Field Crops Research 344 (2026) 110512

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Field pea breeding for integrated adaptation to biotic and abiotic stresses in Mediterranean rainfed agrosystems

Manuel Alejandro Jiménez-Vaquero [a,b,*], Fernando Flores [c], Maria José Cobos [a], Diego Rubiales [a]

[a] *Institute for Sustainable Agriculture, Spanish National Research Council (IAS-CSIC), Córdoba, Spain*
[b] *Programa de Doctorado de Ingeniería Agraria, Alimentaria, Forestal y de Desarrollo Rural Sostenible, Universidad de Córdoba, Córdoba, Spain*
[c] *Departamento de Ciencias Agroforestales, E.T.S.I., Universidad de Huelva, Huelva, Spain*

ARTICLE INFO

Dataset link: Agronomic, phenology, and disease data from rainfed field pea trials in Córdoba (Spain)

Keywords:
Pisum sativum
Orobanche crenata
Legume breeding
Yield stability
Stress resistance
Mediterranean agriculture
MGIDI

ABSTRACT

Context: Improving adaptation of field pea (*Pisum sativum* L.) to Mediterranean rainfed systems requires considering the combined effects of climate factors and key biotic constraints, including parasitic weeds like broomrape (*Oc*) and foliar diseases such as powdery mildew and Ascochyta blight. However, the combination of these stresses remain insufficiently understood.
Objectives: To quantify and compare the performance, stability, and response to stresses of novel pea breeding lines; to identify agronomic and climatic predictors of yield; and to guide pea breeding for adaptation to Mediterranean rainfed systems.
Methods: In this study, nine advanced pea breeding lines developed under the IAS-CSIC breeding programme were compared with five commercial cultivars in multi-environment trials across three seasons. Agronomic, phenological, and disease-related traits were assessed and analysed using Genotype×Environment (G×E) and multivariate approaches to address yield stability and to inform selection under biotic and abiotic stresses.
Results: Among the biotic constraints, *Oc* had the strongest negative impact on grain yield. Higher levels of *Oc* parasitism were favoured by spring rainfall and high temperatures, thereby altering crop–environment interactions. IAS-CSIC breeding lines showed superior resistance to *Oc*, with approximately 50% fewer *Oc* shoots per plant than commercial cultivars. Consequently, they achieved higher yields in *Oc*-infested environments (1742 vs 743 kg ha^{-1}). They also showed higher yields in *Oc*-free environments (3435 vs 2803 kg ha^{-1}), highlighting consistent productivity and successful adaptation to Mediterranean rainfed systems. In *Oc*-free environments, abiotic-stress indices indicated that several breeding lines showed better yield maintenance than commercial cultivars under drier, hotter spring conditions. Rainfall showed beneficial or detrimental impacts on yield depending on the presence or absence of *Oc*. Several agronomic traits (i.e., plant height, crop appearance, lodging, and thermal time during pod filling) were consistent predictors of yield. The impact of powdery mildew on yield was limited under the studied conditions with several lines showing complete resistance. Multi-trait selection enabled the identification of breeding lines combining improved *Oc* resistance with yield stability and no trade-offs in agronomic traits or in response to other biotic stresses, particularly Cartujano, Chicana, and Pepapea.
Conclusions and significance: Altogether, our results provide practical recommendations for growers in the Mediterranean region and methodological guidance for breeders. These findings illustrate the utility of combining resistance introgression, multi-trait selection, and trait-informed modelling as complementary strategies. This integrative framework may also support genetic improvement for adaptation to environments distinct from the original breeding context and exposed to diverse, and novel stresses.

---

* Corresponding author.
E-mail addresses: majimenez@ias.csic.es (M.A. Jiménez-Vaquero), fflores@dcaf.uhu.es (F. Flores), mjcobos@ias.csic.es (M.J. Cobos), diego.rubiales@ias.csic.es (D. Rubiales).

https://doi.org/10.1016/j.fcr.2026.110512
Received 13 September 2025; Received in revised form 16 April 2026; Accepted 21 April 2026

1. Introduction

Grain legumes are multifunctional annual crops with widely acknowledged importance for agriculture and the environment, notably by improving soil fertility (Sinclair and Vadez, 2012; Stagnari et al., 2017). Although legumes were previously well established in European agriculture, their cultivation has progressively decreased. In fact, other crops that have adapted more readily to technological progress and are more profitable for farmers in the short term have often replaced legumes in crop rotations (Magrini et al., 2016). At the same time, demand for protein crops in the animal-feed sector is increasing, but domestic production is insufficient to meet it (van Loon et al., 2023). Today the leading crop in the feed industry is soybean (*Glycine max* (L.) Merr.), but field peas (*Pisum sativum* L.) also have great potential for feed use. Manufacturers are increasingly willing to include higher proportions of pea in their feed formulations, but this will depend on a stable supply. Although peas have long been cultivated in Europe, their cultivation is now recovering rapidly after decades of decline. In the 2022–2023 season, field pea represented 23% of the total acreage devoted to grain and forage legumes in Europe (i.e., 2.9 out of 12.7 Mha) according to FAO (2025). In Spain, 171,259 ha of peas for dry seed production were grown in 2022–2023, making field pea the largest legume crop by cultivated area (Ministerio de Agricultura, Pesca y Alimentación, 2023). Nevertheless, despite this marked increase, field pea cultivation remains far below current demand, forcing large imports to satisfy the industrial requirements. Therefore, field pea acreage is likely to continue increasing in coming years to meet market needs demand and growing societal interest in the environmental benefits of legume cultivation.

The Mediterranean region is characterised by rainy and mild winters, with dry and warm springs, which favours the autumn sowing of spring-type pea cultivars to benefit from winter rainfall and avoid terminal drought and heat in late spring (Flores et al., 2012; Rubiales et al., 2009). The predicted impacts of global warming in the Mediterranean region are particularly severe, involving wider year-to-year variation in rainfall and temperature patterns, with extreme and prolonged droughts and heat waves (Urdiales-Flores et al., 2023). This raises the question of whether the breeding sector is ready to provide farmers with well-adapted cultivars that meet agronomic and market needs. In this context, substantial breeding effort is needed to improve field pea adaptation to Mediterranean rainfed farming systems and their associated biotic and abiotic stresses (Annicchiarico et al., 2017; Rubiales et al., 2021, 2023). Moreover, specific local constraints must be addressed to ensure broad adaptation and high productivity. The major abiotic stresses constraining pea production worldwide are drought (Bagheri et al., 2023) and heat stress during flowering and pod filling (Tafesse et al., 2021; Devi et al., 2023). Accordingly, improving tolerance to these stresses remains a key priority in field pea breeding programmes, particularly for Mediterranean environments (Annicchiarico et al., 2025). In these systems, major biotic constraints affecting pea include foliar fungal diseases such as rust (*Uromyces pisi* (Pers.) de Bary), Ascochyta blight (*Didymella pinodes* (Berk. & A. Bloxam) Petr.; *Ascochyta pisi* Lib.; *Didymella pinodella* (L.K. Jones) Q. Chen & L. Cai), and powdery mildew (*Erysiphe pisi* (DC.) St-Amans; *Erysiphe trifolii* Grev.), as well as pests such as the pea aphid (*Acyrthosiphon pisum* (Harris)) and pea weevils (*Sitona lineatus* (L.) and *Bruchus pisorum* (L.)). In addition, parasitic weeds such as broomrape (*Oc*, *Orobanche crenata* Forsk.,) constitute a key constraint in the region (Rubiales et al., 2009, 2019). Effective breeding to address these constraints requires a better understanding of the biology and genetic diversity of the causal agents and their interactions with the plant.

Within the breeding programme conducted at IAS-CSIC in Córdoba (South Spain), long-term efforts have focused on incorporating resistance to *Oc*, powdery mildew and Ascochyta blight into field pea breeding lines. For this purpose, resistant accessions, elite cultivars and locally adapted breeding lines were used as parental material. Repeated rounds of intra- and interspecific hybridisation were carried out to combine the desired traits into early breeding lines. The resulting trait combinations were subsequently selected and fixed through stringent selection schemes under Mediterranean rainfed conditions (Fondevilla et al., 2017; Rubiales et al., 2009, 2021). The resulting homogeneous advanced lines enabled a detailed assessment of adaptation to Mediterranean rainfed conditions, responses to stress, and yield potential.

It is important to acknowledge the limitations commonly associated with trials conducted in local breeding programmes (e.g., unbalanced designs or contrasting climatic conditions between growing seasons). Consequently, the genotypic differences are often obscured by complex Genotype×Environment (G×E) interactions (Kang et al., 2020). To disentangle this complexity, linear mixed-effects models (LMMs) can be used to partition phenotypic variation into fixed- and random-effect components. When genotypes are treated as random effects, LMMs provide the random-effects matrix required to derive genotype predictions as best linear unbiased predictors (BLUPs) (Henderson, 1975; Searle et al., 2006). These BLUPs are characterised by shrinkage, which pulls estimates towards the mean and can improve predictive accuracy (Robinson, 1991).

We hypothesised that field pea lines bred and selected under Mediterranean rainfed conditions would show improved adaptation and productivity in *Oc*-infested environments compared with widely grown commercial cultivars developed in other regions for broad adaptation. We further hypothesised that *Oc* pressure would interact with seasonal climatic variability to shape crop performance. To test these hypotheses, our objectives were to partition genetic (G), environmental (E), and G×E sources of variation across trials; to quantify the performance and cross-environment stability of advanced lines and commercial cultivars across *Oc*-free and *Oc*-infested environments; to assess the ability of genotypes to maintain yield under abiotic stress in *Oc*-free environments; and to identify agronomic traits and climatic variables that contribute to the prediction of grain yield to inform selection within an integrated multi-trait framework.

2. Materials and methods

2.1. Plant material and experimental design

Nine advanced field pea breeding lines developed within the IAS-CSIC breeding programme were evaluated in multi-environment trials (Table 1). All lines had undergone more than seven generations of selfing and selection and were protected under the Plant Variety Protection status granted by the Spanish Office of Plant Variety Registration (OEVV). In addition, the five most popular commercial cultivars

Table 1
Breeding lines and check cultivars included in the study.

	Name	Genetic background
Breeding lines	Antojo	3064 // Messire / Pf660 / Ballet
	Cartujano	Ps624 / Messire / Cartouche // 3066 / Ps624 / Messire
	Chicana	Ps624 / Messire / Baccara // Chicarrón
	Chiruco	Ps624 / Messire / Baccara / Chicarrón // B99–100 / Messire / Pf660 / Ballet / Ps624 / Messire / Baccara / Babieca
	Forana	Franklin / Ps624 / Messire / B99–100 / Messire / Pf660 / Ballet // Viriato
	Jarana	3066 // Ps624 / Messire
	Pepapea	3062 // Messire / Pf660 / Ballet
	Pichita	3066 // Ps624 / Messire
	Tirana	Lifter // Messire / Pf660 / Baccara
		Country of origin
Check cultivars	Astronaute	Germany
	Chicarrón	Spain
	Enduro	France
	Kayanne	France
	Messire	France

available to farmers were included in the study as check cultivars due to their high yield potential and good adaptation to regional growing conditions.

