging at Vollebekk and Apelsvoll. Finally in 2023 there was quicker plant development in terms of the measured stages of the BBCH scale than in 2022, likely because of the early drought during the spring of 2023. The variation of all the phenotypic traits for the two years and locations separately and the genotypic means across years and locations is presented in the supplementary material (S8 and S9, respectively). The fixed effects of location and of the interaction of year and location were significant for all traits but maximal plant height (Table 1). In 2022 grain yield and protein yield were considerably lower at Bjørke compared to Apelsvoll and Vollebekk. TSW was significantly lower at Vollebekk in 2022 compared to Apelsvoll and Bjørke, while the opposite was observed in 2023. Similarly to TSW, protein content was lower at Vollebekk in 2022 than at Apelsvoll and Bjørke, while the lowest protein yield was measured at Bjørke in 2022. For all the other traits (excluding maximal plant height) the effect of location, although significant, did not follow a clear trend and the year by location interaction likely played a stronger role as proved by the different patterns observed within single years (S8). The significance of the latter interaction indicates that each location-year combination presents distinguished environmental conditions to which genotypes respond differently. Therefore, it justifies a more in depth analysis of the genotype by environment interaction (GEI) for the traits of major agronomic interest, which is presented in the next section.

The variance component analysis (Table 1) reported a significant effect of the genotype variance components (VC) for all traits but grain yield and protein yield which, nonetheless, had a p-value just above 0.1. The genotype by location VC was significant only for protein content, plant height at harvest and BBCH70, while the genotype by year VC was significant only for grain yield, maximal plant height

and BBCH70. For all traits the genotype by year by location VC was strongly significant, proving the strong effect of the within year genotype by location interaction. The replicate VC was also significant for all traits although its magnitude was low relatively to the other VC (Fig. 1).

The genotypic VC had the strongest contribution to the total phenotypic variance for TSW, protein content, maximal plant height and BBCH70 (Fig. 1) which also had the highest broad sense heritabilities (> 0.60, Table 1). Grain yield and protein yield were affected by a strong within year genotype by location interaction as shown in Fig. 1, proving that different genotypes performed differently at different locations within the 2022 and 2023 growing seasons, which were strongly affected by the different weather conditions described above (S2). Plant height at harvest, BBCH60, BBCH89 and to a minor extent BBCH70 were characterized by a high residual error VC because of the strong within trial (field) variation in lodging which affected mainly the recording of plant height at harvest, and the plant development after flowering.

The strongest association among traits (on genotype means across years and locations) were found between grain yield and protein yield, protein yield and BBCH89, plant height at harvest and maximal plant height, maximal plant height and BBCH70 and all combinations of the BBCH measurements (all > 0.50, Table 2). The importance of these associations was confirmed by the magnitude of the genetic correlations (S10) which also showed a strong association (> 0.50) of maximal plant height with all BBCH measurements.

The genetic association between the traits was further investigated through a PCA performed on the adjusted phenotypes, which retains only the genetic component of the variance (Fig. 2a). The genotypes were clustered in three different groups by the HCA performed on the same matrix of adjusted phenotypes (Fig. 2b). One group (blue in Fig. 2a and b) was quite diverse and comprehended genotypes with high values for maximal plant height and plant height at harvest as well as high grain yield (Kazek, Sisu, Nemo top right of Fig. 2a). Belonging to the same group, the genotype Tytus and Ingrid were characterized by high TSW, while Eagle and Mefisto were more similar to the previous subgroup but also characterized by higher protein yield and later development (right side of Fig. 2a). The second group (green in Fig. 2a and b) comprehended genotypes which were characterized by average performance in terms of grain and protein yields (placed near the center of Fig. 2a) although some of them, Colin, Lina, Bagoo and Leva had a later plant development (higher values of BBCH measurements) while Leva, Milwa and

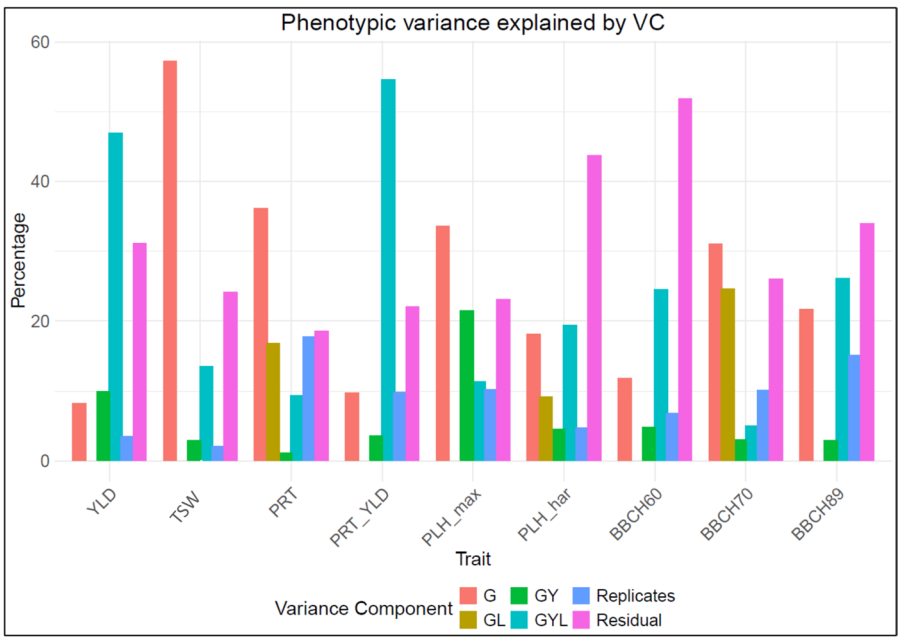


Fig. 1 Percentage of phenotypic variance explained by each variance component. YLD = Grain Yield; TSW = Thousand Seed Weight; PRT = Protein Content; PRT_YLD = Protein Yield; PLH_max = Maximal Plant Height; PLH_har = Plant Height at Harvest; BBCH60 = Full Flowering; BBCH70 = end flowering/first pods final length and BBCH89 = fully ripe

Sokolik also had a higher protein content than all the other genotypes (lower part of Fig. 2a). Finally, the third group (red in Fig. 2a and b) were characterized by lower-than-average performance across years and locations and were positioned in the center and left side of Fig. 2a. It is worth noting that since the multivariate analyses presented in Fig. 2 were performed on adjusted phenotypes, the associations among traits and grouping of genotypes are stable across environments, since they are based only on the genetic part of the phenotypic variance.

