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Characterisation of Grass Pea (*Lathyrus sativus* L.) Genotype Diversity Identified Key Agronomic Traits for Central European Environments

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ABSTRACT

Climate scenarios for Central Europe forecast an increase in average temperature and a higher occurrence of drought and heavy rain events, calling for identifying crops able to tolerate weather extremes. Grass pea (*Lathyrus sativus* L.) is a minor legume crop known for its ability to tolerate temperature extremes, drought and waterlogging as well as for its capability to grow in a wide range of soils. Hence, we investigated the suitability of grass pea in diverse environments across Germany. The objective was to identify agronomical and morphological traits associated with productivity parameters. We characterised 50 grass pea genotypes in six environments, evaluating two parameters related to plant development, six related to agronomy and plant morphology and five related to productivity. Higher grain yield was associated with a higher position of the first pod at plant stem, a total number of at least 20 pods per plant and a minimum of 40 seeds per plant. Genotypes with white flowers or white/blue flower wings had higher yields compared to those with blue flower wings. The study identified relevant breeding traits for selection and release of varieties adapted to Central European conditions.

1 | Introduction

Climate change impacts agricultural systems worldwide. Especially weather extremes, such as drought and heavy rain events, make crop production less stable. The impacts of climate change are particularly relevant for grain legumes grown in Europe, which provide high-quality protein and a range of ecosystem services (Watson et al. 2017). At the same time, grain legumes support the transition towards plant-based diets (Rockström et al. 2025) and can reduce environmental impacts (Notz et al. 2023). However, legume production is generally more variable than that of cereals, making yields less predictable (Reckling et al. 2018).

Field pea (*Pisum sativum* L.), faba bean (*Vicia faba* L.) and soybean (*Glycine max* (L.) Merr.) are the most widely grown grain legumes in Europe (Van Loon et al. 2023). However, the productivity of these crops is highly limited by abiotic factors such as heat stress in pea (Bhandari et al. 2017; Devi et al. 2023) and drought stress in faba bean (Parvin et al. 2019; Mansour et al. 2021) and soybean (Poudel et al. 2023; Du et al. 2024).

Recognised as a resilient crop in the Mediterranean region, grass pea (*Lathyrus sativus* L.) could be a valuable crop to cope with weather extremes and diversify farming systems. Grass pea can endure drought and waterlogging, temperature extremes, and tolerate insect and pest damage (Kumar et al. 2011; Gonçalves

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et al. 2022; Aloui et al. 2023). In addition, the crop copes with moderate salinity and grows on a wide range of soil types (Campbell et al. 1994; Vaz Patto et al. 2006; Lambein et al. 2019). Moreover, under favourable conditions, yields can reach up to 5 t ha⁻¹ (Briggs et al. 1983). However, grass pea production is still hindered by the neurotoxin β -N-oxalyl-L- α , β -diaminopropionic acid (β -ODAP), which can cause paralysis if the crop is consumed as a staple food for prolonged periods (Yan et al. 2006). On the other hand, the presence of L-homoarginine (L-hArg) in grass pea has gained attention for its benefits on cardiovascular health (Boldischar et al. 2025).

Grass pea has received considerable attention in Mediterranean regions, where it holds significant importance in local cropping systems. For instance, screening trials in Spain and Egypt identified genotypes with a large range in yield performance and strong environmental effect on productivity (Rubiales et al. 2020). In Turkey, Oten (2023) identified that days to flowering and the number of pods were important traits when selecting high-yielding genotypes, while Gonçalves et al. (2024) highlighted the number of seeds per plant and the height of the first flower as the most important traits when selecting high-yielding grass pea genotypes.

Together, these studies identified the main traits shaping grass pea yield, emphasising flowering time, pod and seed traits, and strong environmental effects, which reflect the long-term cultivation of grass pea in those regions. However, no comparable evaluations exist for Central Europe. Consequently, it remains unclear whether the same traits drive productivity under cooler climates, leaving an important gap for assessing the crop's potential in Central European cropping systems.

Therefore, the objectives of this study were to analyse grass pea genotypes in diverse locations across Germany, to (i) identify key morphological and agronomical traits that drive productivity, (ii) examine the correlation between observable phenotypic traits and productivity parameters and (iii) assess the influence of genotype origin on agronomical traits and productivity.

2 | Material and Methods

2.1 | Plant Material

Grass pea genotypes were obtained from the gene bank of the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK). Out of 263 genotypes maintained at IPK, based on passport data and seed availability, a total of 96 genotypes were selected for field evaluation during the first year of the study. In addition, four commercial control varieties were added for comparison. Hence, 100 genotypes were used for the first year of evaluation.

After the first year of field evaluation, based on the genotypes' yield performance within locations and the concentration of the neurotoxin β -ODAP, 46 out of the 96 genotypes were selected for a second year of field evaluations. In addition, the four commercial varieties were included as well. Therefore, a total of 50 genotypes were analysed in the second year and were used for this

study. The genotypes include traditional landraces, old varieties and commercial varieties.

For the analysis by origin, the studied genotypes were grouped into three groups, as shown in Table 1. One genotype was excluded from the analysis due to the absence of other genotypes within a similar geographical or climatic context.

A detailed list of the genotypes and commercial varieties used for this study is shown in Table S1.

2.2 | Climate Characterisation

Climatic conditions within the growing season were monitored by a weather station in each location of the study. The monthly average temperature at 2 m, the average monthly soil temperature at -5 cm and the monthly precipitation sum in millimetres were collected during the growing season.

