

ORIGINAL ARTICLE

Agronomic Application of Genetic Resources

Influence of growth habit on yield performance and quality of wheat landraces under continental Mediterranean conditions

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Abstract

Wheat (*Triticum aestivum* subsp. *vulgare* (Vill.) Thell.) is cultivated across a wide range of environments, where growth habit represents a key mechanism of local adaptation. However, modern varieties often lack key traits for sustainable farming, particularly in organic and low-input systems where stress resilience and resource-use efficiency are critical. In contrast, landraces often show greater yield stability under suboptimal conditions. This study assessed the adaptation of spring and winter landraces across two contrasting seasons in a semiarid Mediterranean climate, focusing on yield components, agronomic traits, yield stability, and technological quality. The effects of growth habit, genotype, and environment on the evaluated traits were analyzed, as well as the relationships between agronomic traits and yield across growth habits and environmental conditions. Winter landraces generally outperformed spring types in terms of yield under favorable agroclimatic conditions, while no significant differences were found under dry and hot conditions—though winter types showed greater yield stability. Yield enhancement strategies varied by environment and growth habit. Under favorable conditions, traits such as increased kernel number, early heading, and shorter height improved winter variety performance. Under stress, vegetative development, spike number, and test weight appeared to be critical for winter wheat adaptation, while spring types with greater biomass, test weight, and earliness tended to perform better. Quality analyses revealed that both growth habits exhibited comparable technological quality. These findings highlight the importance of considering growth habit and environmental context when selecting landraces for Mediterranean farming systems. Finally, several genotypes from both habits demonstrated promising adaptation and stability.

Abbreviations: BW, biomass weight; DH, days to heading; GDD, growing degree-days; GEI, genotype $\times$ environment interaction; GH, growth habit; GPC, grain protein content; GS, glutamine synthetase; GY, grain yield; HI, harvest index; KS, number of kernels per spike; LGS_{BH}, length of the growing season before heading; PCA, principal component analysis; PH, plant height; Pi index, genotype superiority measure; Pop, population; SDSS, sodium dodecyl sulfate sedimentation; SN, number of spikes per m²; TKW, thousand kernel weight; TW, test weight.

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Plain Language Summary

Modern wheat varieties are generally less adapted to sustainable farming, especially in organic or low-input systems. Although local varieties (landraces) have been largely replaced due to their lower yields, they often show greater stability under stressful conditions. Wheat can have either a winter or spring growth habit, depending on its need for cold temperatures to flower (required for winter types) and its tolerance to cold (lower in spring types). Growth habit is therefore an important mechanism for local adaptation. In this study, we found that winter landraces produced higher yields than spring types when water was more available. However, under dry conditions, neither growth habit was clearly superior. We also found no major differences in grain quality between the two types. To select the best landraces for each environment, it is important to consider specific agronomic traits—such as number of grains or spikes, biomass, and earliness—depending on their growth habit.

1 | INTRODUCTION

Agricultural practices introduced during the Green Revolution significantly boosted food production and supported global population growth (Fischer, 2022). However, they have also become a major driver of ecosystem degradation and biodiversity loss (Hald-Mortensen, 2023; Kahiluoto et al., 2019). Agroecosystems in dry and semiarid regions, such as the Mediterranean, are particularly vulnerable due to chronic water scarcity and low soil fertility (Jacobsen et al., 2012). These conditions heighten their susceptibility to recurrent droughts, reduced wheat (*Triticum aestivum* subsp. *vulgare* (Vill.) Thell.) yield and yield stability, and exacerbate the accelerating impacts of global climate change (Iglesias et al., 2011). In response, there is a growing awareness of the need to adopt more sustainable agricultural systems as alternatives to conventional cropping practices, alongside the development of crop varieties with good stability under such conditions.

Genotype stability reflects the consistency (or resilience) of a genotype's performance across environments and is particularly relevant for traits such as grain yield (GY) and quality in regions where environmental conditions fluctuate periodically (Kahiluoto et al., 2019). Assessing stability requires evaluating a variety behavior across contrasting environments, typically achieved by testing across two or more localities and/or over several years. Among the various stability parameters available, the Superiority Index of genotypes (Lin & Binns, 1988) is especially useful because it quantifies relative performance across environments, helping identify genotypes with both high performance and stability, as well as those with specific adaptability to low-yielding conditions (Mohammadi et al., 2021; Roostaei et al., 2022).

Some studies have highlighted that modern-bred wheat varieties often lack key traits required for optimal perfor-

mance under sustainable management practices, particularly in organic and low-input systems, where stress resilience and resource-use efficiency are critical (Lammerts Van Bueren et al., 2011). In contrast, landraces are heterogeneous varieties that evolved locally under specific environmental conditions, exhibiting a high capacity to tolerate both biotic and abiotic stresses (Adhikari et al., 2022; Lopes et al., 2015). While wheat landraces generally produce lower yields compared to commercial cultivars, their adaptability to diverse and challenging climatic conditions makes them increasingly valuable in the context of climate change (Carranza-Gallego et al., 2019; Migliorini et al., 2016). Due to their resilience and rusticity, landraces often show greater yield stability and grain quality under suboptimal conditions, making them particularly well-suited for use in sustainable and low-input farming systems (Özberk & Özberk, 2021; Preiti et al., 2022; Zeven, 1998). Furthermore, wheat landraces serve as reservoirs of valuable allelic variation for traits of agronomic interest, contributing to biodiversity enhancement and the stabilization of crop production under rapidly changing climatic conditions (Adhikari et al., 2022). Mediterranean wheat landraces in particular possess substantial genetic diversity and are considered valuable genetic resources for their tolerance to both biotic and abiotic stresses, and for their consistent performance under sustainable agricultural practices (Bektas et al., 2016; Bosi et al., 2022; Frankin et al., 2021; Korpetis et al., 2023; Martínez-Moreno et al., 2022; Ruiz et al., 2019). The comprehensive characterization and evaluation of these landraces are essential for unlocking their potential and effectively utilizing their genetic variability to improve traits of economic and agronomic relevance.

Wheat is cultivated across a wide range of environments, where growth habit (GH) represents a key mechanism of local adaptation (Kamran et al., 2014). The GH, classified as winter, facultative, or spring, is controlled by genes that regulate

responses to vernalization, which, together with photoperiod responses genes, adjust flowering time to ensure alignment with favorable environmental conditions (Gomez et al., 2014). Spring wheat is typically insensitive or only partly sensitive to vernalization, while winter wheat requires a substantial vernalization requirement to trigger flowering (Dreisigacker et al., 2016). In Spain, where agroclimatic conditions vary widely, both spring and winter wheat varieties are cultivated. Similar to other Mediterranean regions, winter types are commonly grown in the north due to their cold tolerance, whereas spring types are predominant in the south, where temperatures are insufficient to meet the vernalization needs of winter wheats (Royo & Briceño-Félix, 2011). However, in the central continental regions, both GHs can be sown in autumn and successfully cultivated. Several studies have highlighted the influence of GH on traits relevant for the agronomic performance of wheat, including GY across diverse environments (He et al., 2020; Mosaad et al., 2008; Sánchez-García et al., 2012), disease tolerance (Lai et al., 2024; Ye et al., 2017), root architecture (Hamada et al., 2012; Thorup-Kristensen et al., 2009; Voss-Fels et al., 2018), and grain quality characteristics (Chung et al., 2003).