Each genotype was sown in a 1 m^2 plot consisting of three parallel rows (spaced 35 cm apart and 1 m long) that served as experimental units for all trials. The 14 genotypes were arranged in a randomised complete block design (RCBD) with plots laid out in a grid and separated by 0.5 m. A sowing density of 45 seeds per plot was used. In each field, three independent blocks were arranged, each containing the same set of genotypes. Trials were conducted in two contrasting sets of field sites within the same experimental farm at Córdoba (Spain). These sets differed in their natural *Oc* infestation status: one comprised fields with high natural soil infestation (*Oc*-infested), whereas the other comprised fields free of infestation (*Oc*-free). Accordingly, *Oc* infestation status was treated as a predefined field condition, whereas foliar diseases were not imposed as controlled experimental factors, and their severities varied with seasonal disease pressure. This trial design was implemented across three growing seasons: 2021–2022 (with two distinct sowing dates), 2022–2023, and 2023–2024 (Table 2). All sowings took place in November or December (in accordance with standard local practices for cool-season legume cultivation), and were carried out under strictly rainfed conditions. Pendimethalin 45% was applied pre-emergence in all environments, and subsequent weed control was performed manually. In each growing season, a combination of deltamethrin 2.5% + fenpyroximate 5% was applied during early pod filling to control aphids and red mite pests.

2.2. Agronomic and phenological assessments

Throughout the crop cycle, flowering onset, pod-filling onset and plot senescence were recorded twice weekly by visual assessment. Senescence was defined as the date when the entire plot canopy (vegetative biomass and pods) had naturally dried down. Thermal time accumulation was calculated by combining these phenological assessments with regional weather data ('Red de Información Agroclimática de Andalucía' database, Instituto de Investigación y Formación Agraria y Pesquera). The daily degree-day increment (DD) was computed from daily maximum and minimum air temperatures as

$$DD = (Tmax + Tmin)/2 - \mathrm{Tbase},$$

where *Tmax* and *Tmin* are the daily maximum and minimum air temperatures, respectively, and Tbase is the base temperature; when (*Tmax* + *Tmin*)/2 was below Tbase, DD was set to 0. Growing degree days (GDD) were then obtained by summing daily DD values from the start to the end of a specific phenological window. A base temperature of Tbase = 2.9°C was used following Olivier and Annandale (1998) and Bourgeois et al. (2000). *Flowering GDD* (thermal accumulation from sowing to flowering onset) was used as the main indicator of phenological earliness in this study.

Crop *Appearance* was defined as a subjective trait established through discussions with participating farmers regarding the crop type they would visually select (Rubiales et al., 2021). It was evaluated on a 1–5 scale, integrating visual traits considered desirable by growers (e.g., erect growth habit, high vegetative density, high pod number per plant, and absence of chlorosis). *Lodging* was scored from 1 (completely erect plants) to 10 (fully lodged plants). *Plot height* was measured once at the beginning of pod filling as the maximum vertical canopy height (distance from soil surface to canopy top) within each plot. Foliar disease severities (*Powdery mildew DS* and *Ascochyta blight DS*) were assessed before senescence as the percentage of symptomatic plant biomass. In *Oc*-infested environments, *Oc* infection level was assessed at harvest by counting emerged *Oc* shoots within each plot and normalising by the number of pea plants to obtain the *Number of broomrapes/plant*. Total dry biomass was recorded at harvest by weighing the whole aboveground biomass of each plot after natural drying in the field, following complete plant senescence. After threshing, seed weight was also recorded, allowing the calculation of harvest index (*HI*) as the ratio of dry seed weight to total dry biomass, and grain yield (*GY*) as the dry seed yield extrapolated to kg ha^{-1}.

2.3. Statistical analysis

Statistical analyses were conducted to compare genotype performance across environments and to quantify how agronomic traits, climatic variables and biotic constraints were associated with yield within each *Oc* infestation condition. In this study, an environment was defined as a unique combination of season, sowing date where applicable, and field condition (*Oc* infestation status). Accordingly, eight environments were considered (Table 2). All analyses were performed in R version 4.3.3 (R Core Team, 2024). For the percentage data (i.e., *DS* variables), an arcsine square-root transformation was applied, and statistical analyses were performed on the transformed data.

2.3.1. Variance analyses

A combined analysis of variance was performed using the R package 'metan' version 1.19.0 (Olivoto and Lúcio, 2020) with all effects treated as random (random-effects ANOVA) to estimate the variance components for the main sources of variation and to detect G×E interactions. The data from all environments were subjected to the Shapiro-Wilk test for normality and Bartlett's test for homogeneity of variances.

2.3.2. Trait-specific genotype performance and stability

The weighted average of absolute scores from the singular value decomposition of the G×E interaction matrix of BLUPs (WAASB) was calculated using 'metan' version 1.19.0 (Olivoto and Lúcio, 2020) as a measure of stability for each agronomic trait across environments (Olivoto et al., 2019). Lower WAASB values indicate greater stability, whereas higher values indicate stronger G×E-driven variation. To visualise the relationship between WAASB the genotype performance for each trait, Trait×WAASB biplots were used.

2.3.3. Multi-trait genotype–ideotype distance index (MGIDI)

The MGIDI was computed using 'metan' version 1.19.0 (Olivoto and Lúcio, 2020) following the methodology of Olivoto and Nardino (2021) in four steps: trait rescaling, factor analysis, ideotype design, and calculation of the MGIDI index. To prioritise traits most closely

Table 2
Summary of the environments analysed, defined by a combination of cropping season/sowing date and field condition.

	Sown	Season	*O. crenata* (*Oc*) infestation status	Soil Type	Soil pH	Average T_{max} (°C)	Average T_{min} (°C)	Rainfall (mm)
CJ-NOV21	08 Nov.	2021–2022	*Oc*-infested	Luvisol	7.6 – 7.7	18.4	5.6	326
SJ-NOV21	08 Nov.	2021–2022	*Oc*-free	Luvisol	7.5 – 7.6	18.5	5.7	326
CJ-DIC21	08 Dec.	2021–2022	*Oc*-infested	Luvisol	7.6 – 7.7	18.9	6.2	316
SJ-DIC21	09 Dec.	2021–2022	*Oc*-free	Luvisol	7.5 – 7.6	18.9	6.3	316
CJ-22	28 Nov.	2022–2023	*Oc*-infested	Luvisol	7.6 – 7.7	18.5	5.7	304
SJ-22	30 Nov.	2022–2023	*Oc*-free	Luvisol	7.5 – 7.6	19.0	6.2	304
CJ-23	22 Nov.	2023–2024	*Oc*-infested	Luvisol	7.6 – 7.7	18.5	7.1	451
SJ-23	23 Nov.	2023–2024	*Oc*-free	Luvisol	7.5 – 7.6	19.1	7.5	461

associated with productivity, trait weights were derived from the Pearson correlation coefficient between each trait and *GY*. The ideotype was defined by assigning desirable target values to each trait, with 0 representing the least desirable expression and 100 the most desirable: *GY*, *HI*, *Plot height*, and *Appearance* were assigned higher target values, whereas *DS* variables, *Number of broomrapes*/plant, *Flowering GDD* and *Lodging* were given lower values.

2.3.4. Correlation analysis of agronomic traits, biotic constraints and climatic variables

Pearson correlations were used to describe associations between agronomic traits, biotic constraints recorded in the trials, and climatic variables. Daily weather data were obtained from the 'Red de Información Agroclimática de Andalucía' database (Instituto de Investigación y Formación Agraria y Pesquera) and summarised at two temporal scales: crop-cycle metrics, calculated over the full crop cycle from sowing to plot senescence; and stage-specific metrics, calculated over three phenological windows. These stages were "Flowering" (from sowing to flowering onset), "Flower–pod" (from flowering onset to pod-filling onset) and "Pod-filling" (from pod-filling onset to senescence). *Rainfall* and *GDD* variables were computed at both temporal scales. Relative humidity variables (*Hmin* and *Hmax*) were summarised only at the crop-cycle scale, whereas air temperature variables (*Tmin* and *Tmax*) were summarised only at the stage-specific scale. In addition, heat-extreme indices were computed as the number of consecutive days with $Tmax > 25°\mathrm{C}$ during Flower–pod (*Flower–pod_NDT>25*) and with $Tmax > 30°\mathrm{C}$ during Pod-filling (*Pod-filling_NDT>30*). Correlation matrices were visualised with the R package 'ggcorrplot' version 0.1.4.1 (Kassambara, 2025), with $p < 0.05$ as the significance threshold.

2.3.5. Abiotic stress-tolerance indices for GY under contrasting seasonal conditions

To characterise genotype performance under contrasting abiotic conditions, a set of widely used stress-tolerance indices was computed from *GY* data. Two *Oc*-free environments were selected based on their marked contrast in mean *GY* and post-flowering seasonal weather patterns (Supplementary Figure S1). SJ-NOV21 was treated as the reference favourable environment (*Yp*), whereas SJ-22 was treated as the stress-prone environment (*Ys*).

For each genotype i, Yp_i and Ys_i correspond to the environment-specific BLUP of *GY* in SJ-NOV21 and SJ-22, respectively. Stress intensity (*SI*) was calculated as

$$SI = 1 - \left(\frac{\overline{Ys}}{\overline{Yp}}\right),$$

where $\overline{Ys}$ and $\overline{Yp}$ are the mean *GY* across genotypes in the stress-prone and favourable environments, respectively.

Based on the contrasting yield data, the following indices were computed for each genotype (Fernandez, 1992; Rosielle and Hamblin, 1981; Fischer and Maurer, 1978; Gavuzzi et al., 1997; Schneider et al., 1997):

- Mean productivity (*MP*) $= \frac{Yp_i + Ys_i}{2}$
- Geometric mean productivity (*GMP*) $= \sqrt{Yp_i \cdot Ys_i}$
- Harmonic mean (*HARM*) $= \frac{2 \cdot (Yp_i \cdot Ys_i)}{Yp_i + Ys_i}$
- Yield index (*YI*) $= \frac{Ys_i}{\overline{Ys}}$
- Stress susceptibility index (*SSI*) $= \frac{1 - (Ys_i / Yp_i)}{SI}$
- Tolerance (*TOL*) $= Yp_i - Ys_i$
- Stress tolerance index (*STI*) $= \frac{Yp_i \cdot Ys_i}{\overline{Yp}^2}$

Higher values of *MP*, *GMP*, *HARM*, *YI* and *STI* indicated better performance across environments and/or under the stress-prone environment, and were assigned better (lower) ranks. Lower *SSI* and *TOL* values indicated a lower *GY* penalty in the stress-prone relative to the favourable environment and were also assigned better (lower) ranks. An overall rank (*RankMean*) was obtained as the arithmetic mean of ranks across indices.

2.3.6. Stepwise multiple linear regression modelling (SMLR) of GY using agronomic traits and climatic variables

To evaluate the influence of agronomic traits and climatic variables on *GY* across all genotypes and environments included in the study, an SMLR analysis was conducted using standardised variables (multi-environment z-scores). The general form of the model was

$$Y = X \cdot \beta + \varepsilon,$$

where Y is the response vector representing *GY* for n observations, X is the $n \times k$ matrix of predictor variables, β is the vector of regression coefficients, and ε is the vector of residuals.

The analysis was performed using the 'stepAIC' function from the R package 'MASS' version 7.3-65 (Venables and Ripley, 2002). To allow bidirectional variable selection, the 'stepAIC' function was configured with direction = "both", enabling both addition and removal of predictors (Venables and Ripley, 2002; Burdett and Wellen, 2022).