Dissection of GEIs for key agronomic traits

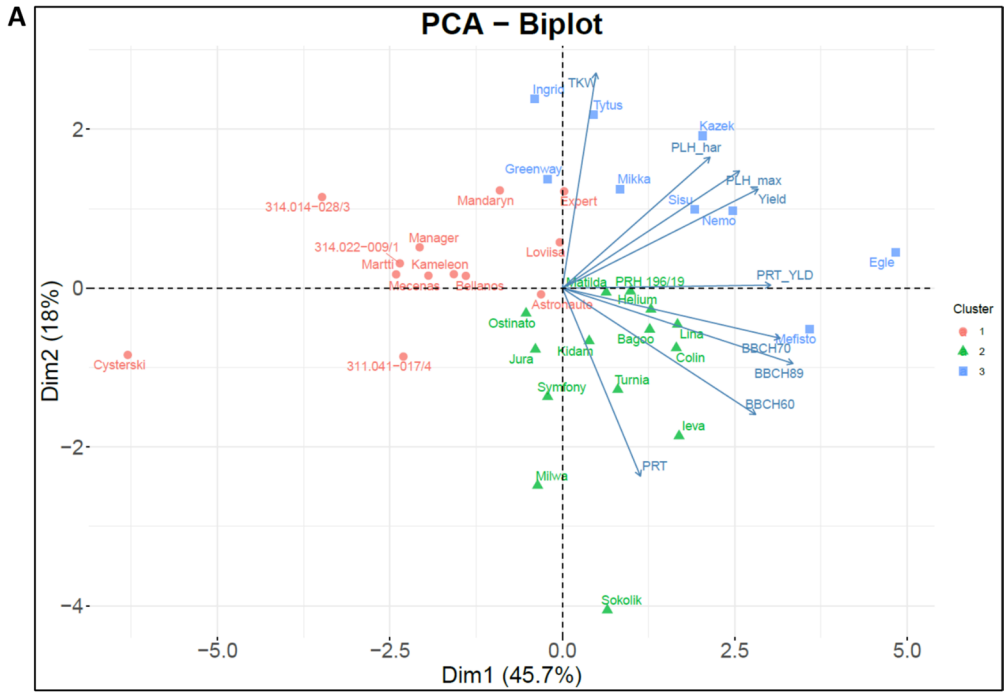
The results of the AMMI analysis for the three traits YLD, PRT and PRT_YLD are presented in Table 3. For all traits the main effects of G, E and GEI were statistically significant. For all traits G accounted for the smallest variation, with E accounting for most of the variation for YLD and PRT_YLD, while GEI explaining most of the variance in PRT. These results are in line with those of the VC analyses based on Eq. 1. The GEI effect was further partitioned into 5 interaction principal components (IPCs). For YLD the first four IPCs were found to be significant ($p < 0.001$) and explained 96.7% of the GEIs variation, while the first three and four IPCs were found to be significant ($p < 0.001$) for PRT and PRT_YLD, explaining 95.2% and 99% of the GEIs variation, respectively (Table 3). For all three traits the first 2 IPCA accounted for the majority of GEI variation (> 82%). The distribution of pea genotypes and test environments based on biplots of AMMI1 (mean response × IPC1 scores) and AMMI2 (IPC1 × IPC2 scores) for the three traits are found in the supplementary material (S11).