Environmental conditions can modulate the expression of the major GH genes and influence heading date after the vegetative phase, thereby affecting GY potential (Lozada et al., 2021). GY in wheat results from the interaction of three main yield components: number of spikes per m², number of kernels per spike, and kernel weight (Moragues et al., 2006; Sánchez-García et al., 2013; Slafer et al., 2014). The plasticity of wheat genotypes determines that these yield components can be strongly influenced by cultivation practices and seasonal conditions, which may, in turn, affect their relative contribution to final yield (Du et al., 2020; Slafer et al., 2014). Guijarro-Real et al. (2025) examined the adaptation of Spanish spring landraces in two distinct localities, one in the South and one in the Centre, and demonstrated that the landraces employed different yield strategies depending on the environmental context. However, as only spring wheat is suitable for cultivation in southern Spain, the effect of GH on the environmental adaptation of wheat varieties was not included in that study.

In the present research, the agronomic performance and quality of both spring and winter landraces were evaluated in two contrasting cropping seasons in a central locality. Thus, the specific objectives were to (i) assess the effects of GH, genotype, and environment on landraces' yield, yield-related traits and grain quality; (ii) investigate the differential yield strategies employed by winter and spring wheats in these cropping seasons; and (iii) identify the landraces with the most stable yields across the two contrasting seasons that might be more suitable for organic and low-input farming systems.

Core Ideas

- Significant yield variation was observed among varieties sharing the same growth habit.
- The selection of optimal agrotypes was influenced by both growth habit and prevailing environmental conditions.
- The two growth habits did not exhibit significant differences under dry and hot environmental conditions.
- Winter genotypes generally exhibited greater yield stability than spring genotypes.
- No growth habit demonstrated superior technological quality.

2 | MATERIALS AND METHODS

2.1 | Plant material

In this study, the Spanish core collection of bread wheat (*Triticum aestivum* subsp. *vulgare* (Vill.) Thell.) landraces, composed of 94 accessions, was analyzed. These accessions were selected to capture the genetic diversity assessed with more than 50K DArT markers distributed across the whole genome, and the geographic and agromorphological diversity of the entire collection of more than 500 Spanish landraces and old cultivars of bread wheat preserved at the National Plant Genetic Resources Centre (Pascual, Fernández, et al., 2020). The 94 accessions are clustered in four genetic populations (Table S1), which differ in their eco-geographical origin and genetic diversity (Pascual, Ruiz, et al., 2020). All the accessions (i.e., genotypes) were homozygous lines derived from GenBank-original accessions by the single-seed descent method. According to the registered data (Giménez et al., 2025), out of the whole core collection, 60 landraces had a spring GH, and the other 34 landraces had a winter GH (Table S1).

2.2 | Sites description and experimental procedure

The study was performed at the INIA experimental farm La Canaleja (Alcalá de Henares, Madrid, Spain: 40°32' N and 3°20' W; 600 m.a.s.l.). The soil was a moderately alkaline (pH close to 8) and nonsaline (0.12 dS m⁻¹) sandy-loam *Calcic Haploxeralf* (Soil Survey Staff, 2022); the Ap horizon (0–15 cm) presented low inherent fertility with mean soil organic carbon content of 6 g kg⁻¹, Kjeldahl soil nitrogen content of 0.7 g kg⁻¹ and main nutrient values of 7 mg Olsen-available P

kg⁻¹ and 300 mg available K kg⁻¹. The region has a semiarid, continental Mediterranean climate, Csa (Köppen-Geiger climate classification, Kottek et al., 2006), characterized by dry summers and irregular precipitation both throughout the year and among years.

Daily meteorological data were recorded over the study period (autumn 2020 to summer 2022) at the weather station located in the experimental site. The length of the growing season before heading (LGS_{BH}) was expressed as thermal time, measured for each variety as cumulative growing degree-days (GDD) from January 1 to the heading date. For a given day, GDD was calculated as the difference between the average air temperature and a base temperature of 0°C (Payero, 2017). When calculating the average air temperature, the upper limit for maximum temperature was established at 25°C (Pask et al., 2012).

The study was conducted over two growing seasons, 2020–2021 (experimental year 2021) and 2021–2022 (experimental year 2022), using an augmented design (Petersen, 1985) with repeated controls (cultivars Aragón 03 and Siete Cerros in both years, and also Califa Sur in 2022) replicated twice in 2021 and three times in 2022. Experimental units consisted of 2 m² plots sown at a density of 400 plants m⁻². Wheat was sown in November and harvested in June. Fertilization was applied both pre-sowing (150 kg ha⁻¹ of 8/12/12 [NPK]) and in spring (223 kg ha⁻¹ of ammonium nitrosulfate, 26% N). Weed control was performed mechanically, and no fungicides or insecticides were applied throughout the experiment.

2.3 | Phenotype evaluation and yield stability

Days to heading (DH) were recorded from January 1 to the date when more than 50% of the main spikes within a plot reached Zadoks stage 55 (Zadoks et al., 1974). At maturity (Zadoks stage 92), five randomly selected plants from the center of each plot were used to measure plant height (PH, cm), from ground level to the top of the main spike, excluding awns. At harvest maturity (Zadoks stage 92), all plants within a 1-m-long row located at the center of each plot were cut at ground level. From each landrace lineal meter, several yield components were evaluated: spike number (SN, m⁻²), number of kernels per spike (KS), GY (kg ha⁻¹), biomass weight (BW, kg ha⁻¹), harvest index (HI), thousand kernel weight (TKW, g), and test weight (TW, kg hL⁻¹). Aerial biomass (tillers and spikes, excluding grain) was oven-dried at 70°C for 48 h before weighing to obtain the dry matter weight. HI was calculated as the ratio of GY to the sum of GY and BW on a dry weight basis. TKW was estimated from two hand-counted subsamples of 100 grains each. KS was calculated by dividing the total grain number by the number of spikes. Grain number was obtained by dividing total grain weight by TKW.

TW was measured using a chondrometer in a 250 mL volume. GY, TKW, and TW were expressed on a 14% moisture basis.