3. Results

3.1. Partitioning of phenotypic variance across environments

The analysis of key agronomic traits revealed distinct contributions of G, E, and G×E components to phenotypic variance (Fig. 1, Supplementary table S1). According to the random-effects ANOVA, their relative contributions differed across traits and environments. Environmental effects contributed strongly to the variance of traits such as *Flowering GDD* (54% of total phenotypic variance), *Lodging* (53%), and *Ascochyta blight* arcsin-*DS* (46%). For these traits, the relative contribution of variance components was similar in *Oc*-infested and *Oc*-free environments. However, this pattern was not observed for other traits. For *Powdery mildew* arcsin-*DS*, the environmental variance component increased from 10% in *Oc*-free to 46% in *Oc*-infested environments. For *GY*, the environmental variance component decreased from 52% in *Oc*-free to 12% in *Oc*-infested environments. For *HI*, the environmental variance component was 32% in *Oc*-free environments but non-significant in *Oc*-infested environments. For *Appearance*, the environmental contribution decreased from 28% in *Oc*-free to 13% in *Oc*-infested environments. Notably, *Powdery mildew* arcsin-*DS* showed the strongest genetic contribution across environments, especially under *Oc*-free conditions (74%). In *Oc*-infested trials, residual variance not explained by G, E, or G×E was relatively high for all traits, particularly for *Appearance*. The within-environment *Block* effect was also tested, but it did not contribute significantly to the variance for any trait (Supplementary tables S1, S2 and S3).

3.2. Genotypic performance and stability analysis for GY

Genotype performance within environments was predicted through BLUPs. Results for *GY* (shown in Table 3) were two- to four-fold higher in *Oc*-free than *Oc*-infested environments, with mean values of 3209 and 1385 kg ha^{-1}, respectively. An exception was 2022–2023, when *Oc*-free yields exceeded *Oc*-infested yields only by 231 kg ha^{-1} on average. All breeding lines outperformed the check cultivars under *Oc*-infested environmemts, although some did not do so in *Oc*-free environments (e.g., Pepapea and Tirana). The best-performing check cultivars were Kayanne and Messire. Among breeding lines, Antojo and Chicana showed the highest mean yields (3977 and 3967 kg ha^{-1} in *Oc*-free environments, and 2243 and 1858 kg ha^{-1} in *Oc*-infested environments, respectively). Cartujano achieved a yield of 1961 kg ha^{-1} under *Oc*-infested conditions, although its performance in *Oc*-free environments

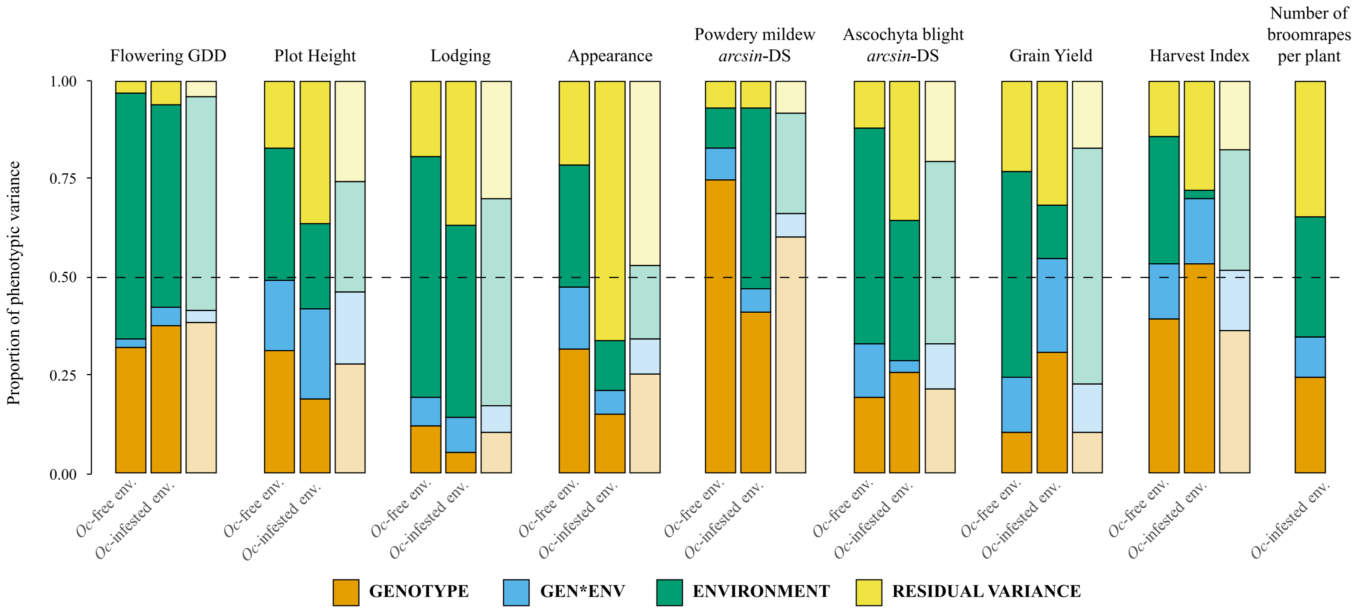

Fig. 1. Relative contribution of genetic (G), environmental (E), and G×E interaction components to the total variance of the traits evaluated in this study. The proportional contribution of each component is represented by the height of the corresponding coloured segment within each stacked bar. Results are shown for *Oc*-free environments, *Oc*-infested environments, and the combined dataset (third bar, shown in transparency). The trait *Number of broomrapes/plant* is displayed only for *Oc*-infested environments.

Table 3
Summary of *GY* values estimated as BLUPs across all tested environments for breeding lines and check cultivars.

Genotype		***Oc*-infested environments**					***Oc*-free environments**					***Genotype Mean***	**SE**
		CJ-NOV21	**CJ-DIC21**	**CJ-22**	**CJ-23**	***Mean***	**SJ-NOV21**	**SJ-DIC21**	**SJ-22**	**SJ-23**	***Mean***		
Breeding lines	Antojo	2871	2401	2828	871	2243	5461	5273	3252	1922	3977	3110	308
	Cartujano	1462	1722	2536	2124	1961	4712	3534	2384	2874	3376	2668	208
	Chicana	1263	1565	2865	1740	1858	5392	4484	2773	3291	3967	2913	284
	Chiruco	1696	1236	2766	1118	1704	5233	3927	2875	2321	3589	2646	275
	Forana	1191	2078	2325	1208	1700	5679	4804	2419	2040	3736	2718	322
	Jarana	1490	1274	2635	1902	1825	5775	3515	2506	2953	3687	2756	281
	Pepapea	2449	1652	2071	945	1779	5207	3504	2374	1581	3166	2473	263
	Pichita	1427	811	1817	1130	1296	3638	2216	1935	2616	2601	1949	178
	Tirana	1228	739	1737	1527	1308	3925	2528	2177	2649	2820	2064	197
	Mean	1675	1479	2398	1396	1742	5003	3754	2522	2464	3435	2589	
Check cultivars	Astronaute	415	523	1649	352	735	4353	3105	2014	1854	2831	1783	277
	Chicarrón	450	612	1579	431	768	5055	2678	1730	1645	2777	1772	302
	Enduro	309	185	731	148	343	3104	2107	1213	1147	1893	1118	205
	Kayanne	654	1213	1627	770	1066	4951	3547	2277	2744	3380	2223	292
	Messire	647	731	1446	390	803	4373	3808	1921	2427	3132	1968	292
	Mean	495	653	1406	418	743	4367	3049	1831	1964	2803	1773	
Environment Mean		1254	1196	2044	1047	1385	4776	3502	2275	2285	3209		

was closer to the overall mean.

GY stability was assessed at the genotype level using WAASB, which summarises the contribution of each genotype to the G×E interaction across environments. The *GY*×WAASB biplot shown in Fig. 2 illustrates the relationship between WAASB values and genotypic mean BLUPs for *GY*. Under *Oc*-free conditions, the breeding lines Chicana, Jarana, Chiruco, and Cartujano showed low WAASB along with high *GY* values (quadrant IV). Genotypes with high mean *GY* but poor cross-environment stability (quadrant II) included the breeding lines Antojo and Forana. The check cultivars Astronaute, Chicarrón and Enduro showed stable but only moderate *GY* (quadrant III). Notably, most breeding lines (i.e., Cartujano, Chicana, Pepapea, Jarana, Forana and Chiruco) fell within quadrant IV for *Oc*-infested environments.

The *GY*×WAASB biplot also differentiated environments according to their mean *GY* BLUPs and WAASB (Fig. 2). Among the *Oc*-free environments, SJ-DIC21 and SJ-23 showed the highest WAASB values. SJ-22 had the lowest WAASB but also showed the lowest mean yield. In *Oc*-infested conditions, WAASB values were high across all environments. Among them, CJ-22 showed the highest mean yield.

3.3. Resistance to Oc and performance under contrasting sowing dates

For the *Number of broomrapes/plant*, the Trait×WAASB biplot (Fig. 3) also revealed consistent patterns. All pea breeding lines clustered in quadrant III, combining low *Oc* infection (ranging from 1.55 broomrapes/plant in Jarana to 0.72 in Cartujano) with low WAASB values. Among the check cultivars, Kayanne showed the lowest *Oc* infection (1.50 broomrapes/plant), whereas Messire showed the highest (3.11). Overall, check cultivars showed higher WAASB scores in the *Oc*-infested environments.

When comparing genotypic yields in *Oc*-infested and *Oc*-free environments (Fig. 4A), breeding lines Cartujano and Pepapea exhibited the

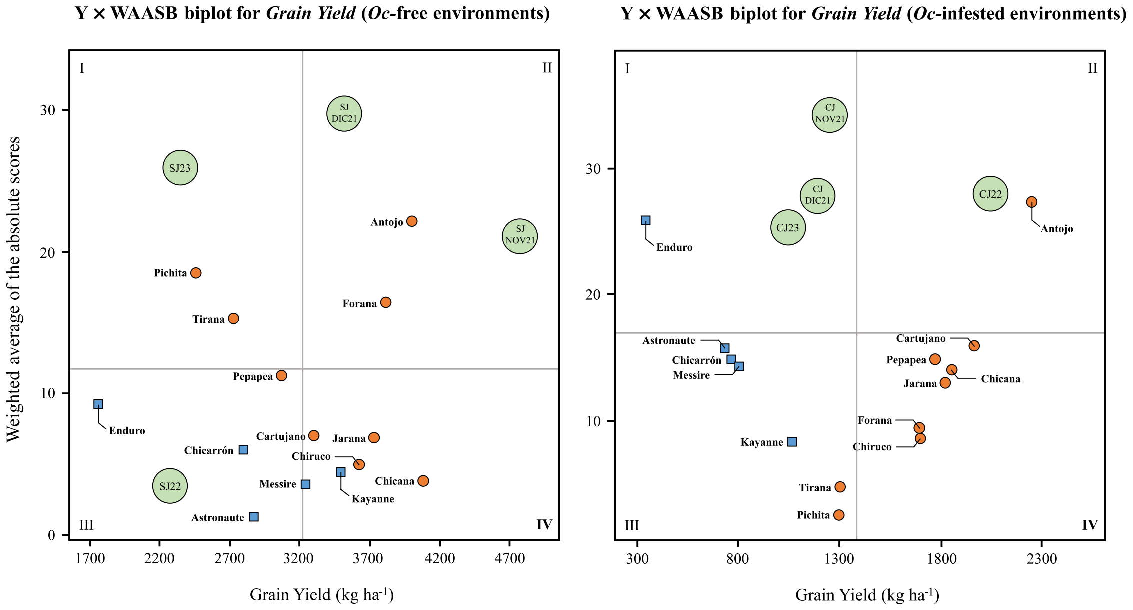

Fig. 2. *GY*×WAASB biplots under different *Oc* infestation conditions. The *GY* values shown correspond to the mean BLUPs of each genotype or environment, whereas WAASB represents the instability index. The grey lines defining quadrants I–IV are set at the overall means of *GY* and WAASB. Environments are shown as green circles, breeding lines as orange dots, and check cultivars as blue squares.