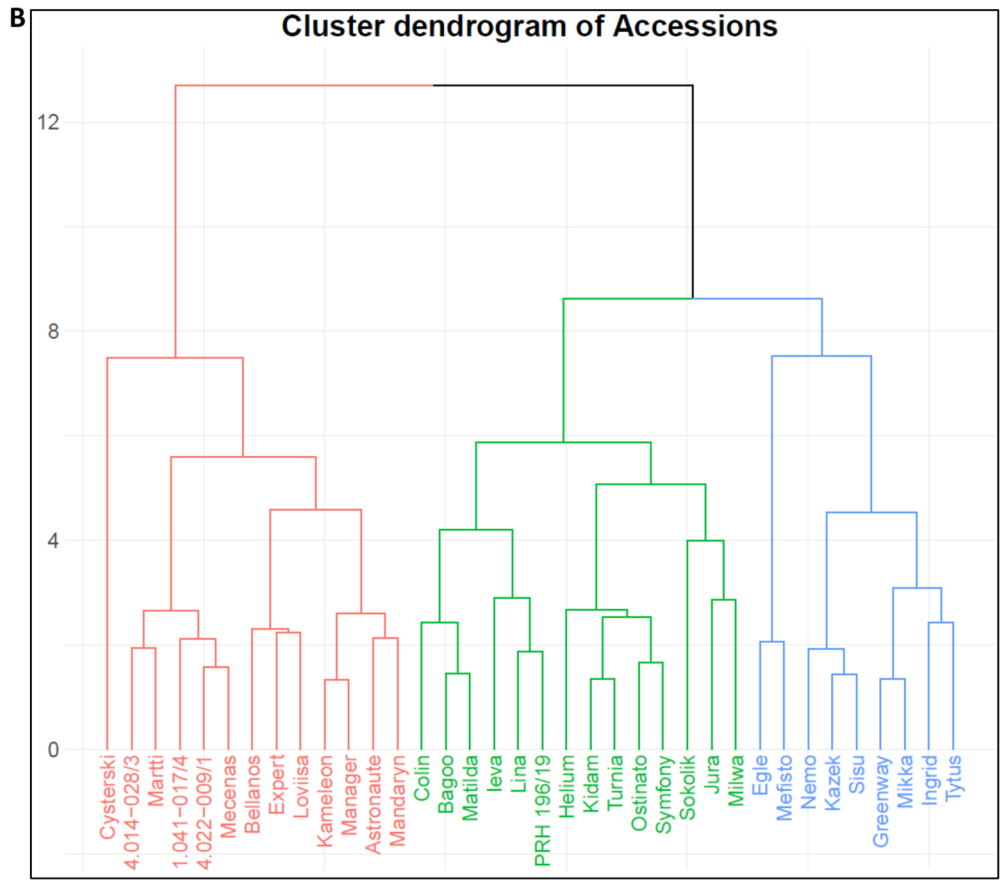
WAAS scores were computed to better characterize ideal genotypes based on stability. With this method, the stability and performance of the genotypes can be presented graphically using biplots of the WAAS scores vs response variables. Figure 3 presents the Y (response) × WAAS biplot with quadrants denoting the four classes of genotypes that simultaneously interpret performance and stability. The perpendicular line to the horizontal axis indicates the overall mean for the trait and discriminates the genotypes' performance above and below the grand mean. The first quadrant represents the most unstable genotypes that have the largest role in GEI. In quadrant II unstable genotypes are included, although with productivity above the grand mean. Genotypes within quadrant III have low productivity but can be considered stable due to the lower WAAS values. The lower this value, the more stable the genotype can be considered. Finally genotypes within the quadrant IV are highly productive and broadly adapted due to the high magnitude of the response variable and high stability performance (higher Y and lower WAAS values). Among the large groups of genotypes included in the IV quadrant, genotypes 7,17 and 12 (Colin, Kazek and Kolin) had the highest YLD while 10, 36 and 30 (Expert, Tytus and Ostinato) had the most stable YLD while still having above average performance. For PRT, genotypes 9, 12, 26 and 33 (Egle, Helium, Mefisto and Sokolik) had high protein content, although the latter was just above the threshold for being considered a stable genotype. Genotype 15 (Jura) was distinguished from the rest for its high stability and relatively high PRT. For PRT_YLD, genotypes 34, 35 and 18 (Synfony, Turnia and Kidam) were those with the best performance and relatively high stability. It is worth nothing that genotypes 10, 18, 34 and 35 (Expert, Kidam, Symfony and Turnia) were all found in quadrant IV for all three traits of major agronomic interest (Fig. 3). Complete ranking of genotypes depending on their WAAS and performance for the three traits is presented in the supplementary material (S12 and S13). It is worth nothing that the reference Norwegian variety Ingrid (14) was largely outperformed for all the considered traits both in terms of performance and stability (Fig. 3, S12 and S13).

LD and Population structure

The LD decay was very rapid for each chromosome (LD plots are shown in the supplementary material S14) perhaps not surprisingly, since genotyping tools such as SNP arrays markers are already selected for being in low LD to avoid redundancy. However, the SNP distribution was even across the chromosomes, providing good coverage of all the genome (S7).

The optimal number of genetic clusters as suggested by the K-means statistic was equal to three (S15). The structurization of the genotypes (complete dataset of 43 genotypes) in three groups partly reflected the geographic origin of the plant material, as shown in Fig. 4a and b. The genomic data clearly distinguish the material in three genetic backgrounds,


A
PCA – Biplot
Dim2 (18%)
Dim1 (45.7%)
Cluster
1
2
3
Ingrid
TKW
Tytus
Kazek
PLH_har
Greenway
Mikka
PLH_max
Yield
Sisu
Nemo
Egle
PRT_YLD
Mandaryn
Expert
314.014−028/3
314.022−009/1
Manager
Martti
Kameleon
Mecenas
Bellanos
Loviisa
Matilda
PRH 196/19
Helium
Astronaute
Ostinato
Lina
Mefisto
Bagoo
BBCH70
Colin
BBCH89
Cysterski
311.041−017/4
Jura
Kidam
Symfony
Turnia
BBCH60
Ieva
PRT
Milwa
Sokolik


B
Cluster dendrogram of Accessions
Cysterski
4.014−028/3
Martti
1.041−017/4
4.022−009/1
Mecenas
Bellanos
Expert
Loviisa
Kameleon
Manager
Astronaute
Mandaryn
Colin
Bagoo
Matilda
Ieva
Lina
PRH 196/19
Helium
Kidam
Turnia
Ostinato
Symfony
Sokolik
Jura
Milwa
Egle
Mefisto
Nemo
Kazek
Sisu
Greenway
Mikka
Ingrid
Tytus

◂**Fig. 2** Results of multivariate analyses of the phenotypic traits measured on 36 genotypes across 2 years and 3 locations. **a** Principal Component Analysis and **b** Hierarchical clustering analysis performed on the matrix on adjusted phenotypes. In both panels the genotypes were colored following the cluster assignment indicated by the HCA performed on adjusted phenotypes

with two major groups comprehending: (1) genotypes with western European origin (up right corner in Fig. 4a and green bars in 4b) and (2) a mixture of genotypes with northern and eastern European origin (low right corner in Fig. 4a and yellow bars in Fig. 3b). The third group was less numerous and was composed exclusively of genotypes bred in Poland, which were clearly distinct from the rest (up left corner in Fig. 4a and purple bars in Fig. 4b).

When considering only the 36 genotypes present in both the 2022 and 2023 field trials at all locations, the HCA analysis of the genomic data highlights once again three major groups as indicated in Fig. 5 and S16. The groups highlighted in Fig. 5 were close to those identified by the DAPC on the whole dataset, with the accessions most closely related in terms of geographic origin having also the shorter genetic distance.

To test the consistency between the classification of the 36 accessions based on the (adjusted) phenotypic and genomic data a simple correlation was performed between the genotypes distance matrixes based on the phenotypic and genomic data, respectively. The moderately high correlation coefficient of $r = 0.47$ ($P < 0.01$), shows that there is consistency in the differentiation of the considered genotypes in terms of their phenotypic and genomic based genetic diversity (Fig. 6).