Technological quality (i.e., grain protein content [GPC] and gluten strength, Table S1) was evaluated in 65 selected accessions out of the 94 of the core collection (37 spring-habit and 28 winter-habit genotypes), which had sufficient seed available and represented all genetic populations in a similar proportion to those of the core collection. GPC on a dry matter basis was estimated by near-infrared reflectance analysis using a PerCon Inframatic 8600 (Perten Instruments AB, Sweden). Gluten strength was determined on 1 g of whole grain flour samples by a sodium dodecyl sulfate sedimentation (SDSS) volume test, according to Dick and Quick (1983), with minor modifications. Technical duplicates were used in protein content measurement and the SDSS tests.

Yield stability of the varieties across the two cropping seasons (experimental years in this study) was evaluated based on GY data using the genotype general superiority measure, namely, Pi index (Lin & Binns, 1988). This index quantifies the distance mean square between a variety's yield and the maximum yield observed in each year, averaged across all tested years. Since the maximum yield represents the upper boundary of performance in each year, a smaller Pi value indicates a closer approximation to this maximum and thus reflects greater general superiority. Therefore, the lower the Pi index, the more stable and superior the variety across years was.

$$Pi = \sum_{j=1}^n (X_{ij} - M_j)^2 / (2n)$$

where X_{ij} be the yield of the i th variety grown in the j th year, and M_j the maximum yield among all the varieties in the j th year. The superiority index was also calculated separately for each of the tested years. Genotypes were ranked from 1 (best) to 94 (worst) based on their Pi values.

2.4 | Statistical analyses

Analysis of variance (ANOVA) was conducted on agronomic traits to evaluate the fixed effects of genotype, year, GH, and genetic population (Pop). All variables met the assumption of homoscedasticity, as confirmed by Levene's test. The statistical significance of main effects and interactions was determined using F -tests, while mean comparisons were conducted using Fisher's protected least significant difference test. Differences between Pi means and between means of the quality parameters were tested using the Student's t -test and the Satterwait's correction if variances were not homogeneous at a significance of $p = 0.05$. To test for pairwise independence among allelic variants at different glutamine synthetase

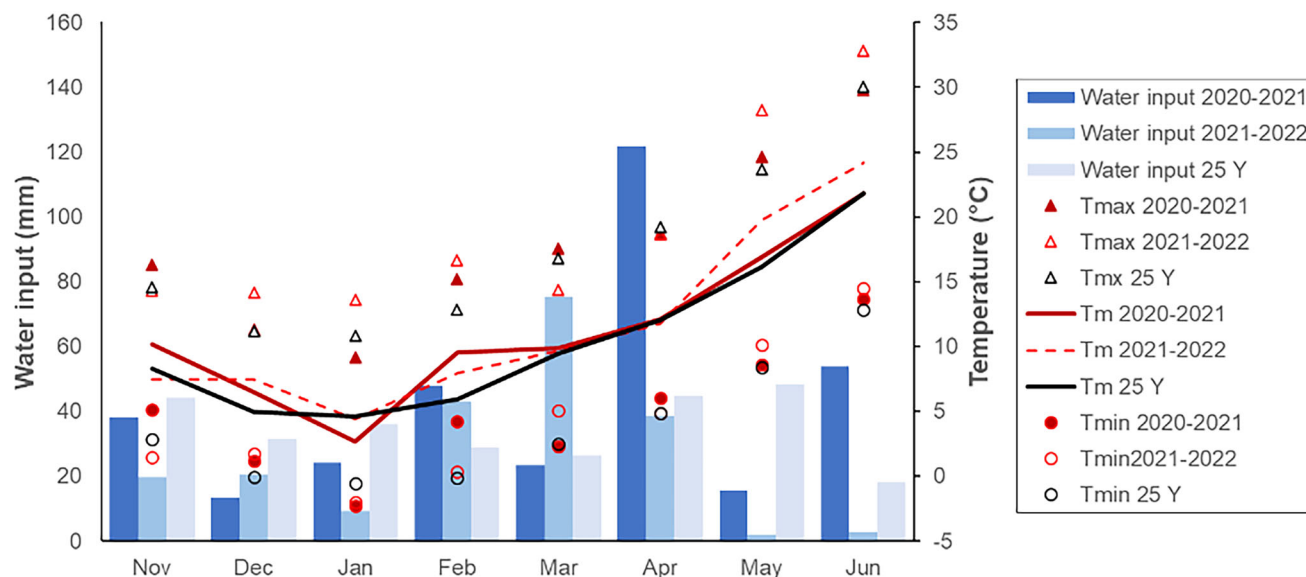


FIGURE 1 Monthly water input and the average mean (Tm), maximum (Tmax), and minimum (Tmin) temperatures corresponding to the field trials during the cropping period in the growing seasons 2020–2021 and 2021–2022, along with the 25-year average (25 years). Y, year.

(GS) and glutenin loci within the diversity panel, contingency chi-square tests were applied. Relationships between variables were assessed through Pearson correlation coefficients ($p = 0.05$). Multivariate relationships among agronomic traits and wheat genotypes were further explored using principal component analysis (PCA). All statistical analyses were implemented with Infostat software, version 6.12 (Di Rienzo et al., 2008). Pi index analyses were conducted in R using the metan library (Olivoto & Lúcio, 2020).

3 | RESULTS

3.1 | Environmental conditions of the growing seasons

The two cropping years analyzed (2021 and 2022) were thoroughly characterized in a previous study (Guijarro-Real et al., 2025). Figure 1 presents the average monthly precipitation, and the minimum and maximum temperatures, during the crop cycle (November to June). In both years, the coldest quarter coincided with winter, while the hottest occurred in spring. The driest period also corresponded to winter. The wettest period was from April to June in 2021, coinciding with the hottest months, whereas in 2022, it extended from February to April. The duration of the pre-heading phase, expressed as thermal time, was longer in 2021 than in 2022 for both winter and spring wheats, with values of 1098 GDD and 1051 GDD in 2021, compared to 1065 GDD and 998 GDD in 2022, respectively (Table S1).

The second year differed from the first by having higher temperatures from heading to maturity (May to June), despite

similar annual mean temperatures in both years (11.2°C for 2021 and 11.7°C for 2022). When comparing water input in 2022 with the 25-year long-term average (1994–2019), 2022 was notably dry (211 mm vs. 278 mm), particularly during the hottest quarter (April–June), which received only 43.5 mm compared to 111 mm in the long-term average (Figure 1). These conditions led to increased water stress during the late stage of the crop cycle in 2022. In contrast, wheat plants did not suffer drought stress in 2021; in fact, water input exceeded the long-term mean (338 mm in 2021). Notably, rainfall in April 2021, right before heading, was substantially greater than in 2022 and the long-term April average (Figure 1).