2.3 | Field Trials Description

The field trials were located at three locations across Germany: the first at the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), located in Gatersleben, at 51°49'43.7" N, 11°16'26.9" E, with loess soil; the second at the University of Hohenheim (UHOH), located near Stuttgart, at 48°44'08.8" N, 09°12'11.8" E, with loamy clay soil; and the third at the research station of the Leibniz Centre for Agricultural Landscape Research (ZALF), located in Dedelow, at 53°36'99" N, 13°80'13" E, with sandy loam soil. The genotypes were evaluated during two growing seasons, 2023 and 2024, resulting in six environments.

Sowing and harvesting dates were dependent on regional climatic conditions, depending on year and location. Dates of sowing were, in 2023, the 5th of April at IPK, the 4th of May at UHOH and the 13th of April at ZALF. In 2024, sowing dates were the 30th of March, the 10th of April and the 23rd of April at IPK, UHOH and ZALF, respectively. Harvest dates varied according to the genotype, location and year. In 2023, harvest dates ranged from the 13th of July to the 23rd of August at IPK, from the 27th of July to the 15th of August at UHOH and from

TABLE 1 | Categorisation of genotypes according to their geographical/climatic group.

Geographical/ climatic region	Number of genotypes	Countries of origin
Western Mediterranean	20	Italy, Spain, Tunisia
Central Eastern European	16	Austria, Azerbaijan, Bulgaria, Czech Republic, Germany, Hungary, Russia, Slovakia, Ukraine
Eastern Mediterranean	13	Albania, Greece, Turkey

the 2nd to the 8th of August at ZALF. In 2024, harvest dates ranged from the 26th of July to the 5th of August at IPK, from the 25th of July to the 13th of August at UHOH and from the 5th to the 30th of August at ZALF.

2.4 | Experimental Design

For the experiment, 50 seeds of each genotype were sown in all locations in both years. Sowing was done mechanically using a trial plot drill at IPK (HALDRUP SP 25) and at ZALF (Hege 80). At UHOH, plots were hand sown. The seeds were sown in two rows; the distance between plant rows varied from 12 to 30 cm depending on the location of the experiment. Seed spacing was 4–5 cm within the row. Genotypes were not replicated within a single site; however, they were evaluated across three locations over 2 years, resulting in six environments. Due to the climbing characteristic of grass pea, a 1 m × 1.5 m metal trellis with a 0.10 m × 0.10 m grid was implemented within the two plant rows of each plot (Figure 1). Moreover, hand-weeding on the plot was conducted when needed, with the objective of avoiding external plant stress due to weed competitiveness.

2.5 | Agronomical and Yield Evaluation

A total of 13 developmental, agronomical, morphological and productivity-related parameters were selected based on the source “Descriptors for *Lathyrus* spp.” (IPGRI 2000) and adapted for our purpose. The parameters were grouped into three categories: the first related to the developmental phases of the genotypes (sowing date and growing degree days to the first flower [GDD1f]); the second related to agronomical and morphological traits (wing colour, plant height [Ph], height



FIGURE 1 | Experimental plot layout illustrating the growth and developmental stage of genotype ‘LAT4015’ at 49 DAS (10 days after first flower).

of the first pod [H1p], number of branches with pods [Nbp], seed colour and seed area [Sa]); and the third related to the productivity of the genotypes (number of seeds per pod [Nsp], number of pods per plant [Npp], number of seeds per plant [Nspl], thousand grain weight [TGW] and yield [Yield]). The full description of the traits evaluated in this study is shown in Table 2. Colours of flower wings and colour of seeds were categorised based on visual scores. Detailed colour scoring criteria are described in Figure S1.

2.6 | Data Analysis

Prior to correlation analysis, data normality for all traits included in the agronomic-productivity correlation analysis and non-metric multidimensional scaling (NMDS) plot were evaluated using the Shapiro–Wilk test (Table S2). As several variables deviated from normality, correlation matrices with heat

TABLE 2 | Descriptors used in the study for development, agronomy and morphology, and productivity-related traits, listed in the order of characterisation.

Trait related to	Acronym	Trait name	Unit
Development	—	Sowing date	day
Development	GDD1f	Growing degree days to first flower	°C
Agronomy and morphology	—	Wing colour	—
Agronomy and morphology	Ph	Plant height	cm
Agronomy and morphology	H1p	Height of the first pod	cm
Agronomy and morphology	Nbp	Number of branches with pods	—
Agronomy and morphology	—	Seed colour	—
Agronomy and morphology	Sa	Seed area	mm ²
Productivity	Nsp	Number of seeds per pod	—
Productivity	Npp	Number of pods per plant	—
Productivity	Nspl	Number of seeds per plant	—
Productivity	TGW	Thousand grain weight	g
Productivity	Yield	Yield	g plant ⁻¹

Note: Growing degree days to first flowering (GDD1f) was calculated according to the formula $(T_{max} + T_{min}) / 2 - T_{base}$, with a base temperature (T_{base}) of 0°C. Days with a minimum temperature below the base temperature were excluded from the calculation.