Discussion

This study identified considerable phenotypic variation for all the evaluated traits, with both location and year playing an important role in determining genotype performance. This confirms the importance of multi-location field trials of diverse material in the preliminary steps of a breeding program, to identify the correct breeding strategy and preselect high performing and stable genotypes (Annicchiarico et al. 2009; Gauch Jr., 2013). In this case, the two testing years were strongly different in terms of the weather conditions under the growing season and thus resulted in clear differences in genotype performance. Year had the strongest contribution to the phenotypic variation for all traits, in particular grain and protein yields were considerably lower at all locations in 2023. Location had a significant effect on all traits, excluding plant height, which was stable across testing locations but was reduced by the suboptimal growing conditions in 2023 as for grain and protein yields.

The weather conditions in 2023 included both an early drought (mid-May to mid-June) and thereafter frequent rain that lasted for the rest of the growth period with several events of unusual intense rainfalls in the period prior to harvest (August). Trials were irrigated during the early drought period to ensure satisfactory canopies, but a faster phenological development was nonetheless recorded. It is likely that the frequent precipitation lasting for the whole period from pod and seed development until maturation was the main reason for the lower grain yield in 2023. This could be due to both the cloudy weather reducing irradiance, and to the severe lodging that could reduce both assimilation and translocation into seeds and increase losses at harvest. Even though the

Table 2 Phenotypic correlations calculated as Pearson correlations on traits genotypic mean across the whole dataset

	TSW	PRT	PRT_YLD	PLH_max	PLH_har	BBCH60	BBCH70	BBCH89
YLD	0.23	− 0.07	0.86***	0.47***	0.34**	0.35**	0.48***	0.49***
TSW		− 0.19	0.12	0.13	0.27	− 0.15	− 0.04	− 0.07
PRT			0.39**	− 0.16	0.11	0.28*	0.11	0.26
PRT_YLD				0.37**	0.32*	0.49***	0.46***	0.55***
PLH_max					0.56***	0.29*	0.52***	0.49***
PLH_har						0.06	0.31*	0.42**
BBCH60							0.68***	0.73***
BBCH70								0.90***

*, **, *** significance at the 0.1,0.05 and 0.01 levels, respectively

Table 3 Analysis of variance for combined and additive main effects and multiplicative interaction (AMMI) analysis for grain yield (YLD), protein content (PRT) and protein yield (PRT_YLD) of 36 pea genotypes evaluated at 6 environments during 2022–2023 cropping seasons

	YLD			PRT			PRT_YLD		
Source	F value	Var. exp. (%)	GEI exp. (%)	F value	Var. exp. (%)	GEI exp. (%)	F value	Var. exp. (%)	GEI exp. (%)
E	144.15***	55.23		11.38***	33.78		80.27***	62.16	
Replication/E	5.21***	0.92		35.40***	6.68		17.14***	1.74	
G	12.31***	6.34		35.73***	26.22		14.52***	5.74	
GEI	6.01***	15.49		4.25***	12.48		8.29***	13.11	
PC1	16.29***	9.35	59.10	9.1***	7.44	52.2	19.84***	8.74	63.8
PC2	7.19***	3.92	24.80	5.55***	4.31	30.2	7.84***	3.28	23.9
PC3	2.3***	1.18	7.50	2.48***	1.82	12.8	2.47***	0.98	7.1
PC4	1.73***	0.84	5.30	0.98	0.68	4.8	1.87***	0.70	5.1
PC5	1.15	0.52	3.30	0	0.00	0	0	0.00	0
Residuals		6.21			6.58			3.55	

weather conditions in 2023 were considered strongly unusual, the increased precipitation in the later part of the growth season with events of very intense rainfalls is in line with climate change predictions for these areas (Sjulgård et al. 2023). The weather conditions observed in 2023 will be more common in Norway; this on one hand highlighted the challenges of grain legumes cultivation in the future, but on the other it resulted in an opportunity for this research project to investigate how different genotypes performed in significantly different testing years. All traits but protein content and BBCH70 had a low, if not absent G × L interaction effect. In particular, for grain and protein yields, the traits with highest interest for plant breeders, the biggest source of variation was the within year G × L interaction. This suggests that the performance of different genotypes at different locations was more strongly affected by the weather conditions that differentiated the two growing seasons than by the different locations. For example, genotypes with earlier development and maturation were more negatively affected by the late harvest induced by the long period with rains and cold temperatures characterizing the second part of the summer in 2023. Some of these genotypes showed also strong lodging, that in combination with the late harvest resulted in heavy yield losses. The significance of the location by year interaction indicated the importance of conducting an analysis of the GEI were every combination of year and location is considered as a distinguished environment. Therefore, an AMMI analysis was performed for the traits yield, protein content and protein yield. The results indicated large E and GEI effects for all of the three traits. Significant GEI effect for grain yield was reported by several studies in field pea across different regions (Daba et al. 2023; Haile and Tesfaye 2024; Maleki et al. 2024; Sharma et al. 2025). The E effect is often reported as the major contributor to grain yield variation in multi-location field trials, and our study is not exception, mainly explained by the largely different climatic conditions experienced in the two growing seasons. However, the significant and relatively high contribution of GEI to the overall variance underlines the importance of dissecting its components to (1) identify the correct breeding strategy for a specific agricultural area and (2) highlight genotypes that can be successfully cultivated in a defined area or as useful addition to breeding programs. Relatively to the two points above, this study