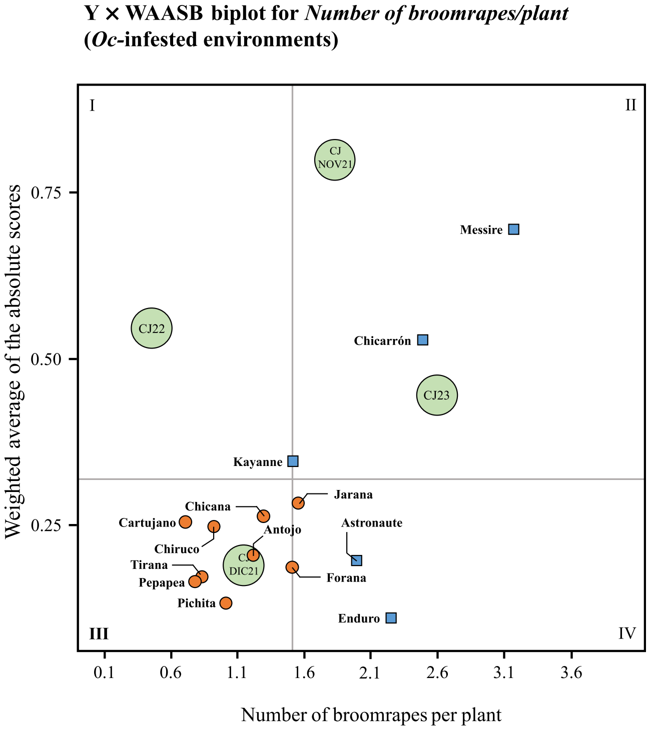

Fig. 3. Trait×WAASB biplot for *Number of broomrapes/plant* under *Oc* infestation. The values shown for *Number of broomrapes/plant* correspond to the mean BLUPs of each genotype or environment, whereas WAASB represents the instability index. The grey lines defining quadrants I–IV are set at the overall means of *Number of broomrapes/plant* and WAASB. Environments are shown as green circles, breeding lines as orange dots, and check cultivars as blue squares.

lowest *GY* penalties (–42% and –44%, respectively). In contrast, other high-*GY* lines (i.e., Chicana, Chiruco, Forana, Jarana) experienced mean losses of about 53%. Among the check cultivars, Astronaute, Chicarrón, Messire and Enduro showed severe mean yield reductions of –73%. Although Kayanne showed fewer broomrapes per plant than other checks, it still experienced substantial *GY* losses under *Oc* infestation (–68%) (Fig. 4A). Furthermore, a positive association between the *Number of broomrapes/plant* and the magnitude of *GY* penalty under *Oc* infestation was observed (Fig. 4B).

We also compared *GY* performance under early sowing (8 November) and late sowing (8–9 December) in the 2021–2022 season. *Number of broomrapes/plant* showed a mean increase of about 70% in early compared with late sowing (Fig. 3). Accordingly, the majority of check cultivars showed higher *GY* in the late sowing, based on both the mean and median across genotypes (Table 3, Fig. 5). In contrast, breeding lines showed a less consistent pattern with a lower mean but a higher median under late sowing, reflecting heterogeneous responses among genotypes (Table 3, Fig. 5).

3.4. Integrating agronomic trait stability and multivariate selection

Additional agronomic traits were analysed using the same WAASB-based approach applied to *GY* (Supplementary figures S2–S8), thereby providing genotype-specific stability profiles for each trait. For *HI*, Cartujano, Forana, Chiruco and Chicana showed values of about 40% with low WAASB. For *Ascochyta blight DS*, Pepapea showed the highest severity (33.5%), whereas Pichita, Chicarrón, Tirana and Enduro showed the lowest values (10.5–12.8%). For *Plot height*, the highest WAASB values were observed at both extremes of the continuous phenotypic distribution, including the tallest genotypes (Pichita and Tirana, >75 cm) and the shortest genotypes (Messire, Chiruco and Chicana, 55–62 cm). The lowest *Lodging* scores were recorded for Tirana (4.4 out of 10), Jarana (4.8), and Enduro (4.9).

To integrate yield performance with the other assessed traits, the MGIDI was computed, with trait weights derived from pairwise Pearson correlations with *GY* (Fig. 6). Within the MGIDI calculation, *Flowering GDD*, *Plot height*, *Appearance* and *Ascochyta blight* arcsin-*DS* loaded onto factor FA1 (Table 4), indicating a shared pattern of variation across genotypes. The second factor (FA2) included *Powdery mildew* arcsin-*DS*, *Number of broomrapes/plant*, *GY* and *HI*, forming a co-variation cluster more closely associated with yield. Together, FA1 and FA2 explained 79% of the total variance. Genotypes were ranked by MGIDI, which represented the distance of each genotype from the ideotype (Fig. 7). Applying a 30% selection threshold, Cartujano, Chicana, Pepapea, and

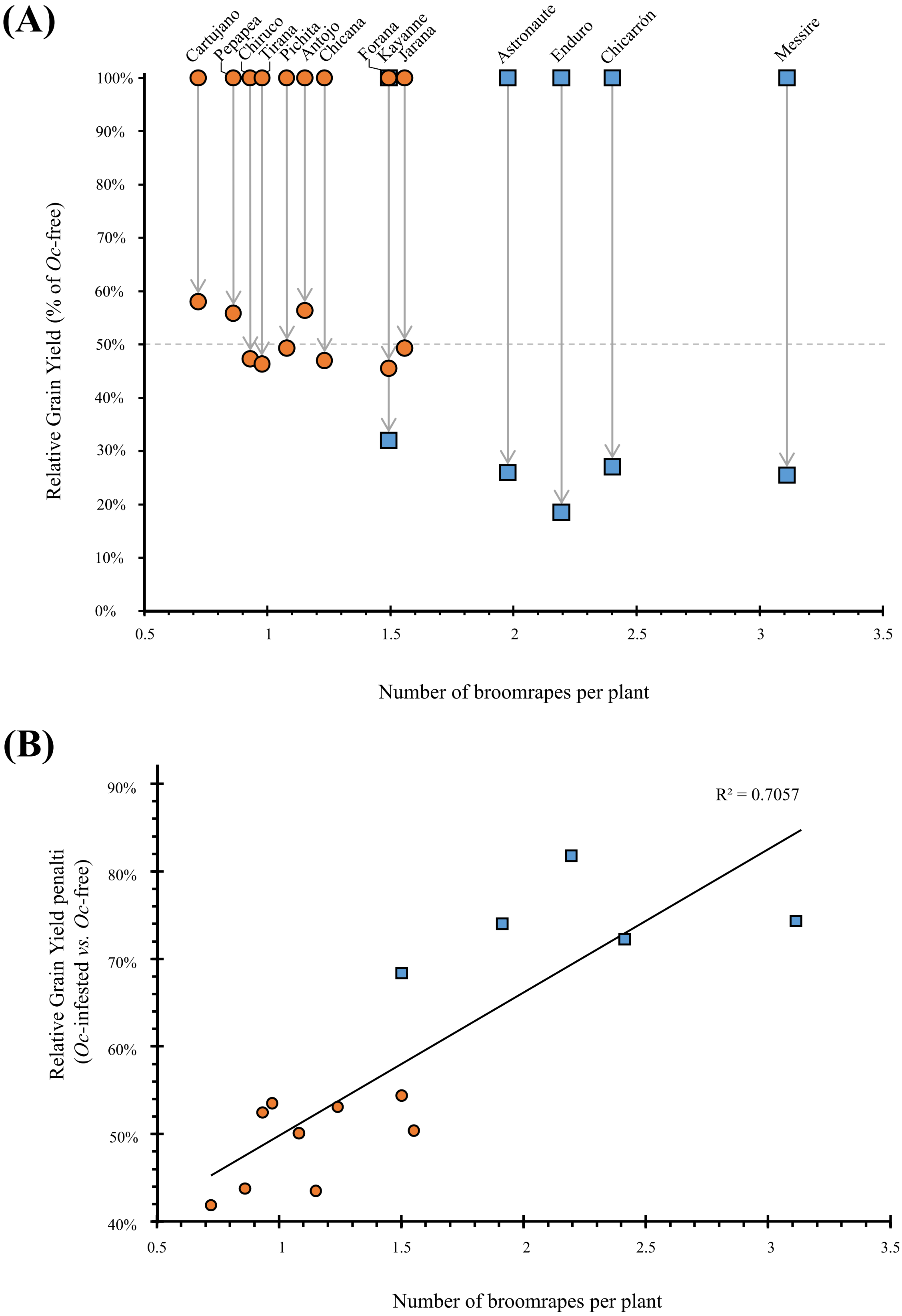

Fig. 4. Genotype-specific *GY* penalties in *Oc*-infested versus *Oc*-free environments. Breeding lines are shown as orange points and check cultivars as blue squares. (A) For each genotype, mean BLUPs for *GY* under *Oc* infection are expressed as a percentage of the corresponding mean BLUPs for *GY* under *Oc*-free conditions and plotted along the horizontal axis according to the mean BLUPs for *Number of broomrapes/plant* in *Oc*-infested environments. The length of the vertical grey arrows represents the magnitude of the *GY* penalty between *Oc*-free (arrow origin) and *Oc*-infested (arrowhead) conditions. The horizontal dashed grey line is set at 50% relative *GY*. (B) The magnitude of the relative *GY* penalty for each genotype is plotted against the mean BLUPs for *Number of broomrapes/plant* in *Oc*-infested environments. A linear regression between the two variables is also shown.

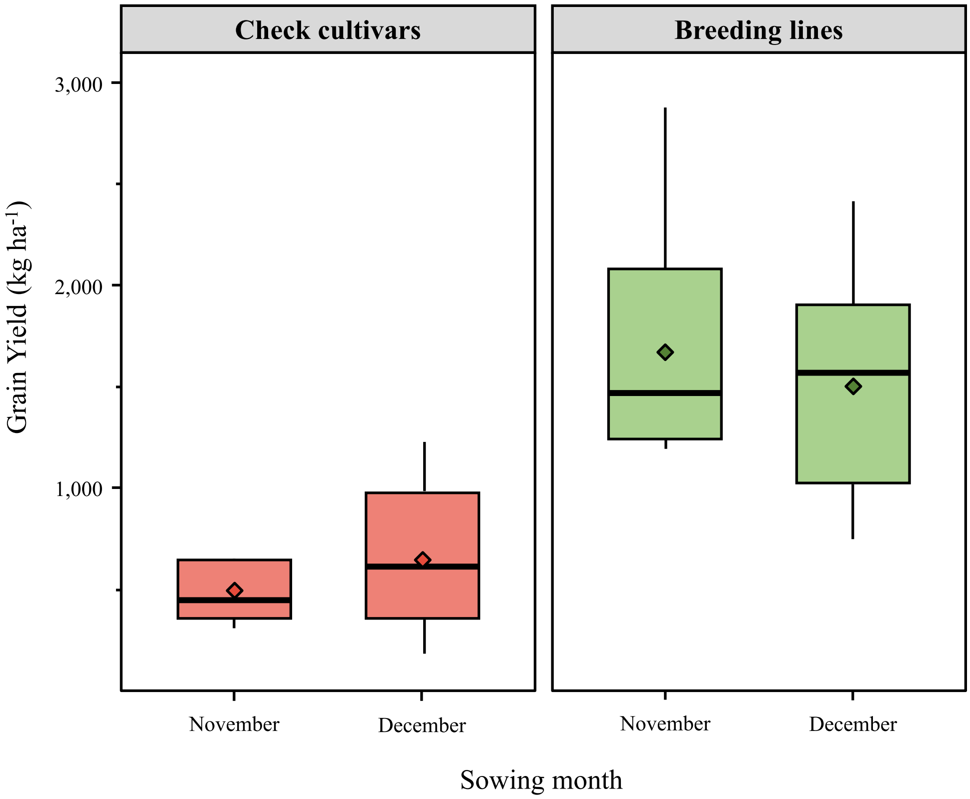

Fig. 5. Distribution of mean BLUPs for *GY* in check cultivars and breeding lines under *Oc*-infested conditions at two different sowing dates in the 2021–2022 growing season. The median is represented by the thick black line within each box, and the mean by the coloured diamond.