maps were generated using Spearman's correlation coefficients to assess relationships among developmental, agronomic, morphological and productivity-related traits. Spearman rank correlations were considered statistically significant at $p < 0.05$, and only moderate ($\rho > 0.4$), strong ($\rho > 0.6$) and very strong associations ($\rho \geq 0.8$) were interpreted. Scatter plots, illustrating the relationships between yield per plant with the other measured traits with both $\rho > 0.4$ and $p < 0.05$, are additionally shown in Figure S2. Flower and seed phenotypic classes were regarded as categorical factors. Due to the observed deviations from normality, differences among phenotypic classes were analysed using the non-parametric Kruskal–Wallis test at a significance level of $p < 0.05$. Pairwise comparisons between groups were performed using Wilcoxon rank-sum tests with Bonferroni correction to adjust for multiple testing only when the Kruskal–Wallis test indicated a significant difference. Furthermore, because of the deviation from normality from several traits, the NMDS plot, using Euclidean distance, was applied to visualise the relationships between agronomic descriptors and genotypes clustered by geographic/climatic regions of origin. Finally, differences among the geographic and climatic regions of origin were further compared by estimated marginal means of the measured traits, using post hoc pairwise comparisons, at a significance level of $p < 0.05$ (Table S3). All statistical analyses were performed using RStudio 2022.07.2, Build 576 (R Core Team 2022).

3 | Results

3.1 | Climate During the Experimental Periods

Weather conditions varied between locations and years of the study (Figure 2A–D). In 2023, UHOH had the highest average air temperature across locations during the season (Figure 2A). However, in 2024, UHOH had the lowest air temperature across the cropping season (Figure 2B), while IPK and ZALF had slightly higher air temperatures until flowering time in June, where temperatures were similar across the studied locations almost until the end of the season.

Precipitation also varied between years and locations. In 2023, IPK had the highest precipitation, with 110 mm in June, while UHOH had the highest precipitation in 2024 (186 mm in June). Soil temperatures were relatively stable across the years, showing that IPK had a higher soil temperature earlier in the cropping season compared to UHOH and ZALF (Figure 2C,D). In June and July, when the primary pod-filling period was occurring, UHOH had lower soil temperatures, while ZALF had higher soil temperatures, despite similar or slightly lower air temperatures at ZALF. Considering that sandy soils warm more quickly than clay-rich soils, this pattern likely reflects variation in soil texture among locations.

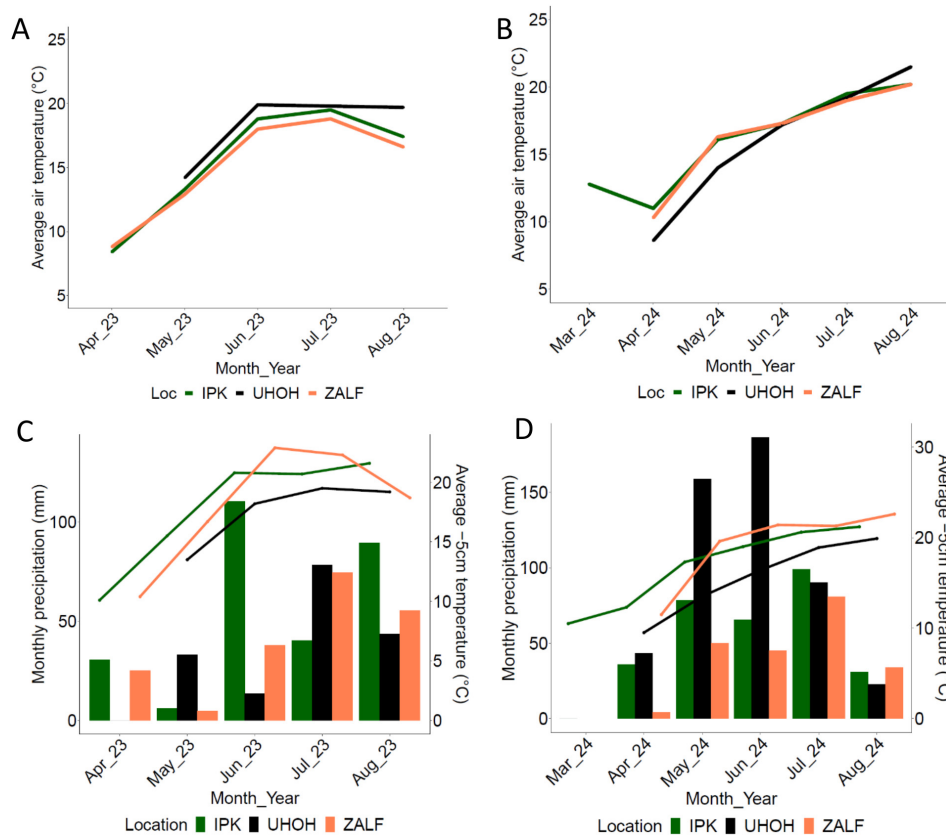


FIGURE 2 | Weather conditions from the day of sowing to the last date of harvest between the locations of the study detailing the monthly average air temperature at 2 m on 2023 (A) and 2024 (B), and monthly precipitation (in bars) and average soil temperature at –5 cm (in lines) for 2023 (C) and for 2024 (D). Data was collected from weather station Gatersleben (IPK), Agrarmeteorologie Baden-Württemberg (UHOH) and WetterKontor (ZALF).

3.2 | Correlation of Agronomical and Productivity-Related Parameters

The productivity-related parameter number of pods per plant was moderate and positively correlated (Figure 3) to the plant height ($\rho=0.47$, $p<0.001$), number of seeds per plant ($\rho=0.58$, $p<0.001$) and yield per plant ($\rho=0.51$, $p<0.001$).