3.2 | Effects of growth habit, environment, and genotype on the agronomic traits

Environmental conditions favored yield in 2021. Mean yields ranged from 661 to 5606 kg ha⁻¹ in 2021, and from 324 to 2911 kg ha⁻¹ in 2022 across landraces. Regarding GH, yields ranged from 324 to 5606 kg ha⁻¹ in winter landraces, and from 438 to 4535 kg ha⁻¹ in spring types (Table S1).

The ANOVA results (Table 1) indicated that the year and, primarily, the genotype explained a significant portion of the variation in most agronomic traits. Significant effects of year and genotype were observed for all traits, except for year on KS and genotype on BW. No significant interactions among the fixed effects were found. Mean comparisons between years indicated that 2021 had higher values than 2022 for SN, GY, BW, TKW, HI, and DH, but lower values for TW. Overall, 2021 was a favorable growing season, in contrast to 2022, which presented unfavorable conditions for the

TABLE 1 Sum of squares for the effects of genotype, growth habit, year, and their interactions on the evaluated agronomic traits. Mean values for winter and spring growth habits, as well as for the 2 years, are presented.

Source of variation	Sum of squares (%)								
	KS	SN (m ⁻²)	GY (kg ha ⁻¹)	BW (kg ha ⁻¹)	HI	TKW (g)	TW (kg hL ⁻¹)	DH	PH (cm)
Gt	80.5***	48.0*	44.8***	50.8	55.6***	50.4***	43.7***	87.5***	69.6***
GH	0.1	0.2	1.2*	0.0	2.2***	2.5***	1.1**	5.1***	0.3
W habit	14.1	410	1921a	8047	0.17a	34.3a	81.1a	123a	125
S habit	13.8	395	1723b	7982	0.15b	32.3b	80.1b	120b	123
Y	0.1	20.0***	32.1***	8.1***	26.7***	33.0***	43.4***	0.5*	18.2***
2021	14.0	466a	2288a	8696a	0.18a	36.5a	77.6b	121a	131a
2022	13.8	334b	1301b	7315b	0.13b	29.5b	83.3a	120b	117b
Gt × Y	17.2	32.8	22.2	38.8	13.2	13.8	11	6.1	9.4
GH × Y	0.3	0.1	0.7	0.8	0.0	0.0	0.2	0.2	0.0

Note: Means followed by different letters are significantly different at $p = 0.05$.

Abbreviations: BW, biomass weight; DH, days to heading; GH, growth habit; Gt, genotype; GY, grain yield; HI, harvest index; KS, number of kernels per spike; PH, plant height; S, spring habit; SN, number of spikes per m²; TKW, thousand kernel weight; TW, test weight; W, winter habit; Y, year.

*, **, and *** indicate significance at $p = 0.05$, 0.01, and 0.001, respectively.

TABLE 2 Mean values and standard deviation of the evaluated traits separated by growth habit and year.

Trait	Winter habit		Spring habit	
	2021	2022	2021	2022
KS	14.6 ± 5.9	13.7 ± 5.1	13.7 ± 4.3	13.8 ± 4.0a
SN (m ⁻²)	480 ± 155a	340 ± 136b	458 ± 151a	331 ± 91b
GY (kg ha ⁻¹)	2511 ± 944a	1331 ± 5504c	2162 ± 850b	1284 ± 453c
BW (kg ha ⁻¹)	9025 ± 2604a	7068 ± 2412b	8509 ± 2619a	7455 ± 1771b
HI	0.19 ± 0.05a	0.14 ± 0.04c	0.18 ± 0.04b	0.13 ± 0.03d
TKW (g)	37.8 ± 4.8a	30.7 ± 4.5c	35.7 ± 5.5b	28.8 ± 4.7d
TW (kg hL ⁻¹)	77.9 ± 3.4c	84.2 ± 3.0a	77.0 ± 4.4c	82.8 ± 3.6b
DH	123 ± 5a	123 ± 5a	120 ± 8b	119 ± 7c
PH (cm)	131 ± 17a	118 ± 13b	130 ± 15a	116 ± 14b

Note: For each trait, different letters between columns indicate significant differences ($p = 0.05$).

Abbreviations: BW, biomass weight; DH, days to heading; GY, grain yield; HI, harvest index; KS, number of kernels per spike; PH, plant height; SN, number of spikes per m²; TKW, thousand kernel weight; TW, test weight.

evaluated agronomic traits. The effect of GH was less pronounced, but it significantly influenced GY, HI, TKW, TW, and DH, with winter genotypes displaying higher values than spring types.

Although the growth habit × year interaction was not statistically significant for any trait, mean values separated by GH and year (Table 2) indicated that the superiority of winter over spring genotypes in GY and TW was significant only in 2021 and 2022, respectively. Notably, DH was higher in 2021 than in 2022 only for spring genotypes. In terms of thermal time, winter genotypes exhibited a longer average pre-heading period than spring genotypes, with values of 1074 and 1032 GDD, respectively (Table S1).

When winter and spring types were analyzed separately, the ANOVA results were similar to those obtained when all

landraces were analyzed together, particularly concerning the effects of year and genotype on the traits studied (Table S2). However, among the winter genotypes, no significant differences were observed in SN, as the genotype effect was not significant.

The combined effect of genetic population and year was also examined (Table 3). Populations showed significant effects on all traits except SN. Overall, the effect of year was stronger than that of population, except for KS and DH, where the year effect was not significant. Among populations, Pop 3 had the highest yield and TW, along with favorable values for TKW, BW, and HI. However, this superiority was mainly evident in 2021 (Table S3). Comparisons between Tables 1 and 3 showed that the population effect was greater than that of GH for all the variables analyzed.

TABLE 3 Sum of squares for the effects of population and year, and their interactions on the evaluated agronomic traits. Mean values of the four genetic populations are presented.

Source of variation	Sum of squares (%)								
	KS	SN (m ⁻²)	GY (kg ha ⁻¹)	BW (kg ha ⁻¹)	HI	TKW (g)	TW (kg hL ⁻¹)	DH	PH (cm)
Pop	19.5***	1.5	10.0***	3.9*	6.7***	5.7**	11.8***	11.7***	4.4*
Pop 1	10.1c	442	1,543c	7,991ab	0.14b	34.9a	80.0b	126a	130a
Pop 2	15.1a	395	1,884b	8,092ab	0.17a	32.5b	81.1b	119b	123bc
Pop 3	16.9a	410	2,492a	9,260a	0.18a	36.5a	83.5a	119b	129ab
Pop 4	12.3b	383	1,501c	7,390b	0.15b	31.7b	78.2c	122b	120c
Y	0.7	11.5***	25.0***	7.4***	15.6***	22.4***	25.8***	0.0	11.2***
Pop × Y	1.7	0.6	1.7	0.9	0.4	0.6	1.1	0.5	1.3

Note: Means followed by different letters are significantly different at $p = 0.05$.