Kayanne were selected for their proximity to the ideotype. The four selected genotypes showed a mean reduction of 50 °C·d to flowering compared with the full set of genotypes, representing a 7.77% increase in reproductive earliness. For the remaining FA1 traits, the direction of change in the selected genotypes was opposite to that defined by the ideotype (Table 4, columns *g* and *f*). *Plot height* decreased by about 1 cm on average, *Lodging* increased slightly by 0.12 on the 1–10 scale, *Appearance* also declined modestly (–4.58%) and susceptibility to Ascochyta blight increased by 6.79% arcsin-*DS*. For the traits grouped under FA2, the selected genotypes showed 14.9% and 10.4% increases in *GY* and *HI* respectively. Both traits were strongly correlated (r = 0.81). Additionally, the *Number of broomrapes/plant* decreased by 25% in the selected genotypes; this trait was negatively correlated with *GY* (r = –0.64). *Powdery mildew* arcsin-*DS* decreased only slightly (–0.15%).

3.5. *Abiotic stress tolerance screening in Oc-free environments*

Stress-tolerance indices were computed from *GY* in two *Oc*-free environments with contrasting seasonal conditions (Table 2). Total rainfall was broadly comparable between SJ-NOV21 (*Yp*) and SJ-22 (*Ys*), but its temporal distribution differed markedly (Supplementary figure S1). In particular, the SJ-22 post-flowering period (defined by median flowering and senescence dates at the environment level) was characterised by markedly reduced rainfall (15.4 mm vs 189.6 mm in SJ-NOV21) and higher maximum temperatures (mean *Tmax* 26.7°C vs 20.5°C), with a substantial increase in the frequency of hot days (e.g., 37 vs 10 days with *Tmax* >25°C; 7 vs 0 days > 30°C). The resulting stress intensity was *SI* = 0.52.

Across genotypes, indices that captured performance in both environments (*MP*, *GMP*, *HARM* and *STI*) pointed to lines with high yield potential independently of the abiotic stress level (Table 5). Antojo showed the highest *Ys* and accordingly high *MP*, *GMP*, *HARM* and *STI* values. Chiruco and Chicana also showed *Ys* values above the stress-prone environment mean ($YI > 1$) together with $SSI < 1$, which translated into low *RankMean* values. At group level, the check cultivars showed lower *Ys* values than the breeding lines, with generally higher *RankMean* values. Within the breeding lines, the indices distinguished contrasting response profiles (Table 5). Jarana and Forana expressed high *Yp*, but showed larger absolute *GY* penalties under the stress-prone environment (higher *TOL*) and higher stress susceptibility ($SSI \geq 1$). Tirana combined lower *Yp* with lower relative susceptibility ($SSI < 1$) and a smaller relative *GY* penalty between environments. In contrast, Chicarrón combined low *Ys* with high susceptibility (high *SSI*) and large yield losses (high *TOL*).

3.6. *Predictive modelling of GY based on agronomic traits and climatic variables*

To identify predictors of *GY*, we built SMLR models integrating key agronomic traits, biotic stress and climatic variables. The three growing seasons included in this study represented contrasting rainfall and temperature patterns. The 2021–2022 season was near average, with typical winter rainfall. The 2022–2023 season was notably warmer and drier, which led to shortened phenological cycles. The 2023–2024 season had more typical rainfall and milder temperatures (Supplementary figure S1).

We examined Pearson correlations among crop-cycle and stage-specific climatic variables separately for *Oc*-free and *Oc*-infested environments (Fig. 8) and fitted independent SMLR models. The model for *Oc*-free environments showed high predictive performance (R^2 = 0.8546; adjusted R^2 = 0.8140) (Table 6). Among climatic predictors, *Rainfall* showed a negative regression coefficient for *GY*. *Hmin* had a positive coefficient despite a small negative pairwise correlation with *GY* (r = –0.33). *Flower–pod Tmin* and *Pod-filling GDD* also showed positive coefficients, while *Flower–pod GDD* had a negative coefficient.

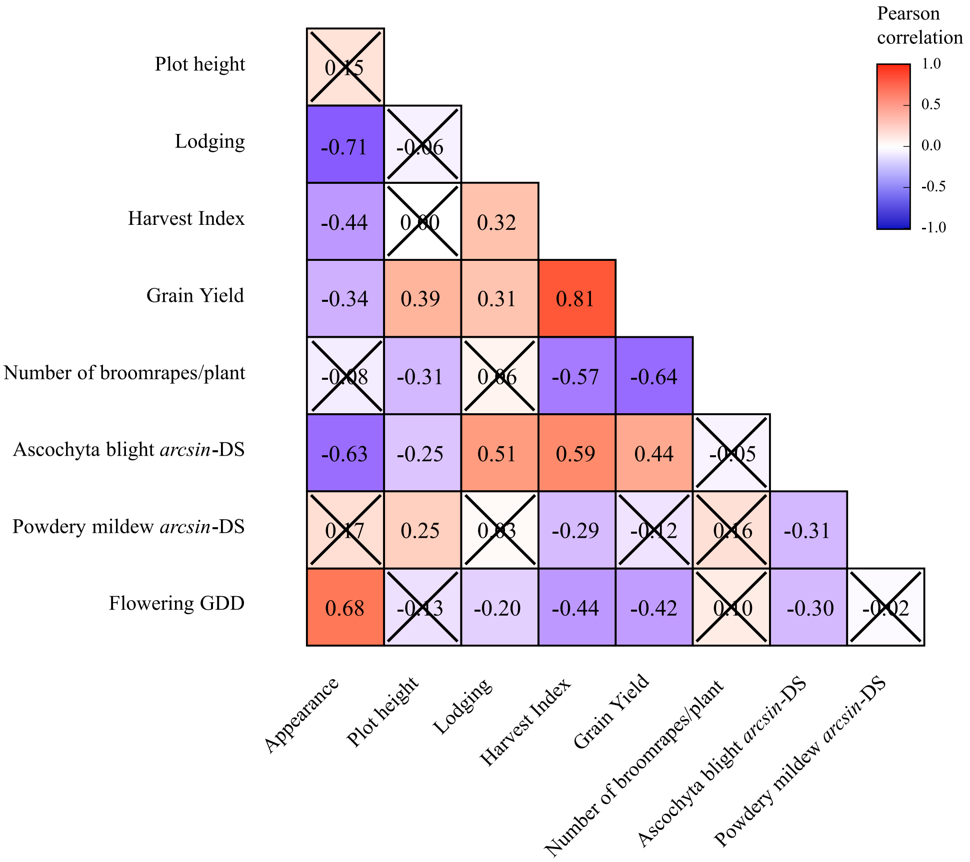

Fig. 6. Pearson correlation coefficients among the assessed traits. Correlations were computed using the BLUPs obtained for each trait. Non-significant correlations ($p > 0.05$) are marked with a cross.

Table 4
Summary of the performance of genotypes selected by MGIDI (Selectionindex = 30%) compared to the full genotype pool for the agronomic traits evaluated.

Trait	Factor [a]	Xo [b]	Xs [c]	SD [d]	SD% [e]	Target direction [f]	Goal [g]
Flowering GDD	FA1	643.00	593.00	−50.00	−7.77	Decrease	Achieved
Plot height	FA1	68.90	67.90	−0.97	−1.41	Increase	Not achieved
Lodging	FA1	5.68	5.80	0.12	2.11	Decrease	Not achieved
Appearance	FA1	2.45	2.34	−0.11	−4.58	Increase	Not achieved
Ascochyta blight arcsin-*DS*	FA1	24.70	26.40	1.68	6.79	Decrease	Not achieved
Powdery mildew arcsin-*DS*	FA2	62.00	61.90	−0.09	−0.15	Decrease	Achieved
Number of broomrapes/plant	FA2	0.77	0.57	−0.19	−25.00	Decrease	Achieved
GY	FA2	2297.00	2536.00	239.00	10.40	Increase	Achieved
HI	FA2	0.33	0.38	0.05	14.90	Increase	Achieved

[a] Variation factor to which the trait is assigned in the principal component analysis implicit in the MGIDI method.
[b] Overall mean value for the trait in the genotype pool.
[c] Mean value of the trait within the subset of selected genotypes.
[d] Gain or loss for each trait in the selected subset relative to the complete genotype pool (in the original units).
[e] Scaled gain or loss for each trait in the selected subset relative to the complete genotype pool (in percentage ratio)
[f] Target direction for trait change.
[g] Trait optimisation outcome. 'Achieved' when the observed change follows the target direction; 'Not achieved' when it opposes it.

Among agronomic traits, *Plot height* and *Lodging* retained positive and significant effects consistent with their positive pairwise correlations with *GY*.

The model built for *Oc*-infested environments exhibited statistically significant predictive performance, although it was slightly lower than that for *Oc*-free environments ($R^2 = 0.7997$; adjusted $R^2 = 0.7437$) (Table 7). For this model, the *Number of broomrapes/plant* had a negative regression coefficient for *GY*, with a pairwise correlation of $r = -0.66$. Among climatic variables, *Hmax*, *Pod-filling GDD* and *Pod-filling_NDT> 30* showed positive regression coefficients in this model. *Rainfall* also had a positive regression coefficient despite a small negative pairwise correlation with *GY* ($r = -0.30$). By contrast, *Pod-filling Tmax* showed a negative coefficient for *GY*. The SMLR model for *Oc*-infested environments retained positive coefficients for agronomic traits including *Appearance*, *Lodging*, *Plot height*, and *Ascochyta blight DS*.