The number of seeds per pod was strong and negatively correlated with the seed area ($\rho=-0.65$, $p<0.001$) and to the thousand grain weight ($\rho=-0.61$, $p<0.001$). The number of seeds per plant was moderate and positively correlated to the height of the first pod ($\rho=0.43$, $p<0.001$) and to the number of pods per plant ($\rho=0.58$, $p<0.001$). In addition, a very strong and positive correlation was identified between the number of seeds per plant and the yield per plant ($\rho=0.88$, $p<0.001$).

Thousand grain weight was strongly and negatively correlated with the number of seeds per pod ($\rho=-0.61$, $p<0.001$). A very strong and positive correlation between thousand grain weight and seed area was also identified ($\rho=0.96$, $p<0.001$).

Yield per plant was moderate and positively correlated with the number of pods per plant ($\rho=0.51$, $p<0.001$) and the height of the first pod ($\rho=0.42$, $p<0.001$), showing that genotypes with a higher first pod exhibit higher yield potential. In addition, a very strong positive correlation between yield per plant and the number of seeds per plant was also observed ($\rho=0.88$, $p<0.001$). Scatter plots illustrating these relationships are provided in Figure S2 and normality tests in Table S2.

3.3 | Productivity-Related Parameters and Phenotype

Characterisation of wing colour of the grass pea genotypes indicated 20 genotypes with white/blue wings, 17 had either blue or pink wings and 13 genotypes had white wings. For seed coat colour, 23 genotypes had a white/brown seed coat, 15 had a brown seed coat and 12 genotypes had a white seed coat colour. The complete colour categorisation is presented in Figure S1, and detailed genotype-level phenotype descriptions are presented in Table S1.

The number of seeds per pod differed significantly among wing colour and seed colour categories (Figure 4C,D, $p<0.001$),