Abbreviations: BW, biomass weight; DH, days to heading; GY, grain yield; HI, harvest index; KS, number of kernels per spike; PH, plant height; Pop, population; SN, number of spikes per m²; TKW, thousand kernel weight; TW, test weight; W, winter habit; Y, year.

*, **, and *** indicate significance at $p = 0.05$, 0.01, and 0.001, respectively.

TABLE 4 Sum of squares for the significant effects of GS2A locus and year on the evaluated agronomic traits. Mean values of the two GS2A alleles *NoDel* and *Del* are presented.

Source of variation	Sum of squares (%)			
	KS	GY (kg ha ⁻¹)	HI	TW (kg hL ⁻¹)
GS2A	4.7**	3.0**	2.3**	2.8**
<i>NoDel</i>	14.7a	1,901a	0.17a	81.1a
<i>Del</i>	12.6b	1,595b	0.15b	79.6b
Year	0.1	31.3***	27.3***	43.0***

Note: Means followed by different letters are significantly different at $p = 0.05$.

Abbreviations: GY, grain yield; HI, harvest index; KS, number of kernels per spike; TW, test weight.

*, **, and *** indicate significance at $p = 0.05$, 0.01, and 0.001, respectively.

Furthermore, differences in allele frequencies of the GS genes *GS1A*, *GS2A*, and *GS2D*, previously characterized by Pascual et al. (2023), were examined between the two types of GHs. The analysis revealed that winter wheats had a significantly higher frequency of the *NoDel* allele at *GS2A* (71% in winter vs. 57% in spring; $\chi^2 = 3.93$, $p < 0.05$), while no significant differences were observed for the *GS1A* and *GS2D* alleles. The *NoDel* allele at *GS2A* was associated with positive effects on KS, GY, HI, and TW, compared to the *Del* allele (Table 4).

3.3 | Impact of agronomic traits on yield performance in winter and spring landraces

Multivariate PCA analysis was conducted to explore the relations between agronomic traits and yield in winter and spring genotypes (Figure 2). PCA biplots were generated separately for winter and spring genotypes in each year. The first two principal components accounted for between 64% of the total variance (for winter types in 2022) and 57% (for spring types in 2021).

Overall, BW, TW, and SN were the traits most strongly associated with GY in the tested landraces, except for winter types in 2021, where the influence of KS (positive), DH (negative), and PH (negative) on GY was more pronounced (Figure 2a,b). In spring wheats, GY was also positively associated with KS in both years, and negatively associated with DH in 2022; however, the influence of both traits on GY was limited (Figure 2c,d). KS was negatively associated with DH regardless of year or GH. PH was closely associated with GY in the winter types in both years, albeit with opposite signs (negative in 2021 and positive in 2022), whereas it was unrelated in the spring wheats.

3.4 | Yield stability of the landraces

The yield stability of the 94 genotypes was evaluated based on their GY-Pi values across the two environments (Table S4). On average, Pi values were lower for winter genotypes (3307×10^3) than for spring genotypes (3854×10^3), indicating greater yield stability in the winter genotypes. In 2021,

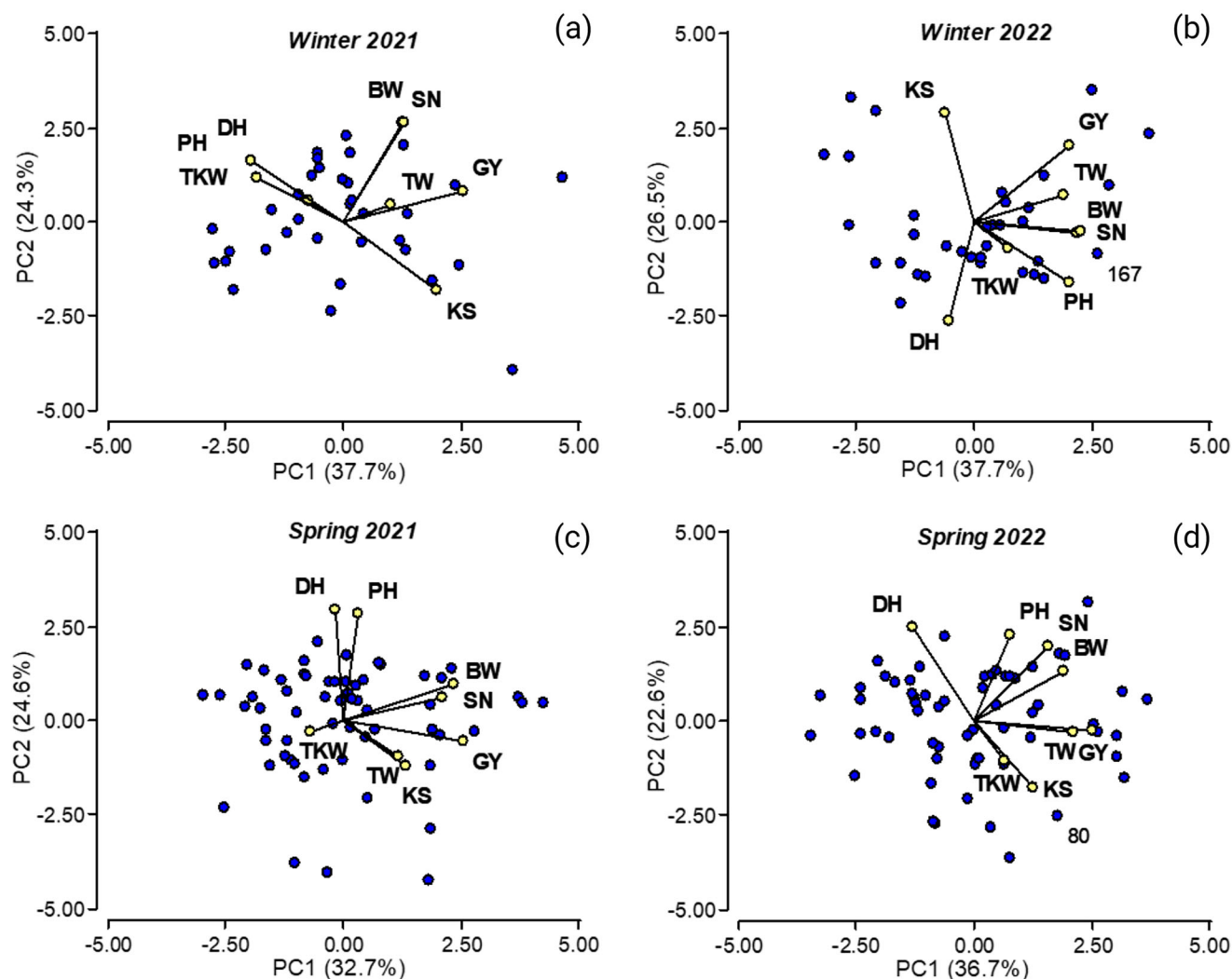


FIGURE 2 Principal components analysis biplots of the first and second principal components (PC1 and PC2) of the landraces based on the agronomic traits. (a) winter genotypes in 2021, (b) winter genotypes in 2022, (c) spring genotypes in 2021, and (d) spring genotypes in 2022. BW, biomass weight; DH, days to heading; GY, grain yield; HI, harvest index; KS, number of kernels per spike; PH, plant height; SN, number of spikes per m²; TKW, thousand kernel weight; TW, test weight.