4. Discussion

Although a number of commercial field pea cultivars are available to growers in Mediterranean countries, the genetic backgrounds of most cultivars reflect breeding origins outside the Mediterranean region (Martin-Sanz et al., 2011). Developing local breeding programmes for

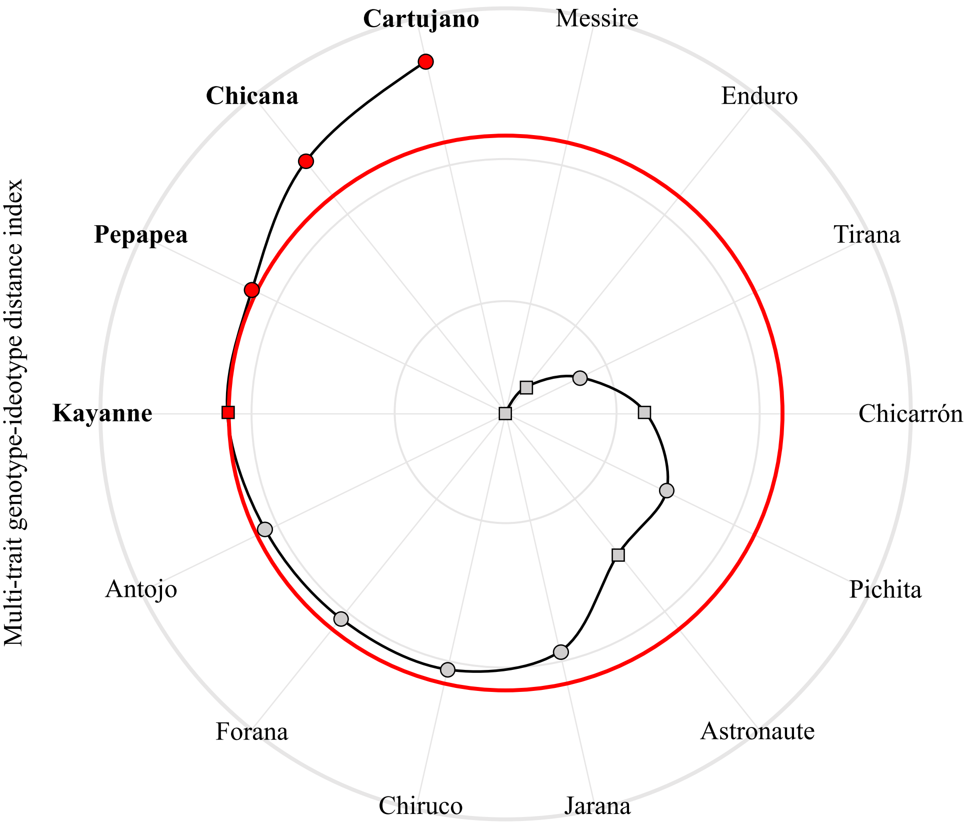

Fig. 7. Ranking of breeding lines and check cultivars based on the MGIDI, expressed as the distance from the ideotype. The selection threshold (red circumference) is set at 30% of the genotype pool, and the red points within this threshold represent genotypes selected as closest to the ideotype. The ideotype is represented by the outer grey circle.

Table 5
Stress-tolerance indices for *GY* across a potential vs stress-prone environments.

Genotype	***Yp*** [a] (kg) **SJ-NOV21**	***Ys*** [a] (kg) **SJ-22**	***MP*** [b]	***GMP*** [b]	***HARM*** [b]	***YI*** [b]	***SSI*** [b]	***TOL*** [b]	***STI*** [b]	***RankMean*** [c]
Jarana	5775	2506	4141	3804	3495	1.10	1.08	3270	0.43	**6**
Forana	5679	2419	4049	3707	3393	1.06	1.10	3260	0.43	**7**
Antojo	5461	3252	4356	4214	4076	1.43	0.77	2209	0.60	**2**
Chicana	5392	2773	4083	3867	3663	1.22	0.93	2619	0.51	**4**
Chiruco	5233	2875	4054	3879	3711	1.26	0.86	2357	0.55	**3**
Pepapea	5207	2374	3790	3515	3261	1.04	1.04	2833	0.46	**7**
Chicarron	5055	1730	3392	2957	2577	0.76	1.26	3325	0.34	**12**
Kayanne	4951	2277	3614	3357	3119	1.00	1.03	2674	0.46	**8**
Cartujano	4712	2384	3548	3352	3166	1.05	0.94	2329	0.51	**7**
Messire	4373	1921	3147	2898	2669	0.84	1.07	2452	0.44	**11**
Astronaute	4353	2014	3183	2961	2754	0.89	1.03	2339	0.46	**9**
Tirana	3925	2177	3051	2923	2801	0.96	0.85	1749	0.55	**8**
Pichita	3638	1935	2786	2653	2526	0.85	0.89	1703	0.53	**9**
Enduro	3104	1213	2159	1941	1745	0.53	1.16	1891	0.39	**13**
Mean	4776	2275								

[a] *Yp* and *Ys* denote BLUPs of *GY* in the potential (SJ-NOV21) and stress-prone (SJ-22) broomrape-free environments, respectively. Genotypes are ordered by *Yp* value.

[b] Stress-tolerance indices. Higher values indicate better performance for *MP*, *GMP*, *HARM*, *YI* and *STI*, whereas lower values indicate better performance for *SSI* and *TOL*.

[c] *RankMean* is the mean of genotype ranks across indices; lower values indicate a more favourable overall profile

specific agroclimatic contexts is essential for producing better-adapted cultivars. Breeding within target environments promotes the accumulation of favourable alleles through selection pressures imposed by specific local conditions (Annicchiarico and Iannucci, 2008).

The results of the multi-environment study presented here highlight this point, and *Oc* provides a clear example. In our study, this root-parasitic plant was the main constraint on field pea cultivation, as widely reported for the Mediterranean region (Rubiales, 2018, 2023). *Oc* infestation directly reduced grain yield and altered crop phenology. Furthermore, it also affected performance indirectly by changing how agronomic traits, and other stresses influenced yield. Genotypes that were more resistant to *Oc* also showed smaller yield penalties between *Oc*-infested and *Oc*-free environments. Within the *Oc*-infested environments, CJ-22 proved particularly informative for discriminating yield under parasite pressure. Compared with the check cultivars, our breeding lines showed more stable yield responses under infestation and

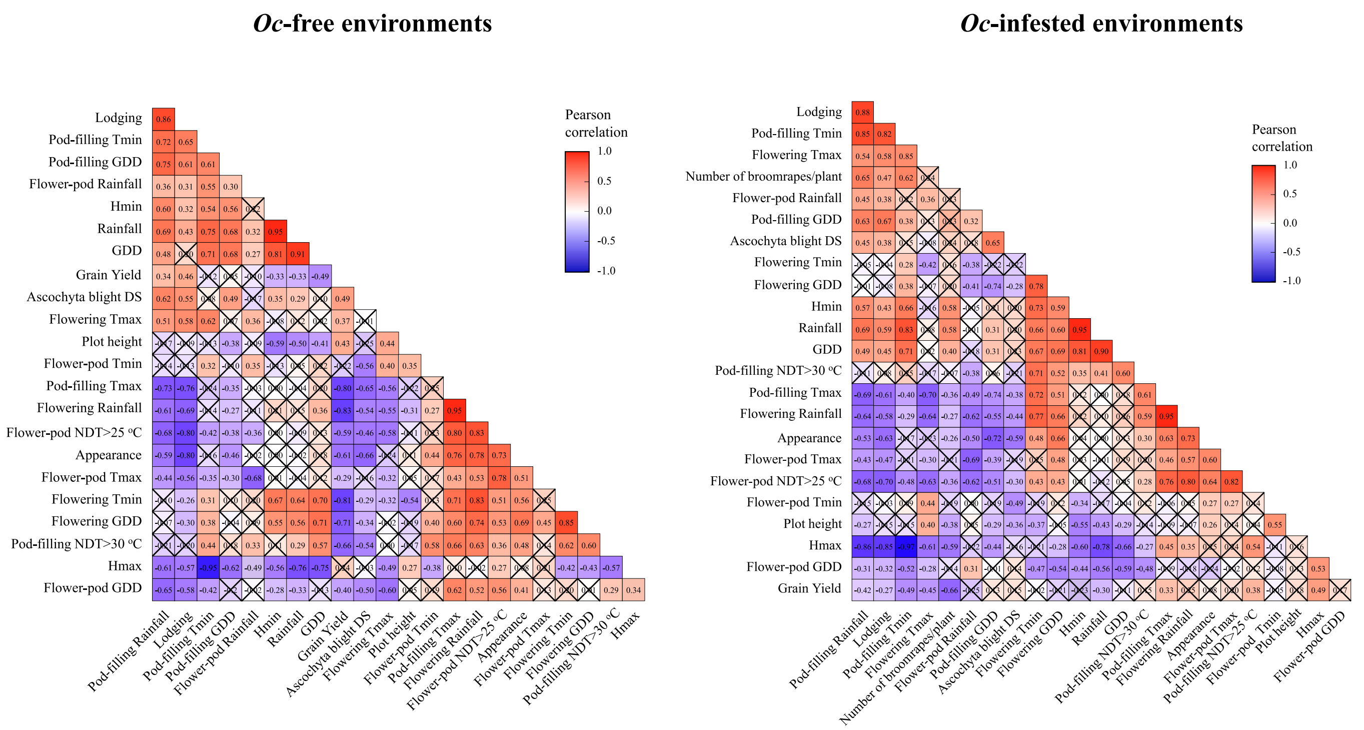

Fig. 8. Pairwise Pearson correlation heatmap of agronomic traits, biotic constraints and climatic variables in *Oc*-free and *Oc*-infested environments. Correlations were computed using the BLUPs obtained for each variable. Non-significant correlations (p > 0.05) are marked with a cross.

Table 6

Coefficients and adjustment quality indexes of the step-wise regression model designed for *GY* prediction in *Oc*-free environments.

Coefficient	Estimate [a]	SE [b]	*t*	Pr (>| *t* |)	[c]
(Intercept)	3209.45	72.75	44.117	< 2e−16	***
Rainfall	−7402.33	2966.44	−2.495	0.01650	*
Hmin	4322.82	1756.04	2.462	0.01792	*
Pod-filling GDD	1825.25	724.11	2.521	0.01550	*
Lodging	1146.07	433.19	2.646	0.01134	*
Flowering GDD	894.04	691.63	1.293	0.20303	
Pod-filling Tmin	857.93	585.57	1.465	0.15016	
Appearance	788.35	317.03	2.487	0.01686	*
Flower-pod GDD	−452.16	128.11	−3.529	0.00101	**
Pod-filling_NDT> 30	−400.41	242.80	−1.649	0.10641	
Flower-pod Tmin	374.35	138.63	2.700	0.00987	**
Ascochyta blight DS	348.00	155.42	2.239	0.03038	*
Plot height	324.81	148.37	2.189	0.03406	*

Residual standard error: 544.4 on 43 degrees of freedom
Multiple R^2*: 0.8546*
Adjusted R^2*: 0.8140*
F-statistic: 21.06 on 12 and 43 DF, p-value: 3.429e−14

[a] Estimated effect of the predictor variable on the *GY* (change on *GY* in original units by variation of 1-SD of the predictor)
[b] Standard Error of the estimated coefficient.
[c] Significance level: 0.001(***), 0.01(**), 0.05(*), 0.1(.), 1()

appeared less affected by variation in parasite pressure across environments.

Various mechanisms of resistance to *Oc* have been reported in pea wild relatives and landraces (Pérez-de-Luque et al., 2005) and some genetic markers and maps are already available (Valderrama et al., 2004; Fondevilla et al., 2010; Delvento et al., 2023; Wohor et al., 2025). However, these traits typically show complex quantitative inheritance, and even the more resistant sources provide only partial protection. The first breeding lines with high levels of resistance to *Oc* infection were developed in Andalucía in the early 2000s (Rubiales et al., 2009, 2021) and were further improved in subsequent years (Rubiales et al., 2021). Several of the resulting lines are protected by OEVV but have not yet been commercialised. The breeding lines evaluated in this study carry genetic contributions from Ps624 (IFPI 2348) and/or Pf660 (IFPI 3260). Ps624 is a *P. sativum* landrace with high levels of incomplete resistance,

Table 7

Coefficients and adjustment quality indexes of the step-wise regression model designed for *GY* prediction in *Oc*-infested environments.