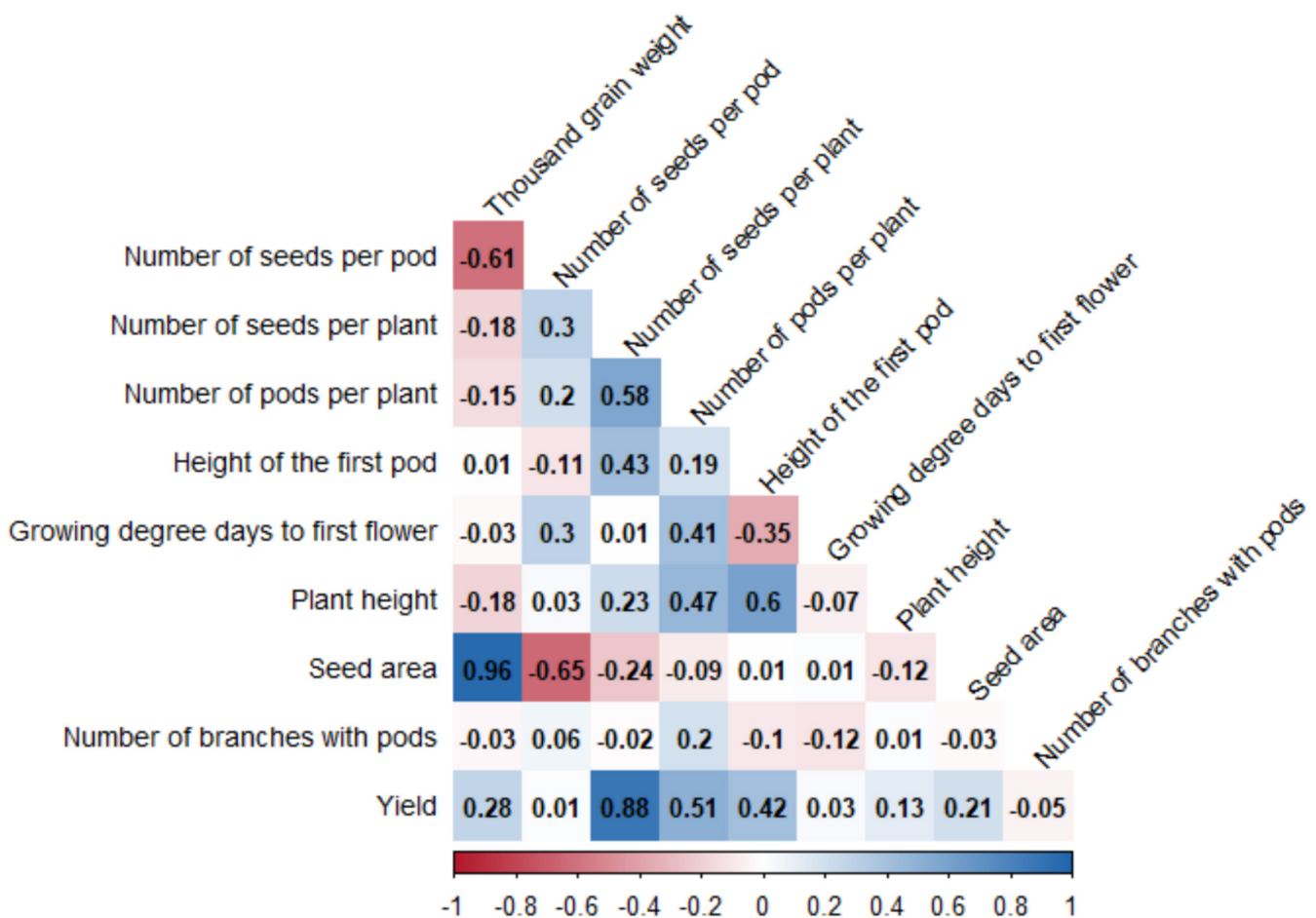


FIGURE 3 | Correlation matrix heat maps showing Spearman correlation coefficients ($df=298$) among agronomical and productivity-related traits of 50 grass pea genotypes evaluated across three locations and two cropping seasons. Correlations are colour-coded from blue (positive correlation, +1.0) to red (negative correlation, -1.0). Traits included: Growing degree days to first flower ($^{\circ}\text{C}$); plant height (cm); height of the first pod (cm); number of branches with pods; seed area (mm^2); number of seeds per pod; number of pods per plant; number of seeds per plant; thousand grain weight (g); and yield (g plant^{-1}).

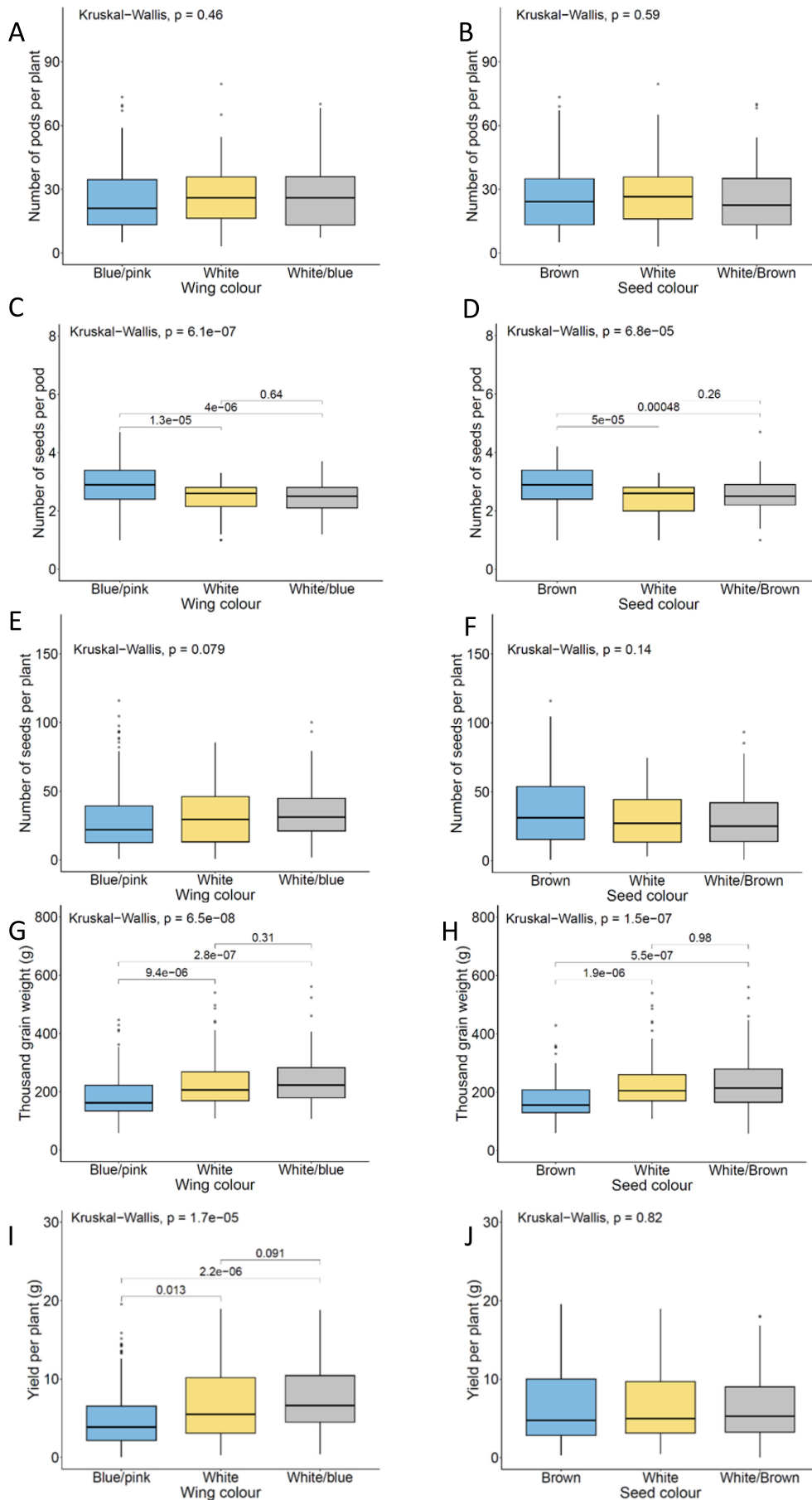


FIGURE 4 | Legend on next page.