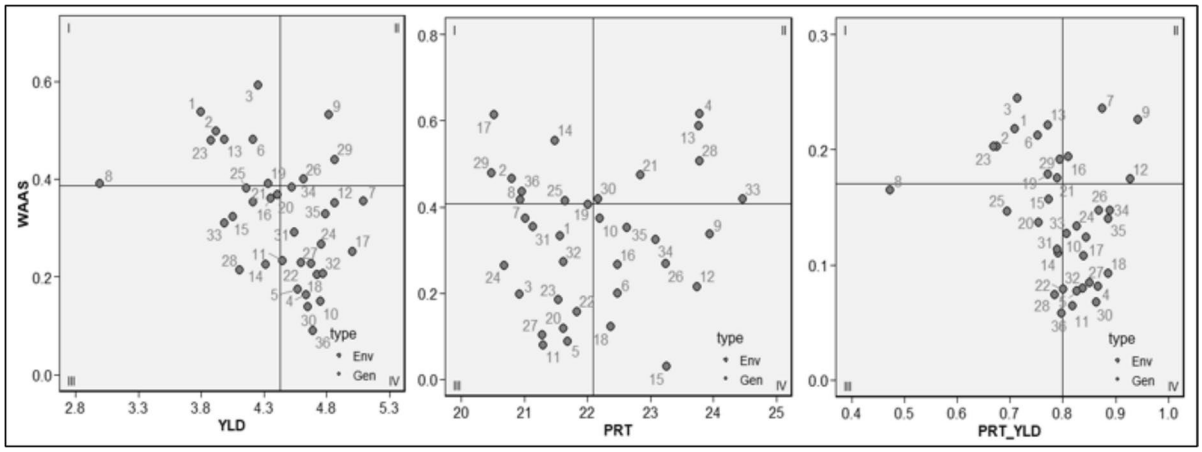


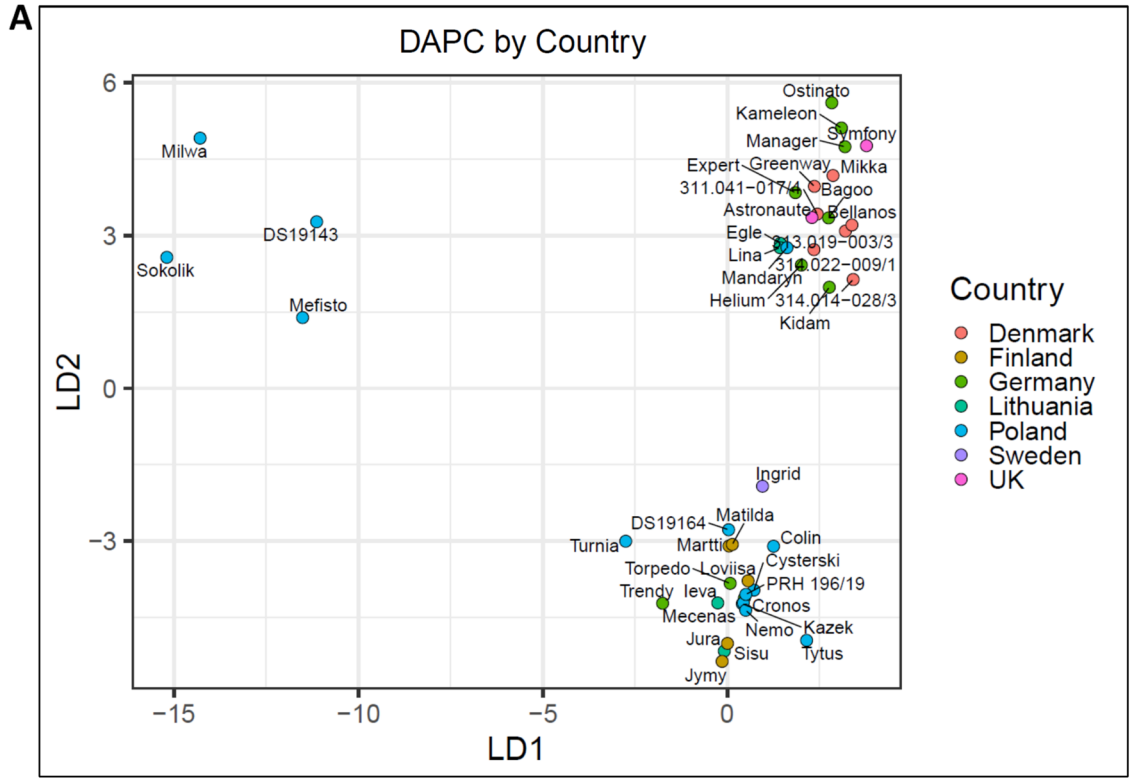
Fig. 3 Biplot of mean response variable (YLD, PRT and PRT_YLD) and weighted average of absolute scores for the genotypes (WAAS). See S9 for genotypes codes

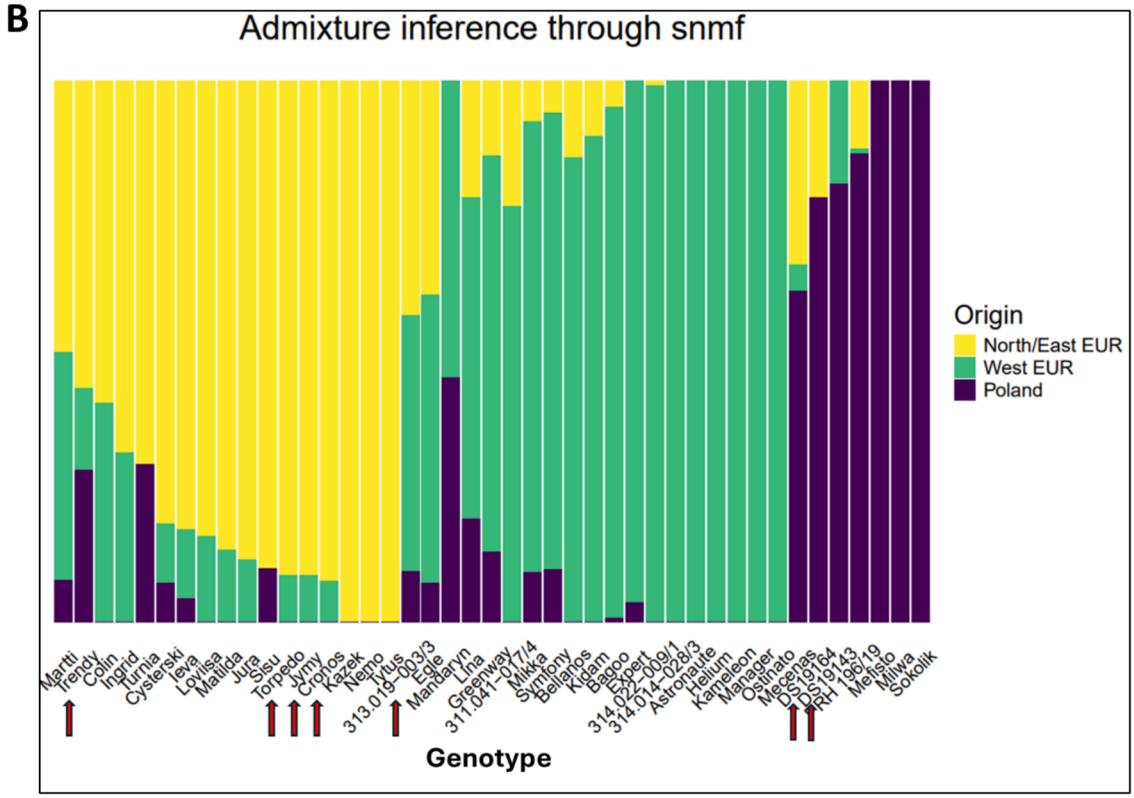
provided an important contribution, since it identified genotypes (1) that are more stable and high performing than the reference Norwegian variety Ingrid and (2) with high performance for specific trait of interest such as protein content which can be introduced in breeding programs aiming at the improvement of such trait.