Coefficient	Estimate [a]	SE [b]	*t*	Pr (>| *t* |)	[c]
(Intercept)	1385.04	50.90	27.214	< 2e−16	***
Hmax	1242.41	256.39	4.846	1.67e−5	***
Rainfall	724.50	247.88	2.923	0.00551	**
Pod-filling_NDT>30	523.94	156.49	3.348	0.00170	**
Lodging	491.20	221.42	2.218	0.03186	*
Pod-filling Tmax	−480.42	219.01	−2.194	0.03372	*
GDD	−401.34	195.61	−2.052	0.04632	*
Appearance	398.23	163.55	2.435	0.01912	*
Pod-filling GDD	299.43	109.49	2.735	0.00903	**
Number of broomrapes/plant	−292.16	86.63	−3.372	0.00159	**
Ascochyta blight DS	213.12	93.00	2.292	0.02688	*
Plot height	165.61	82.44	2.009	0.05087	.
Flower-pod_NDT> 25	134.33	100.68	1.334	0.18917	

Residual standard error: 380.9 on 43 degrees of freedom
Multiple R^2*: 0.7997*
Adjusted R^2*: 0.7437*
F-statistic: 14.30 on 12 and 43 DF, p-value: 2.458e−11

[a] Estimated effect of the predictor variable on the *GY* (change on *GY* in original units by variation of 1-SD of the predictor)
[b] Standard Error of the estimated coefficient.
[c] Significance level: 0.001(***), 0.01(**), 0.05(*), 0.1(.), 1()

mainly through reduced *Oc* establishment (Castillejo et al., 2004; Die et al., 2009; Rubiales et al., 2005). Meanwhile, Pf660 is a wild *P. fulvum* accession that also provides high incomplete resistance to *Oc* (Rubiales et al., 2021).

In the absence of commercially available cultivars with sufficient levels of resistance or tolerance to *Oc*, scheduling strategies such as late-winter sowings are recommended in southern Spain to partially escape *Oc* infection (Fernández-Aparicio et al., 2011; Joel et al., 2007; Rubiales et al., 2003). The breeding material now available enables us to re-evaluate recommendations of this kind. According to our findings, late sowing remains a useful strategy for reducing *Oc* infection in susceptible genotypes, such as the check cultivars. However, the more resistant breeding lines still achieved higher yields when sown one month earlier, despite being exposed to greater infection levels than under late sowing. This suggests that these genotypes may combine *Oc* resistance with some degree of tolerance, contributing to sustain pod filling under infestation. Consistent evidence comes from the trials conducted by Perea-Torres et al. (2021) in the same geographical region, that reported significantly lower yields for these breeding lines when they were sown late in February. Importantly, phenological earliness was associated with higher *GY* under both *Oc*-free and *Oc*-infested conditions in our study, suggesting that the advantage of early flowering is not solely due to temporal escape from *Oc*. The performance of our breeding lines suggests that genetic resistance and tolerance traits can reduce growers' reliance on scheduling strategies by providing well-performing materials with diverse cycle lengths.

The influence of climatic factors on *Oc* aggressiveness is well established in the literature (Arjona-Berral et al., 1987). In line with this, we observed marked inter-seasonal differences in *Oc* infection levels and a strong contribution of the environmental component to variation in this trait. In our dataset, *Rainfall* was a strong explanatory factor for *GY*, although it was also strongly correlated with *Oc* infestation level, as previously reported (Pérez-de-Luque et al., 2004; 2016). More specifically, our results suggest that the effect of rainfall depended on crop stage. Rainfall during the vegetative phase was associated with lower *GY*, whereas rainfall during pod filling showed the opposite effect. This apparent inconsistency may reflect the ability of our breeding lines to maintain good performance under high *Oc* pressure, likely through nutrient-allocation dynamics (Arnaud et al., 1999). Likewise, higher temperatures were associated with increased *GY* but also promoted *Oc* infection, leading to a complex mixed effect on yield under *Oc* infestation. It is widely recognised that improving heat tolerance is a key breeding target for field pea adaptation to warm agrosystems, and for broadening the cultivation window (Devi et al., 2023). In view of our results, heat tolerance may gain additional value in Mediterranean environments for its contribution to crop resilience under *Oc* infestation.

According to the First Mediterranean Assessment Report published by MedECC, climate projections for the Mediterranean Basin consistently indicate continued warming and drying. They also point to an increasing frequency of droughts and extreme events such as heat waves. These trends have direct implications for rainfed agriculture by increasing the risk of yield losses (Ali et al., 2022; Mrabet et al., 2020). These climatic projections should remain a central focus of field pea breeding, which should prioritise adaptation to prolonged drought episodes (Bagheri et al., 2023) and to high temperatures during reproductive development (Devi et al., 2023).

The three growing seasons covered by this study captured a representative range of climatic profiles typical of Mediterranean rainfed conditions (Mrabet et al., 2020). Nevertheless, one limitation of the present study is that all field sites were located within the same experimental farm. As a consequence, beyond the difference in natural *Oc* infestation between field sites, the experimental environments do not represent additional variation in soil conditions (Atlin et al., 2000). An additional limitation is the 1 m^2 plot size, which increases the relative contribution of border rows and may introduce some interplot interference. Indeed, modest biases have been reported associated with this experimental limitation in crop variety trials, including field peas (Talbot et al., 1995; Wang et al., 2013). Genotype responses may therefore show some variation under other farm contexts and plot scales not represented here, although the present results still remain informative for Mediterranean rainfed systems.

Within this context, the abiotic stress-tolerance analysis provides a useful approach to explore genotype responses under drier and hotter springs. As no consistent differences in the biotic stress pressures were observed between the contrasting environments (SJ-NOV21 vs SJ-22), performance differences can therefore be mainly attributed to abiotic variation (e.g., rainfall patterns, thermal conditions). Within this contrast, Chicana and Chiruco combined comparatively high yield in the stress-prone environment with favourable stress-tolerance index values. This is consistent with their favourable positioning in the $GY\times$WAASB biplot and suggests that both genotypes are not only productive but also able to maintain performance under late-season drought and heat stress. Notably, Antojo illustrates that the abiotic stress-tolerance and the $GY\times$WAASB analyses capture different dimensions of adaptation: despite its favourable abiotic stress-tolerance index, Antojo showed a lower yield stability across the broader set of *Oc*-free environments (according to WAASB). Overall, most breeding lines exhibited better yield maintenance than the commercial check cultivars under stress-prone conditions, indicating improved adaptation to abiotic stresses. Nevertheless, these interpretations should remain cautious, as the comparison was based on a single seasonal contrast between two environments rather than on controlled stress treatments.

The SMLR approach allowed us to capture the combined effects of climatic variables and agronomic traits on *GY*. This arises from the ability of the SMLR methodology to handle hierarchical, unbalanced datasets with multiple G×E interactions, which are common in agroclimatic studies (Madden and Ojiambo, 2024). For some climatic predictors, the sign of the regression coefficient differed from that of the corresponding pairwise correlation with *GY*, which can be explained by the strong collinearity among several of these variables. This was particularly evident for *Hmin* in *Oc*-free environments, as its regression coefficient became positive once covariation with rainfall variables was accounted for. A similar collinearity pattern may explain the positive coefficient of *Rainfall* in *Oc*-infested environments, despite its negative pairwise correlation with *GY*.

Analysing *Oc*-infested and *Oc*-free environments separately also allowed us to distinguish between regression coefficients shared across models and those specific to infestation status. Predictor variables common to both SMLR models include agronomic traits such as *Lodging*, *Plot height*, and *Appearance*. Annicchiarico and Iannucci (2008) reached similar conclusions, reporting that harvest index and plant height were more informative than yield itself at early breeding stages. For *Lodging*, its positive correlation with *GY* likely reflects the effect of increasing pod load towards maturity, which may be specially pronounced in the high-*HI* genotypes included in this study. Lodging has received considerable attention since the first *afila*-type pea cultivars were developed. This trait is largely under major-gene control and confers a more erect growth habit, thereby improving suitability for mechanised harvest (Pesic et al., 2013). Because nearly all genotypes in the studied panel were *afila*-type, with Messire as the only exception, genetic effects on *Lodging* were likely limited in this study. This interpretation is further supported by the analysis of variance. Much of the remaining variation in *Lodging* can therefore be attributed to environmental drivers, with rainfall during pod filling emerging as the most important. However, a meaningful genotypic component remained, potentially reflecting differences in other architectural traits or in stem lignin content (Banniza et al., 2005).

Among the coefficients retained specifically in the *Oc*-free model, climatic drivers of *GY* showed a stage-dependent pattern mainly linked to the reproductive period. Within this model, the negative effect of *Flower–pod GDD* suggests that a greater thermal accumulation during the flowering stage may have constrained pollen viability or fertilisation.

Nevertheless, the effects of high temperature were more evident in the accumulated thermal time than in the extreme heat events, as no variables related to heat extremes were retained in the final equation. Meanwhile, the positive contribution of *Flower–pod Tmin* to the model suggest that cooler conditions during this stage limited pod set.

By contrast, the SMLR model for *Oc*-infested environments retained a broader and more complex combination of temperature-related predictors, including accumulated thermal time, maximum temperatures and extreme heat events. In addition, the *Oc*-infested model exhibited a lower predictive performance compared with the *Oc*-free one. Taken together, these results support the hypothesis that *Oc* disrupts the underlying relationships between crop performance and environmental factors.

Ascochyta blight is caused by a fungal complex involving up to four ascomycete species, with *D. pinodes* being the most widespread (Khan et al., 2013). This soil- and seed-borne disease is favoured by wet microclimates and mild temperatures during winter and spring. Pycnidiospores are dispersed from infected biomass by splashing rain or dew droplets, and the disease therefore progresses upwards to the apex under conducive conditions (Roger and Tivoli, 1996). Good resistance levels governed by quantitative resistance loci have been reported in wild relatives of peas (Fondevilla et al., 2007, 2008), but most commercial cultivars range from moderately to highly susceptible. In our study, *Ascochyta blight DS* was positively correlated with *GY* and *HI*, and proved to be a relevant predictor of *GY*. This association was also evident in SJ-NOV21, which combined the highest *GY* observed in our study with the highest mean Ascochyta blight severity. This agrees with previous reports that early sowings are associated with greater Ascochyta blight pressure (Khan et al., 2013). Our results may indicate that certain climatic conditions simultaneously favour pod filling and fungal development in Mediterranean rainfed systems (e.g., higher *Hmin*, rainfall during pod filling and delayed canopy drying).

This co-variation may apply to the late-stage Ascochyta blight infections observed here in adult plants. However, early infections at the seedling stage often led to different outcomes, including detrimental effects on development and yield (Moussart et al., 1998; Roger et al., 1999). A dedicated study targeting seedling-stage infection under comparable Mediterranean rainfed conditions would therefore complement our findings. In addition, the genotypes tested in this study also tended to prioritise nutrients allocation to seeds over vegetative growth (as reflected in their high *HI*). This limits their ability to develop secondary shoots and hinders their capacity to recover (Tivoli and Banniza, 2007), which may explain why high-*HI* genotypes also showed higher disease severity. These findings highlight the need to distinguish genetic resistance from recovery mechanisms, so that each trait can be evaluated and targeted separately in breeding. Although Ascochyta blight did not have a detrimental effect on yield under the conditions of this study, it remains a breeding priority due to its effects on seed quality (Tivoli et al., 1996).