FIGURE 4 | Boxplot of the distribution of the genotypes ($df=298$) for productivity-related traits grouped by wing and seed colour. Traits include: number of pods per plant compared with wing colour (A) and seed colour (B); number of seeds per pod compared with wing colour (C) and seed colour (D); number of seeds per plant compared with wing colour (E) and seed colour (F); thousand grain weight (g) compared with wing colour (G) and seed colour (H); and yield per plant compared with wing colour (I) and seed colour (J). Kruskal–Wallis p values are indicated in the upper left corner of each panel. Pairwise comparison (Wilcoxon rank-sum tests with Bonferroni correction) was performed only when the Kruskal–Wallis test indicated a significant difference ($p < 0.05$) and is represented by the numbers on top of brackets within each subplot.

where genotypes with blue/pink flowers and brown seeds had a significantly higher number of seeds per pod than light coloured flower wings and seeds.

Thousand grain weight (TGW) differed significantly among wing colour (Figure 4G, $p < 0.001$) and seed colour categories (Figure 4H, $p < 0.001$). Genotypes with light-coloured wings (white or white/blue wings) had a significantly ($p < 0.001$) larger TGW, compared to blue flowers (Figure 4G). Seeds with a lighter (white or white/brown) seed coat also tend to have a larger TGW compared to brown seeds ($p < 0.001$) (Figure 4H).

There was no difference in the number of pods per plant when grouped according to their wing (Figure 4A) or seed colour (Figure 4B) ($p \geq 0.05$). The number of seeds per plant (Figure 4E,F) also revealed no significant relation to seed colour or wing colour ($p \geq 0.05$). Yield per plant varied significantly with wing but not seed colour (Figure 4I,J). Higher median yields were observed in genotypes with white and white/blue wing colour compared to blue/pink wing genotypes.

3.4 | Agronomical and Productivity-Related Parameters and Geographic/Climatic Groups

The number of seeds per pod (Nsp) was higher in genotypes with an Eastern Mediterranean or Central Eastern European origin compared to Western Mediterranean origins (Figure 5). Genotypes with a Western Mediterranean origin had a lower number of seeds per plant compared to Eastern Mediterranean and Central Eastern European genotypes. Thousand grain weight (TGW) and seed area (Sa) were higher in genotypes with a Western Mediterranean origin. Eastern Mediterranean genotypes had a significantly higher number of pods per plant (Npp) than Western Mediterranean genotypes. However, Central Eastern European genotypes did not significantly differ from either of the regions. Plant height (Ph) was significantly higher in genotypes with a Central Eastern European origin, while the Western Mediterranean genotypes had the lowest plants. Eastern Mediterranean genotypes had an average value and did not differ from any of the other groups. Grain yield was not significantly different between the origins. There were also no significant correlations between height of the first pod (H1p), number of branches with pods (Nbp) and growing degree days to first flower (GDD1f) across the origins.

PERMANOVA revealed a significant difference in overall trait composition between groups (pseudo- $F=19.37$, $R^2=0.12$, $p=0.001$). Multivariate dispersion did not differ significantly among groups ($p=0.335$). The NMDS ordination resulted in a stress value of 0.21. Estimated marginal means of all analysed traits across geographic and climatic regions of origin are provided in Table S3.

4 | Discussion

4.1 | Correlation of Agronomical and Productivity-Related Parameters

The number of pods per plant was positively correlated with plant height, number of seeds per pod and yield. Similar plant height association was reported by Gonçalves et al. (2024), highlighting that taller plants are correlated to genotypes which can produce more pods per plant and, consequently, more yield. Moreover, the positive correlation described in our study between the number of pods per plant and the number of seeds per pod and yield per plant is consistent with results from other grass pea studies (Basaran et al. 2013; Mandal et al. 2015) and in other legume species, such as broad bean, soybean and common bean (Li and Yang 2014; Umburanas et al. 2022; Stoilova et al. 2025). These results indicate that genotypes producing more pods per plant tend to possess other traits that enhance yield levels, making this parameter a valuable selection criterion for genetic improvement of grass pea for temperate climates.

A strong negative correlation was observed between the number of seeds per pod and both seed area and TGW. This is consistent with findings from prior studies (Campbell 1997; Mandal et al. 2015). Although Mandal et al. (2015) also reported a negative correlation between the number of seeds per pod and yield, we did not identify this correlation in our study. The contrasting relationships observed among studies may be explained by the large genetic variability of grass pea (Abate et al. 2018) and differences in climatic and management conditions between the study regions.

The number of seeds per plant is considered a key factor shaping other productivity-related traits in many legumes. For instance, positive correlations between seed yield and the number of seeds per plant have been reported in broad bean (Li and Yang 2014) and white lupin (Tobiasz-Salach et al. 2023). In our study, this trait was also positively correlated with characteristics such as the number of pods per plant, yield per plant and the height of the first pod, which aligns with recent findings in grass pea (Gonçalves et al. 2024).

Although we identified a positive correlation between TGW and yield per plant ($p < 0.001$), indicating that heavier seeds contribute to higher productivity under Central European conditions, this correlation was relatively weak ($\rho=0.243$). In contrast, Gonçalves et al. (2024) observed no significant correlation under Mediterranean conditions. Together, these findings emphasise that this correlation must be interpreted with caution and that local conditions may affect trait interactions, highlighting the importance of region-specific selection.