winter landraces also showed lower Pi values (5220×10^3 in winter vs. 6284×10^3 in spring), confirming their superior performance under that year's conditions, while in 2022, Pi values were comparable between winter and spring types (1394×10^3 vs. 1424×10^3). The GY-Pi values were also calculated for each genetic population (Table S5). Based on these values, Pop 3 was the most stable for GY and outperformed the other populations, whereas Pop 4 showed the least stability.

Based on Pi values, several winter and spring landraces were identified among the 15 top genotypes for yield performance (high and stable GY) in both years. Noteworthy winter accessions included BGE052284 “Aragones” and BGE052289 “Amorebieta y Gordejuela,” while spring accessions BGE052225 “Trigo tremesino,” BGE052231 (no local name), and BGE052283 “Cabezorro” also ranked among the best landraces.

3.5 | Effect of growth habit on technological quality

The analyses of the glutenin composition of the landraces (Table S1), as reported in López-Fernández et al. (2021), revealed significant differences in the *GLU-A1* alleles between both GHs ($\chi^2 = 12.96$, $p < 0.01$). The *y* allele was more frequent in spring genotypes (35% vs. 3%), whereas the *a* allele was more common in winter genotypes (18% vs. 8%) (Table S1). In contrast, the differences for *GLU-B1* and *GLU-D1* alleles were not significant ($\chi^2 = 19.45$ and 11.35 , respectively; $p > 0.05$), although *Glu-B1f* and *Glu-D1a* were more common in spring genotypes (25% vs. 9%, and 77% vs. 53%), while *Glu-B1e* and *Glu-D1c* predominated in winter genotypes (65% vs. 32%, and 41% vs. 15%) (Table S1).

Mean comparisons between years indicated that SDSS test and protein content values were higher in 2021 for both GHs.

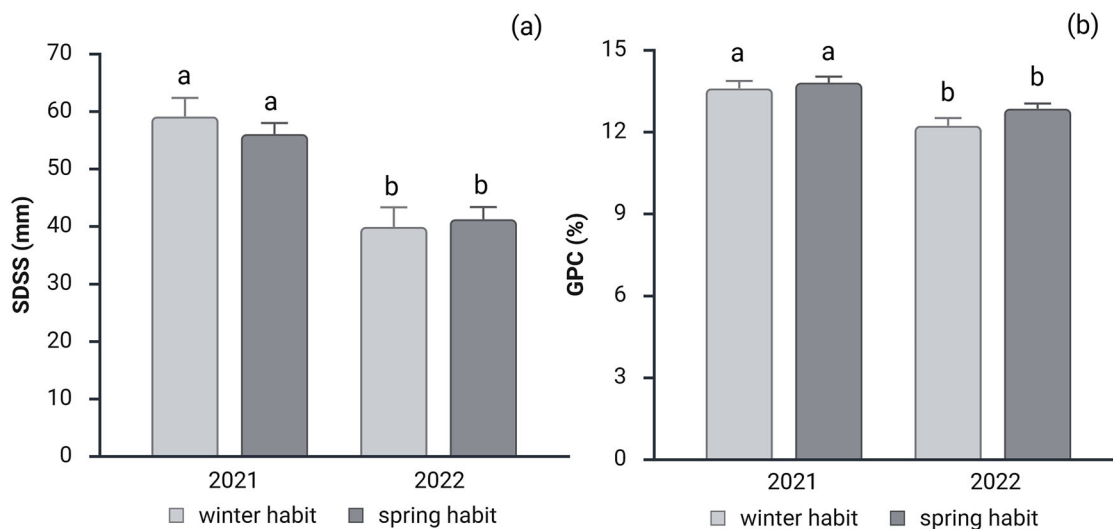


FIGURE 3 Effect of year and growth habit on the quality parameters (a) sodium dodecyl sulfate sedimentation (SDSS) test and (b) grain protein content (GPC). Means followed by different letters are significantly different at 5% level. The error bars indicate standard error.

Comparisons between winter and spring genotypes revealed no significant differences in any year (Figure 3).

4 | DISCUSSION

The diverse climatic conditions in Spain have promoted the adaptation of both spring and winter wheat landraces. In these landraces, GH is primarily regulated by vernalization *VRN1* homoeologous loci. In our study, all winter landraces carried the recessive *vrn-1* alleles, which are associated with delayed heading (Giménez et al., 2025; Royo et al., 2020). In contrast, spring landraces possessed the dominant *VRN1* alleles, which were absent in winter types. Both winter and spring genotypes mainly carried the photoperiod-sensitive *ppd-B1* allele, which was unrelated to GH (Giménez et al., 2025). Average heading occurred in mid-spring, around early May, with spring landraces heading a few days earlier than winter types. This observation aligns with previous findings showing that spring wheats with similar photoperiod sensitivity to winter types tend to have earlier heading under long-day conditions (Košner & Žůrková, 1996). Consequently, winter landraces exhibited a longer vegetative period (Pinthus, 1967; Thorup-Kristensen et al., 2009).

In addition to DH, other relevant agronomic traits were affected by GH. Overall, winter landraces displayed higher values of GY, HI, TKW, and TW. These findings are consistent with previous studies reporting that winter wheats generally outperform spring wheats in terms of yield and HI (Bektas et al., 2016; Ye et al., 2017). However, other authors have found no significant effect of GH on TKW (Pirevatlou et al., 2011).

4.1 | Impact of the climatic conditions on yield performance in winter and spring landraces

The two cropping seasons evaluated in this study showed contrasting climatic conditions, which is quite typical of dry Mediterranean regions characterized by erratic amounts and distribution of rainfall (Guijarro-Real et al., 2025; Lázaro et al., 2001). These irregular weather conditions led to a wide range in mean yields, from 324 kg ha⁻¹ in 2022, the environment with the lowest water input, to 5606 kg ha⁻¹ in 2021, which had the highest water input during grain filling. Despite these environmental differences, genotype performance remained stable across seasons at the central location tested (genotype × environment interaction [GEI], i.e., genotype × year, was not significant for any of the traits evaluated).