The strong difference in genotype ranking for grain yield between 2022 and 2023 (results not shown) suggests that breeding efforts for Norway should target the development of pea varieties with broad adaptation for the whole region rather than different varieties having specific adaptation to different subregions. This approach is justified by the fact that: (1) the major pea/grain growing region in Norway is restricted to a relatively delimited area with similar climatic conditions; (2) the strongest source of genotype by environment interaction is temporal (different years with different weather conditions) rather than geographical (different locations with different weather conditions); (3) pea is still considered a minor crop in Norway which does not allow for major investments in terms of breeding. Therefore, the identification of genotypes with stable, even if average, yield performance will likely result in higher grain and protein yields over time, and an increased adoption of this crop which is still considered by farmers (together with faba bean) less reliable than cereals because of heavy yield losses in unfavorable years (de Visser et al. 2014).

The relatively high TSW, protein content and maximal plant height h^2 values confirms previous findings in Pisum sativum by (Singh and Singh 2011; Tolessa 2017; Ali et al. 2021; Uhlarik et al 2022) which also found high h^2 for the same traits. This work found that phenological development and maturation time, measured as days to end of flowering (BBCH_70) and days to full ripe (BBCH_89) had also quite high $h^2$and genotypic VC, with the traits being stable across environments both in terms of different years and locations. The stability of these traits is particularly relevant for the selection of the right material for cultivation in Norway, which favors early maturing genotypes because of the challenges of wet and cool autumns which often hinder harvesting of late maturing material (Carlson-Nilsson et al. 2021).

Trait association was investigated through correlation and PCA on adjusted phenotypes, to identify associations that are based on the genetic component of the phenotypic variance and thus, that are stable across different environments. Grain yield had the highest correlation with protein yield, but none of these traits were significantly correlated with grain protein content. This was also found in other studies (Carlson-Nilsson et al. 2021; Ferrari et al. 2016; Mohammed et al. 2018). One of the main goals of Norwegian agriculture is that of increasing grain legume production to replace imported protein feed ingredients. Thus, the increase of protein yield (as protein production per unit area) over time is a more relevant goal than the increase of grain


A
DAPC by Country
LD1
LD2
Milwa
DS19143
Sokolik
Mefisto
Ostinato
Kameleon
Symfony
Manager
Expert
Greenway
Mikka
311.041−017/4
Bagoo
Astronaute
Bellanos
Egle
313.019−003/3
Lina
314.022−009/1
Mandaryn
Helium
314.014−028/3
Kidam
Ingrid
DS19164
Matilda
Turnia
Martti
Colin
Torpedo
Loviisa
Cysterski
Trendy
Ieva
PRH 196/19
Cronos
Mecenas
Nemo
Kazek
Jura
Sisu
Tytus
Jymy
Country
Denmark
Finland
Germany
Lithuania
Poland
Sweden
UK


B
Admixture inference through snmf
Genotype
Origin
North/East EUR
West EUR
Poland

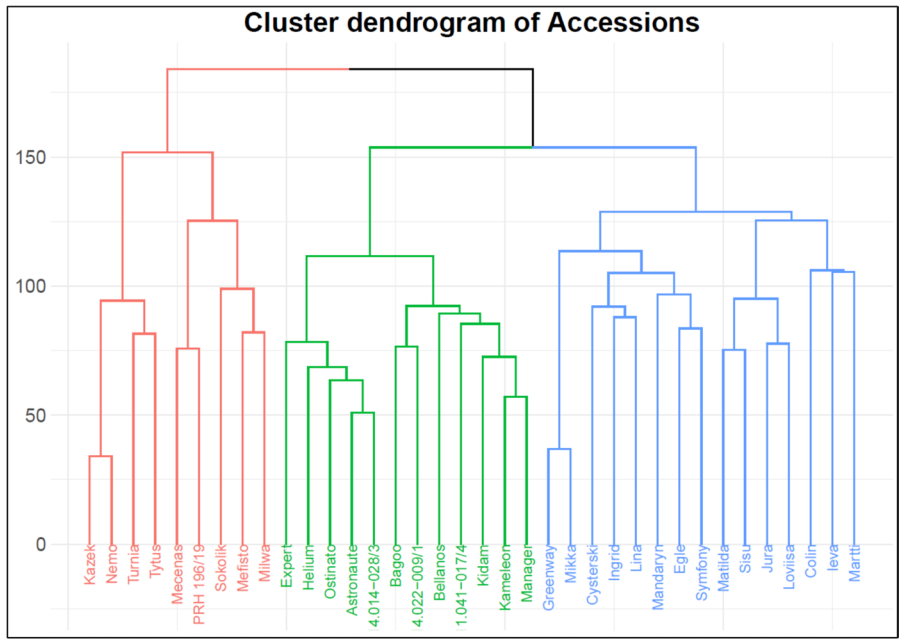
◂**Fig. 4** Results of population genetic structure performed on the genotypic matrix of filtered and imputed SNPs for all the 43 genotypes for which genotypic data were available. **a** Discriminant analysis of principal components (DAPC) and **b** sNMF analysis for admixture inference. The genotypes in both figures were color coded depending on their country of origin (breeder provenance) in figure **a** and for macro-area of origin in figure **b**. The genotypes highlighted by the red arrows in figure **b** are those absent from the phenotypic dataset