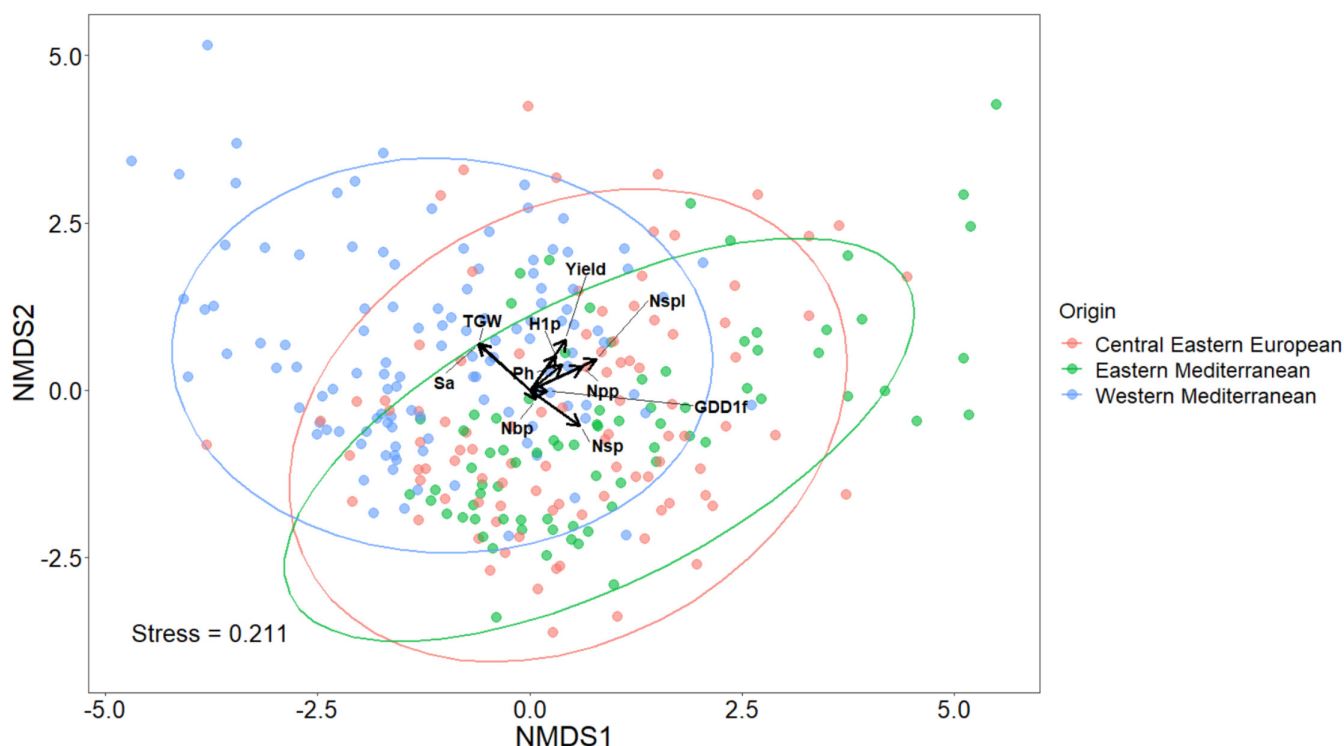


FIGURE 5 | NMDS ordination of the 49 genotypes analysed by geographical/climatic origin with the agronomic and yield-related trait vectors. Distribution based in two-dimensional space, where points represent the genotypes, coloured by the geographic/climatic origin. Black arrows represent the traits, and the arrow direction indicate increasing values while length reflects how strong is the association with the ordination. Trait abbreviation are as follows: GDD1f, growing degree days to first flower; Ph, plant height; H1p, height of the first pod; Nbp, number of branches with pods; Sa, seed area, Nsp, number of seeds per pod; TGW, thousand grain weight; Nspl, number of seeds per plant; Npp, number of pods per plant; and Yield, yield per plant. The stress value (bottom left) shows the fit of the NMDS plot with the original data.

Genotypes with a higher first pod tended to produce greater yields in our study ($\rho=0.42$), which is in accordance with earlier studies showing that first pod height can influence plant architecture and harvestability, reducing yield losses (Beiküfner et al. 2019; Kuzbakova et al. 2022). However, even though we found a correlation between the height of first pod and yield, this is probably a complementary trait rather than the main factor influencing productivity. In the single plot-based assessment, absolute grain yield per unit area varied widely across locations, with yield averages of 268 g/m² at IPK, 465 g/m² at UHOH and 946 g/m² at ZALF (data not shown). This wide yield range is likely driven by environmental variation across the studied sites.

Our study indicates that under German conditions, genotypes with higher first pods, a higher number of seeds per plant and a higher number of pods per plant were strongly and positively correlated with higher yields. However, a clear definition of breeding objectives is crucial for optimising selection strategies and achieving meaningful genetic improvement.

4.2 | Productivity-Related Parameters and Phenotype

We found no significant relation between wing or seed colour and the number of pods per plant. Tsialtas and Irakli (2024) found that white/blue flowers had a slightly higher number of pods per plant, although no significant difference among the groups was observed. Our findings suggest that the number of

pods per plant is more closely related to the genotype collection used for the study rather than to a specific wing or seed colour group.

In our study, genotypes with white/blue flowers showed slightly higher yield performance than other flower colour groups; however, the same pattern was not observed in seed colour. While Tsialtas and Irakli (2024) reported no association between yield and flower or seed colour, Gonçalves et al. (2024) describe higher yields in genotypes with lighter seed colour. We therefore assume that differences in genetic material and growing conditions can explain the distinct patterns we could observe in our study. In addition, Thirumalai et al. (2025) described a linkage between seed colour and agro-morphological traits in pea, noting that the number of pods per plant and seed yield per plant varied across seed-colour classes. Furthermore, similar linkages were described in common vetch (Tiryaki et al. 2016). These findings suggest that, in some legume species, colour traits may be associated with productivity-related parameters. Therefore, wing and seed colour may serve as useful indicators for selecting high-yielding grass pea genotypes for Germany, although their relevance may vary under different environmental conditions.