The first year was characterized by a higher accumulation of GDD until heading than in 2022 (LGS_{BH}: 1075 GDD in 2021 vs. 1010 GDD in 2022), along with increased humidity and milder temperatures during the reproductive phase. These conditions favored spike and grain development (Rezzouk et al., 2023; Royo et al., 2006; Sánchez-García et al., 2012), positively influencing GY. Winter genotypes were better able to exploit these favorable conditions than spring genotypes, showing superior performance in GY, HI, and TKW in agreement with other studies (Sánchez-García et al., 2012; Ruiz et al., 2019). Their longer vegetative period, likely a result of vernalization requirements, may have helped avoid late frost damage during spike formation, which likely affected grain development in the spring landraces (Mosaad et al., 2008).

The PCA analyses revealed that, in 2021, winter landraces with early heading, lower plant height, and higher KS achieved better yield performance. Notably, the negative impact of late heading was particularly relevant in this case, which seemed to be due to the strong negative correlation between KS and DH in 2021 ($r = -0.66$, $p < 0.0001$). Given the strong genotypic effect on these traits (PH, DH, and KS), selecting winter landraces adapted to 2021 conditions appears to be relatively straightforward. In contrast, in spring wheats, BW was the trait that influenced the most on GY in 2021, whereas DH and PH were unrelated to GY. Other studies (Guijarro-Real et al., 2025; Sánchez-García et al., 2012) showed that high minimum temperatures and elevated thermal time before heading enhance KS in spring landraces more than in winter landraces. However, in our study, spring landraces did not surpass winter types in KS under the higher LGS_{BH} of 2021. This is likely because, in Mediterranean continental regions, increased thermal time results mainly from a longer vegetative period, rather than from higher pre-heading temperatures, as is common in southern locations and is known to have a positive effect on KS (Guijarro-Real et al., 2025).

The second year was characterized by a particularly dry and hot spring, subjecting wheat plants to combined drought and heat stress. As previously reported (Guijarro-Real et al., 2025), 2022 was an unfavorable environment for GY. These conditions favored an increase in TW, and a reduction in DH and LGS_{BH} . TW, a measure of grain density, is commonly used as a predictor of flour extraction efficiency (Gibson et al., 1998). The influence of water regime during the ripening period on TW is well-documented (Sánchez-García et al., 2015). Our findings align with previous studies, which indicate that TW tends to decrease with increased rainfall and later maturity, and increase under drought conditions and earlier maturity (Çeçen et al., 2024; Rharrabti et al., 2001; Saint Pierre et al., 2008).

Higher ambient temperatures under long days are known to accelerate the transition to the reproductive stage (Hemming et al., 2012). A shortened pre-flowering period may enable plants to escape terminal stresses during grain filling, which are known to adversely affect GY (Rezzouk et al., 2023; Royo et al., 2006). However, this reduction in vegetative duration was not observed in the evaluated winter wheat genotypes, which exhibited similar DH values in both years. Despite their shorter crop cycle, spring wheats did not show a clear advantage over winter wheats in 2022, although both GHs exhibited distinct yield-enhancement strategies. Earliness provided a slight benefit for GY in the selection of spring landraces adapted to stress conditions. In contrast, earliness had a negligible impact on GY in winter landraces under the same conditions, with other agronomic traits playing a more significant role in determining yield performance. Overall, wheats with higher biomass, TW, and SN performed better,

regardless of their GH. Previous research has highlighted the spike number trait as a key yield component, serving as an important source of carbon and nitrogen during grain filling, thereby contributing to yield and facilitating adaptation to Mediterranean environments (Vicente et al., 2018). Among the spring landraces, those with higher KS showed superior adaptation, whereas this trait had little influence on yield in winter wheats, likely due to delayed heading and the resulting exposure to high temperatures in June, which negatively impacted KS (Rezzouk et al., 2023).

Vegetative growth, as measured by BW, played a more critical role in GY performance of winter wheats under the 2022 stress conditions. Additionally, winter taller landraces performed better, consistent with the strong correlation found between PH and BW in this and other studies (Slafer & Araus, 2007). Taller genotypes are generally better adapted to arid and semiarid environments, where greater vegetative biomass and thus increased reserves for grain filling can contribute to improving yield stability (Lopes et al., 2014; Slafer & Araus, 2007). Although BW has been shown to positively influence GY under drought and heat stress conditions (Landi et al., 2017; Lopes et al., 2015), vegetative development, especially PH, was less relevant for GY in spring wheats. Nevertheless, PH remains a valuable trait for breeding, due to its association with yield, biomass, lodging resistance, and drought tolerance, a factor of increasing importance under future climate scenarios (Lopes et al., 2014).

It is worth noting that winter landraces had better TW values than spring landraces in 2022, which contributed positively to GY. The positive relation between LGS_{BH} and TW (Rharrabti et al., 2001) may have conferred an advantage for winter types under these conditions. Other research has also highlighted the importance of TW as a key trait for selecting drought-tolerant genotypes (Mokhtari et al., 2022), in addition to its relevance as a parameter for industrial quality.

4.2 | Genotypic differences between winter and spring wheats

The strong effect of genotype on all agronomic traits, except for BW, revealed that a substantial portion of the phenotypic variation in the analyzed landraces is constitutive, accounting for over 40% of the variation. This highlights the high potential of the Spanish wheat gene pool for the identification and selection of favorable agronomic traits. This set of landraces was previously characterized at the genomic level, and the accessions clustered into four genetic populations, each representing a different gene pool (Pascual, Ruiz et al., 2020). These genetic populations partially explained the genotypic differences observed among landraces for most traits, with the exception of SN. Nonetheless, there remain genetic

factors influencing the analyzed traits that are not captured by population structure alone.

Some populations included both GHs, suggesting a relatively high genetic similarity between winter and spring types, and highlighting the complex genetic architecture underlying flowering-time regulation in wheat. Previous studies have also reported low genetic differentiation between both GHs (Cavanagh et al., 2013; Sánchez-García et al., 2015), noting that the spring GH can arise from independent mutations in multiple genes (Zhang et al., 2008). These findings are consistent with the limited overlap observed between highly differentiated SNPs and candidate flowering-time loci (Cavanagh et al., 2013). However, certain populations, such as Pop 3 and Pop 4, exhibited a high frequency (approximately 90%) of a single GH, reflecting a degree of genetic differentiation related to GH and potentially to flowering-time genes within these landraces.