protein content by itself. Therefore, the high correlation between grain yield and protein yield is positive news in the current context, where the farmers are simply paid for the tonnage of grain produced with no premium paid for improved quality for example in terms of protein content. Yield (both grain and protein yield) was positively correlated with BBCH measurements as well as maximal plant height and to a lesser extent plant height at harvest, suggesting that taller genotypes with longer vegetative cycle results in higher yields. These findings are in line with previous literature (Ali et al. 2021; Carlson-Nilsson et al. 2021; Uhlarik et al. 2022) and indicate that despite the cool and wet harvesting season that often characterize cultivation areas in Norway (as we experienced in 2023), genotypes with longer growing cycles outperformed early genotypes in terms of grain yield. However, it is worth nothing that the early maturing genotypes might have been penalized in terms of grain and protein yields because they were harvested too late, resulting in pod shattering. For logistical reasons all plots at all field trials considered in this work were harvested at once.

The results of HCA on the matrix of adjusted phenotypes indicated the classification of the tested genotypes in three different groups, characterized by distinct adaptation pattern. Of these three groups, one included genotypes with lower-than-average performance in terms of grain yield (red in Fig. 2a and b), and thus might not be suggested for cultivation in Norway. However, such low yielding genotypes might still be useful if they are carrying traits that are considered useful by plant breeders. In this study this might be the case for some very early genotypes which could be used as a source of earliness in a breeding effort aiming at creating early types which could extend the cultivation areas or be cultivated as a pre-crop to winter cereals. Most of the high yielding and stable genotypes belonged to one of the remaining two groups, blue or green in Fig. 2a and b). Within this group genotypes Colin, Kazek, Kidam, Expert, Eagle and Ostinato were highlighted by the AMMI analysis as the highest ranked in terms of stability and performance. Plant height seems to be important for achieving a high grain yield, however, considering the susceptibility of pea to lodging especially in wet conditions, plant height at harvest is probably a better predictor of a genotype that is less prone to lodging. Finally, among the third group (green in Fig. 2a and b), some genotypes might be considered as a source of genetic diversity for higher protein content. In particular genotypes Symphony, Sokolik, Mefisto and Kidam were also top ranked by the AMMI analysis conducted on protein content. Considering that the trait was not significantly correlated with grain yield and that a considerable genetic diversity was identified (high G VC and h^2), an increase of protein content of the high yielding genotypes might be achieved through crossing with those having higher protein content without compromising their productivity. Most of the genotypes with high protein content had eastern European origin, something which was observed in a previous study considering a wider panel of genotypes (Jha et al. 2013). The results of the structure analyses performed on genomic data confirmed that this material has indeed a different genetic background and therefore, might carry genes associated with higher protein content that can improve this trait in higher yielding genotypes of western European origin such as those in blue in Fig. 2a and b.

To complement the evaluation of genetic diversity in terms of phenotypic traits measured in the field, this study used molecular markers to measure the diversity at the genomic level. The most popular method for finding associations between a phenotypic trait with molecular markers is perhaps genome wide association study (GWAS). GWAS requires a sufficient number of evaluated genotypes to identify reliable trait-marker associations, especially for quantitative traits which are strongly affected by E and GEI variations. The number of evaluated genotypes in this work was not sufficient to perform a GWAS. However, the analysis of population structure clearly identified diverse genotypes in terms of their genomic makeup that can be used as source of useful diversity for several traits.

The different analyses performed to evaluate population structure identified three main clusters which