The number of seeds per plant did not differ significantly among wing or seed colour groups. Considering that seed number is a complex, often quantitative trait (Wallace et al. 1993), the observed variation from our results, although not significant, most likely reflects the genetic variation among the genotypes studied and the environmental conditions under which the study was

conducted. Therefore, the number of seeds per plant should not be associated with a specific wing or seed colour.

Our findings also showed a clear association between the wing and seed colour to the number of seeds per pod and TGW, where genotypes with blue flower wings and brown seeds had a higher number of seeds per pod and smaller TGW. These findings are also confirmed by other studies, for example, Jackson and Yunus (1984) and Tsialtas and Irakli (2024). Although a higher number of seeds per pod might seem positive, our findings did not correlate this with a higher yield. Grass pea marketability preferences are not related to TGW; however, darker seeds usually have a higher concentration of tannins, another antinutritive compound in addition to β -ODAP (Gonçalves et al. 2024). Furthermore, Boldischar et al. (2025) reported that TGW was positively correlated to higher L-hArg concentration using the same plant material of our study, although a positive correlation between L-hArg and β -ODAP was also identified ($r=0.40$, $p<0.01$).

Therefore, selection of genotypes with white or white/brown seeds should be considered when larger TGW is desired and when aiming for a reduced concentration of tannins and increased concentration of L-Arg.

4.3 | Productivity-Related Parameters and Geographic/Climatic Groups

Grouping genotypes by geographic and climatic origin revealed significant differences for the number of seeds per pod, TGW and seed area. Genotypes from a Central Eastern European origin showed intermediate values for these traits. Moreover, we identified that genotypes from this region were significantly taller compared to Western Mediterranean and not Eastern Mediterranean genotypes. Although yield differences were not significant, this latter group included genotypes with taller plants, longer GDD to first flower and slightly lower yield.

Studies analysing genotypes with a Mediterranean origin, including both Eastern and Western Mediterranean regions as described here, have reported associations between higher TGW and Mediterranean environments (Grela et al. 2012; Basaran et al. 2013). However, our study demonstrated that genotypes with a Western Mediterranean origin had a significantly larger TGW than genotypes with an Eastern Mediterranean origin, suggesting differences when allocating genotypes into two geographical pools within the Mediterranean region. Although seeds were significantly larger, the total number of seeds per plant was significantly lower in genotypes with this origin, suggesting a trade-off between seed size and the number of seeds produced by the plant.

In contrast to TGW, the number of seeds per pod was significantly higher in Eastern Mediterranean genotypes, while Western Mediterranean genotypes had a smaller number of seeds per pod. Therefore, our results imply an inverse relationship between the number of seeds per pod and TGW across the two Mediterranean pools. Furthermore, we identified that genotypes with an Eastern Mediterranean origin had a significantly higher number of pods per plant, suggesting a

compensatory strategy of these genotypes, in which smaller seed size is compensated by a higher number of pods per plant and a greater number of seeds per pod.

Despite the absence of significant differences in yield per plant among the geographic or climatic groups, our findings suggest that, when larger TGW is the main breeding objective, genotypes originated from Western Mediterranean countries may be most suitable for selection under German conditions, while when the number of seeds per pod is the main breeding aim, Eastern Mediterranean genotypes may offer greater potential. Ultimately, defining clear breeding priorities will determine the optimal choice of genotypes for selection.

5 | Conclusion

Our study identified key traits for selection of grass pea genotypes and varieties for successful cultivation under Central European conditions for the first time. We found that, for the selection of grass pea genotypes for Central Europe, a high number of seeds per plant, a high number of pods per plant and high first pods are the most important traits that are significantly correlated with high yields and should be prioritised in breeding programmes. Genotypes with white/blue wings and white/brown seeds had the highest TGW, while the origin of genotypes might only be relevant for specific breeding objectives, such as TGW, the number of seeds per pod and the number of seeds per plant.

Our results highlight desirable traits to support future breeding programmes and genotype selection and reveal that commercial varieties currently available for cultivation can be optimised. Variety improvement is therefore urgently needed to broaden the choice of higher-yielding varieties for farmers and enhance grass pea productivity in Central Europe.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Detailed characterisation data of the 50 grass pea genotypes used in this study. **Figure S1:** Visual categorisation of flower wing: (A) blue, (B) white/blue and (C) blue/pink and seed colour (D) brown, (E) white/brown and (F) white. **Table S2:** Shapiro–Wilk normality test for traits used in correlation analysis presented in Figures 4 and 6. Normality was assessed using the Shapiro–Wilk test ($p = 0.05$). **Figure S2:** Scatter plots with the distribution ($df = 298$) between the yield per plant and (A) number of seeds per plant, (B) number of pods per plant and (C) height of the first pod. Data include all 50 genotypes across six environments. **Table S3:** Estimated marginal means of the analysed traits across geographic and climatic regions of origin, with pairwise comparisons at $p < 0.05$. *Means with the same letter are not significantly different at 0.05 significance level based on Tukey-adjusted pairwise comparisons of estimated marginal means.