Interestingly, Pop 3 and Pop 4 showed the highest and lowest GY-performance, respectively, and were also the most genetically distinct from modern cultivars (Pascual, Ruiz, et al., 2020). Pop 3 exhibited greater yield stability, particularly in 2021, which aligns with the predominance of winter GH in this group. Additionally, landraces in Pop 3 displayed higher protein content and TKW values (López-Fernández et al., 2021). This population also had the lowest genetic diversity and harbored low-diversity genomic regions on several chromosomes, likely reflecting historical selection for adaptive traits suited to Spanish agro-environmental conditions (Pascual, Ruiz, et al., 2020).

Our study showed that Spanish winter landraces differed from the spring ones in the higher frequency of the *NoDel* allele compared to the *Del* allele at the GS *GS2A* gene. The *NoDel* allele was associated with higher values of GY and the yield components KS and TW, both associated with a better performance of winter habit in 2021. These results are consistent with the high frequency of the *NoDel* allele in Pop 3 and a much lower frequency in Pop 4 found in this study and by Pascual et al. (2023). These results support the existence of distinct gene pools within Spanish wheat landraces, offering valuable genetic resources for future wheat improvement programs.

4.3 | Relation between growth habit and technological quality

Analysis of the association between GH and glutenin composition affecting gluten quality showed increased variability among spring varieties, largely attributable to unique alleles present in a single genotype. For *GLU-D1*, the locus with the greatest influence on end-use quality (López-Fernández et al., 2021), no significant differences were found between spring and winter GHs. At the *GLU-A1* and *GLU-B1* loci, differences

were observed in the distribution of certain alleles positively associated with gluten quality. Specifically, *Glu-A1y* and *Glu-B1f* were more frequent in spring genotypes, whereas *Glu-A1a* was more common in winter genotypes. Overall, these findings suggest no consistent advantage of one GH over the other in relation to the presence of favorable *GLU-I* glutenin alleles. This conclusion aligns with the similar gluten strength associated with both GHs in the samples analyzed. Comparable results were observed when analyzing the SDSS test values reported by López-Fernández et al. (2021), which included 189 landraces (44 mm for winter vs. 51 mm for spring, t -test = 1.61, p = 0.11). Additionally, no significant effect of the habit on protein content was detected. In contrast to our results, other studies have reported that spring types showed higher values for both SDSS and protein content than winter types (Chung et al., 2003; Maghirang et al., 2006).

4.4 | Yield stability according growth habit

An important objective in the use of landraces for cultivation is to identify and select genotypes that combine high yield potential with stability across a range of environmental conditions. Landraces have undergone long-term adaptation to specific local environments over centuries, and these adaptive processes largely predate the current dynamics of climate change. Nevertheless, their present behavior likely reflects both their historical adaptation and their intrinsic capacity to cope with the increasingly warmer and more erratic conditions now affecting Mediterranean environments. This underscores the need to select landraces that consistently perform well in diverse environments, demonstrating both adaptability and resilience. Therefore, evaluating landrace performance across contrasting growing seasons provides valuable insights into their resilience, their potential contribution to input reduction in agricultural systems, and their relevance for addressing the challenges posed by ongoing global warming. In this study, winter landraces generally exhibited greater yield stability across the two contrasting environments, as reflected by their lower Pi values. In modern varieties, Sánchez-García et al. (2012) similarly reported that GEI for yield was less pronounced in winter cultivars than in spring types. Modern winter varieties demonstrated broader adaptation, largely attributed to the consistent expression of KS. In contrast, modern spring varieties showed greater stability for TKW, probably because of their earliness to avoid terminal stresses.

There is growing interest in identifying varieties adapted to low-input and organic farming systems. Notably, improved cultivars tend to include a higher proportion of spring types than winter types (Sun et al., 2009). In this context, several countries have launched breeding programs targeting winter wheat (Lammerts van Bueren et al., 2011). Winter

wheat varieties have also been reported to carry a higher frequency of disease resistance alleles (Lai et al., 2024; Ye et al., 2017). Furthermore, the presence of winter *vrn* alleles has been linked to enhanced root development, in addition to their key role in regulating GH. Winter wheats with extended vegetative periods generally develop larger root systems that improve water and nutrient uptake, a trait less prevalent in spring types (Hamada et al., 2012; Thorup-Kristensen et al., 2009; Voss-Fels et al., 2018).

Our results identified a group of varieties that ranked among the best- yielding and stable across the two growing seasons. Most of these genotypes originated from the northern or central regions of the country, in agreement with previous findings (Guijarro-Real et al., 2025). Among them, the landrace BGE052283 “Cabezorro” has previously shown strong performance and stability in a southern environment (Guijarro-Real et al., 2025). Particularly remarkable was the winter accession BGE052284 “Aragones,” which achieved the highest GY in the harsh, drought-prone 2022 cropping season. This landrace is closely related to Aragón 03, a traditional variety recently reintroduced for its excellent adaptation to Mediterranean continental conditions. Consistent with previous findings for spring landraces (Guijarro-Real et al., 2025), the five selected landraces outperformed the modern spring cultivar “Califa Sur” in 2022. While this study offers an initial insight into varietal stability, our findings should be interpreted with caution. The stability results rely on the observations made during only two cropping seasons at one site, which, inevitably, represents a limitation. Further studies across more locations and years will be required to verify the stability of these varieties under broader conditions.

5 | CONCLUSIONS

A key requirement for the use of landraces in sustainable farming systems is their capacity to deliver both high yield potential and stable performance across diverse environmental conditions. Our results indicated that, when cultivating landraces in continental Mediterranean regions, GH is an important factor to consider, as winter and spring types respond differently to agroclimatic variability. Both GH types differed not only in yield and some yield-related traits but also in specific genetic factors, such as allelic variation in GS genes. Overall, winter landraces showed superior yield performance over spring types. However, selecting the most suitable variety within each GH type remains essential, as genotype played a major role in overall performance. Consequently, both winter and spring landraces with promising levels of stability and adaptation can be selected. The selection of optimal agrotypes varied depending on both GH and environmental conditions. In dry and hot environments, selection should prioritize landraces with greater biomass and spike

number, while earliness may also be advantageous in spring types. Under conditions of higher water availability, winter landraces that headed earlier and had shorter height achieved superior performance. Although technological quality did not differ markedly between GHs, winter types exhibited higher TW, a trait strongly correlated with yield across both seasons but also relevant for commercial grain quality. The genetic differences observed among the analyzed populations representing distinct gene pools provide valuable information to guide the selection of promising accessions for breeding and sustainable cultivation.

AUTHOR CONTRIBUTIONS

Magdalena Ruiz: Conceptualization; formal analysis; funding acquisition; resources; writing—original draft; writing—review and editing. **Diana Martin-Lammerding:** Data curation; formal analysis; methodology; writing—review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Most of the data are included in the [Supporting Information](#). Raw data will be made available on request.

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SUPPORTING INFORMATION

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