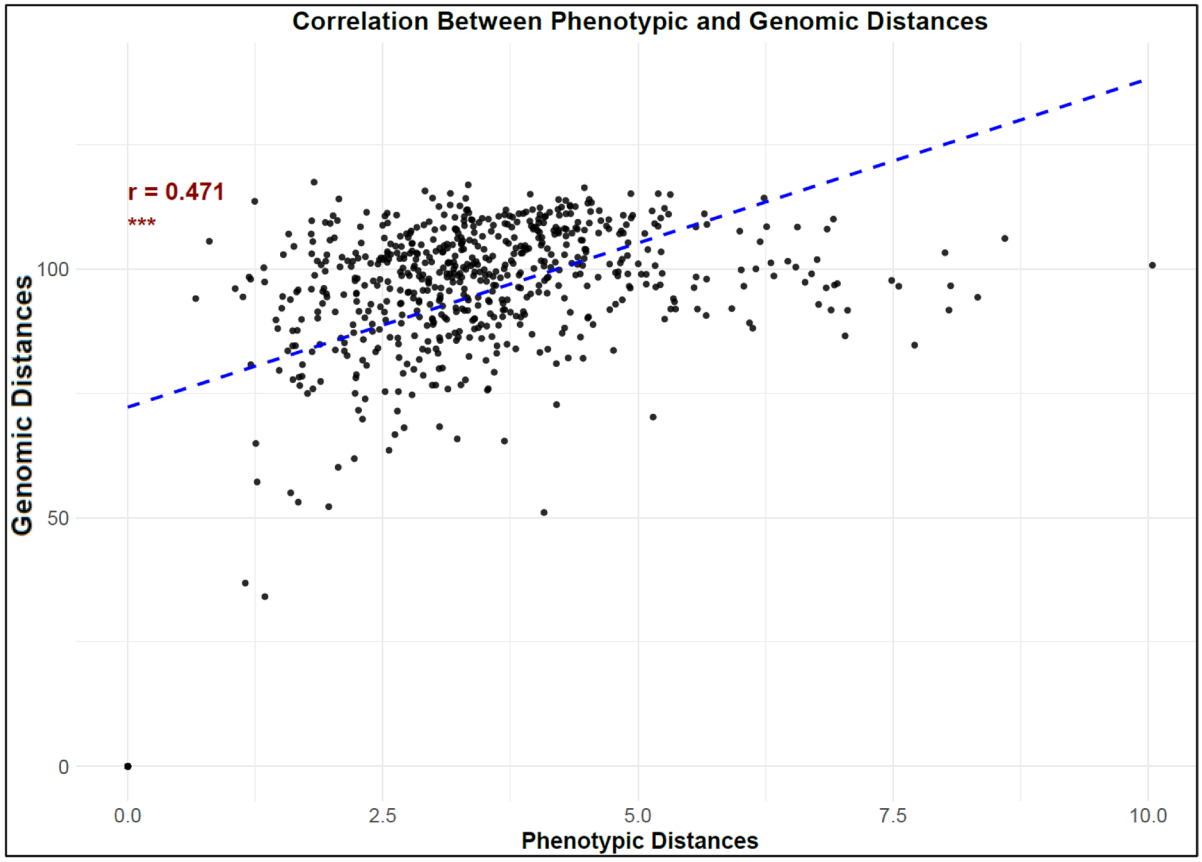


Fig. 5 Hierarchical clustering analysis (HCA) performed on the matrix of filtered and imputed SNPs for the 36 accessions included in the field trials in 2022 and 2023 at all locations

Fig. 6 Results of correlation analysis between measures distance matrixes based on the (adjusted) phenotypic and genomic data, respectively, for the 36 genotypes present in the 2022 and 2023 field trials at all locations

partially coincided with the different geographic origin of the genotypes. Genotypes with different provenances are often characterized by distinct phenotypes and geographic origin is often associated with structurization at the genomic level (Annicchiarico et al. 2017a, b; Crosta et al. 2022; Pavan et al. 2022). The climatic conditions at the place of origin of a genotype often induce new mutations that will be gradually fixated within the population if it is useful for adaptation to that specific environment (Zanotto et al. 2021). In the process of plant breeding, new genotypes that are source of useful traits are useful only if they indeed carry new genes that are associated with the trait of interest. Therefore, the selection of parents for new crosses with the aim of trait improvement should be done from genotypes belonging to different genetic pools. The results of this study were promising to this extent, since: (1) high yielding and stable genotypes were identified among different clusters and (2) genotypes with high protein content belonged to a different cluster than those with high and stable grain yield. From a breeding perspective this suggests that there is the potential for improving grain yield by crossing different high yielding genotypes belonging to different genomic clusters. Also, the protein content of high yielding genotypes can be improved through crossing with genotypes with high protein content belonging to a different genomic cluster. These results are of high relevance for the long-term strategy of improving plant protein production by unit area, or protein yield.

Furthermore, the relatively high and strongly significant correlation between the measure of genetic distance between genotypes at the phenotypic and genomic levels, indicates that the observed phenotypic diversity is indeed associated with different alleles carried by different genotypes. In future breeding efforts a wider panel of plant material should be evaluated in field trials and genotyped with the same or similar tools. SNP chip technology proved reliable in describing genetic diversity (Tran et al. 2023, 2022), is repeatable over time and allows to join different datasets since the tested markers are always the same (and often associated with relevant phenotypic traits). This is particularly useful for the development of genomic selection models, which requires the availability of a lot of phenotypic and genotypic data from many different genotypes across different environments (Annicchiarico et al. 2019; Annicchiarico et al. 2017a, b; Crosta et al. 2023), something which is often not realistic within a single research project.

In this perspective, this study was successful in exploring available genomic tools for describing genetic diversity in a considerably small collection of pea genotypes, and to relate it to the observed phenotypic diversity for several important agronomic traits. A future step should be the evaluation of a larger number of genotypes and building a dataset of genotypic and phenotypic observations robust enough for developing a genomic prediction model. This process works iteratively, progressively including new genotypes with the goal of improving the traits, and it was demonstrated as being more time and resource effective than traditional breeding schemes (Crosta et al. 2022). At the same time the evaluation of new genotypes done in such research projects (particularly varieties and advanced breeding lines) has an important value for cultivar recommendations for farmers as well as data sharing to the providers (collaborating breeding institutions) of such genotypes. Therefore, we foresee a continuation of the current project as pre-breeding activity for the Norwegian environment which might result in the longer terms into a Norwegian based breeding program for pea.

Acknowledgements We thank the staff at SKP Friland at Vollebekk and the staff at Bjørke and Apelsvoll for the excellent agronomic management of the field trials. We also acknowledge Guro Augusta Rogstad Sørheim, Chloé Grieu, and Vilde Gadderud for help with data collection at Vollebekk, Apelsvoll, and Bjørke, respectively.

Author's contributions Stefano Zanotto: conceived the idea for this study, formal analyses, writing original draft, review, and editing., Jon Arne Dieseth: investigation, review and editing, Muath Alsheikh: investigation, review and editing, Susanne Windju: investigation, review and editing, Wendy Waalen: investigation, review and editing, Chloé Grieu: investigation, review and editing Anne Kjersti Uhlen: project administration and funding, review, and editing.

Funding Open access funding provided by Norwegian University of Life Sciences. The research was supported by the project "Future Protein Crops" funded by the Foundation for Research Levy on Agricultural Products (FFL), the Agricultural Agreement Research Fund (JA) in Norway, and industry partners (NFR Project No. 326701). The research was also supported by the project "GreenPlantFood" funded by the Reseasch Council of Norway and industry partners (NFR Project No. 319049).

Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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