Pea powdery mildew is caused by the ascomycete fungi *E. pisi* and *E. trifolii*. Infection, mycelial growth, and ascospore release are favoured by cool, mildly humid nights and hot, dry days (Fondevilla and Rubiales, 2012). Monogenic sources of resistance to powdery mildew (based so far on *er1*, *er2* and *Er3* major resistance genes) offer near-complete resistance and are already available for breeding purposes (Devi et al., 2022). Powdery mildew infection was observed in all environments considered in this study, but it showed no significant effects on yield. The most resistant genotypes in our panel carry the *Er3* gene, introgressed from the wild accession Pf660 (Fondevilla et al., 2007, 2011; Rubiales et al., 2021). Pepapea also carries the more widespread *er1* gene. Combining all available powdery mildew resistance genes within the same genetic background would improve the durability of resistance in commercial cultivars (Banyal et al., 2022; Devi et al., 2022). For efficient gene pyramiding, developing robust molecular markers and further investigating the genetic basis of the resistance mechanisms (Pheirim et al., 2022) are essential tasks.

The MGIDI approach was useful for identifying genotypes with balanced agronomic profiles by integrating performance, stability and responses to stress (Olivoto and Nardino, 2021). Our results indicate Cartujano, Chicana and Pepapea as closest to the ideotype, with Kayanne ranking highest among the check cultivars. The three breeding lines combined good *Oc* resistance with stable yields of about 1900 and 3500 kg ha^{-1} under *Oc*-infested and *Oc*-free conditions, respectively. These genotypes share contributions from Ps624 and Messire in their pedigrees. Across the other assessed traits, the selected genotypes generally showed values close to the panel mean, while still outperforming the check cultivars in most cases. The main unfavourable shift in the selected subset was a moderate increase in Ascochyta blight susceptibility. Although this did not translate into a yield penalty, it remains relevant from a breeding perspective and should be addressed in future breeding efforts. Genotypes not selected under the MGIDI threshold may still be valuable for specific breeding targets. Tirana and Pichita showed lower stability in *Oc*-free environments but may be useful as breeding material, combining strong resistance to Ascochyta blight with stable yields in *Oc*-infested environments (about 1300 kg ha^{-1}, therefore outperforming all check cultivars). Forana, Antojo and Pepapea are valuable sources of powdery mildew resistance for breeding programmes. Likewise, the erect growth habit of lines such as Tirana and Jarana could also contribute to improve appearance and suitability for mechanised harvest in new breeding material.

5. Conclusions

The results of this study illustrate how major biotic stresses interact with local abiotic conditions to shape field pea performance in Mediterranean environments. Our study confirms that *O. crenata* is a major constraint on field pea cultivation in the region, as it directly reduced yield and altered how local abiotic conditions influenced performance, especially during pod filling. In this context, spring rainfall and high temperatures can favour the development of *Oc*. Compared with the check cultivars, the advanced breeding lines developed showed greater resistance to *Oc*, resulting in higher yields and smaller yield penalties under *Oc* infestation. The abiotic stress-tolerance analysis in this study showed that some genotypes maintained relatively high yields under the drier and hotter seasonal conditions. Altogether, these results suggest that selection of this breeding material under Mediterranean rainfed conditions improved yield robustness against the combined pressures of biotic stress and terminal drought. More broadly, this reinforces the value of selection within target environments for achieving adaptation to multiple stresses. Overall, the field pea lines developed within the IAS-CSIC breeding programme represent a clear improvement in adaptation to rainfed Mediterranean conditions, as reflected in their superior yield relative to the check cultivars.

This study also supports early sowing in resistant lines, as it led to higher yields despite greater *Oc* pressure. While early sowing tended to increase late-season Ascochyta blight severity, the disease did not reduce yield under the conditions of this study. Some breeding lines also showed moderate resistance to Ascochyta blight, making them potentially useful in breeding for this trait. However, further work is warranted to clarify the relationship between Ascochyta blight severity and yield in genotypes with high harvest index. Powdery mildew was observed in susceptible genotypes across environments, but it had no significant effect on yield under the conditions of this study. In addition, powdery mildew resistance in several of the breeding lines supports the successful introgression of the *Er3* gene from a wild *Pisum* relative.

Beyond practical recommendations for growers, these results also guide future breeding efforts in Mediterranean environments and further highlight the value of landraces and wild *Pisum* spp. as sources of adaptive and stress-resistance traits.

CRediT authorship contribution statement

Diego Rubiales: Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Maria José Cobos:** Writing – review & editing, Validation, Resources, Investigation, Data curation, Conceptualization. **Fernando Flores:** Writing – review & editing, Writing – original draft, Software, Methodology, Formal analysis, Conceptualization. **Jiménez-Vaquero Manuel A.:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Data curation, Conceptualization.

Funding

This research was funded by the EU Horizon Europe COUSIN (grant number 101135314) and BELIS (grant number 101081878); by Spanish Government projects CPP2022-009742, PID2023-146215OB-I00 (MICIU/AEI/10.13039/501100011033) and by the FPU programme (grant number FPU20/04024) (MCIU/10.13039/100014440).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Carmen M. Ruiz-Pastor for the valuable technical assistance provided during data collection and for the preparation and handling of plant material throughout all field trials.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2026.110512.

Data availability

The original datasets can be accessed through the following link: Agronomic, phenology, and disease data from rainfed field pea trials in Córdoba (Spain) (DIGITAL.CSIC)

References

Ali, E., Cramer, W., Carnicer, J., Georgopoulou, E., Hilmi, N.J.M., Le Cozannet, G., Lionello, P., 2022. Cross-Chapter Paper 4: Mediterranean Region. In: Pörtner, H.-O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., Rama, B. (Eds.), Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York, pp. 2233–2272. https://doi.org/10.1017/9781009325844.021.

Annicchiarico, P., Iannucci, A., 2008. Adaptation strategy, germplasm type and adaptive traits for field pea improvement in Italy based on variety responses across climatically contrasting environments. Field Crops Res. 108 (2), 133–142. https://doi.org/10.1016/j.fcr.2008.04.004.

Annicchiarico, P., Laouar, M., Thami-Alami, I., Crosta, M., Nazzicari, N., Pecetti, L., Russi, L., 2025. Comparison of phenotypic selection of inbred lines, genomic selection of inbred lines, and evolutionary populations for field pea breeding in three Mediterranean regions. Front. Plant Sci. 16, 1565087. https://doi.org/10.3389/fpls.2025.1565087.

Annicchiarico, P., Romani, M., Cabassi, G., Ferrari, B., 2017. Diversity in a pea (*Pisum sativum*) world collection for key agronomic traits in a rain-fed environment of Southern Europe. Euphytica 213, 245. https://doi.org/10.1007/s10681-017-2033-y.

Arjona-Berral, A., Mesa-García, J., García-Torres, L., 1987. Phenology and growth of *Orobanche crenata* Forsk (broomrape) in four legume crops. Weed Res. 27 (5), 349–360. https://doi.org/10.1111/j.1365-3180.1987.tb00772.x.

Arnaud, M.-C., Véronési, C., Thalouarn, P., 1999. Physiology and histology of resistance to *Striga hermonthica* in *Sorghum bicolor* var. Framida. Aust. J. Plant Physiol. 26 (1), 63–70. https://doi.org/10.1071/PP98070.

Atlin, G.N., Baker, R.J., McRae, K.B., Lu, X., 2000. Selection response in subdivided target regions. Crop Sci. 40 (1), 7–13. https://doi.org/10.2135/cropsci2000.4017.

Bagheri, M., Santos, C.S., Rubiales, D., Vasconcelos, M.W., 2023. Challenges in pea breeding for tolerance to drought: status and prospects. Ann. Appl. Biol. 183 (2), 108–120. https://doi.org/10.1111/aab.12840.

Banniza, S., Hashemi, P., Warkentin, T.D., Vandenberg, A., Davis, A.R., 2005. The relationships among lodging, stem anatomy, degree of lignification, and resistance to mycosphaerella blight in field pea (*Pisum sativum*). Can. J. Bot. 83 (8), 954–967. https://doi.org/10.1139/b05-044.

Banyal, D.K., Dixit, H., Chaudhary, J., Malannavar, A.B., Thakur, N., 2022. Deciphering diversity at er loci for diversification of powdery mildew resistance in pea. Sci. Rep. 12, 16037. https://doi.org/10.1038/s41598-022-19894-y.

Bourgeois, G., Jenni, S., Laurence, H., Tremblay, N., 2000. Improving the prediction of processing pea maturity based on the growing-degree day approach. HortScience 35 (4), 611–614. https://doi.org/10.21273/HORTSCI.35.4.611.

Burdett, H., Wellen, C., 2022. Statistical and machine learning methods for crop yield prediction in the context of precision agriculture. Precis. Agric. 23, 1553–1574. https://doi.org/10.1007/s11119-022-09897-0.

Castillejo, M.Á., Amiour, N., Dumas-Gaudot, E., Rubiales, D., Jorrín, J.V., 2004. A proteomic approach to studying plant response to crenate broomrape (*Orobanche crenata*) in pea (*Pisum sativum*). Phytochemistry 65 (12), 1817–1828. https://doi.org/10.1016/j.phytochem.2004.03.029.

Delvento, C., Arcieri, F., Marcotrigiano, A.R., Guerriero, M., Fanelli, V., Dellino, M., Curci, P.L., Bouwmeester, H., Lotti, C., Ricciardi, L., Pavan, S., 2023. High-density linkage mapping and genetic dissection of resistance to broomrape (*Orobanche crenata* Forsk.) in pea (*Pisum sativum* L.). Front. Plant Sci. 14, 1216297. https://doi.org/10.3389/fpls.2023.1216297.

Devi, J., Mishra, G.P., Sagar, V., Kaswan, V., Dubey, R.K., Singh, P.M., Sharma, S.K., Behera, T.K., 2022. Gene-based resistance to *Erysiphe* species causing powdery mildew disease in peas (*Pisum sativum* L.). Genes 13 (2), 316. https://doi.org/10.3390/genes13020316.

Devi, J., Sagar, V., Mishra, G.P., Jha, P.K., Gupta, N., Dubey, R.K., Singh, P.M., Behera, T. K., Prasad, P.V.V., 2023. Heat stress tolerance in peas (*Pisum sativum* L.): Current status and way forward. Front. Plant Sci. 13, 1108276. https://doi.org/10.3389/fpls.2022.1108276.

Die, J.V., Román, B., Nadal, S., Dita, M.Á., González-Verdejo, C.I., 2009. Expression analysis of *Pisum sativum* putative defence genes during *Orobanche crenata* infection. Crop Pasture Sci. 60 (5), 490–498. https://doi.org/10.1071/CP08274.

FAO, 2025. FAOSTAT statistical database. Food and Agriculture Organization of the United Nations. ⟨https://www.fao.org/faostat/⟩ (accessed 10 June 2025).

Fernandez, G.C.J., 1992. Effective selection criteria for assessing plant stress tolerance. In: Kuo, C.G. (Ed.), Proceedings of an International Symposium on Adaptation of Vegetables and Other Food Crops in Temperature and Water Stress. AVRDC, Tainan, pp. 257–270.

Fernández-Aparicio, M., Westwood, J.H., Rubiales, D., 2011. Agronomic, breeding, and biotechnological approaches to parasitic plant management through manipulation of germination stimulant levels in agricultural soils. Botany 89 (12), 813–826. https://doi.org/10.1139/b11-075.

Fischer, R.A., Maurer, R., 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust. J. Agric. Res. 29 (5), 897–912. https://doi.org/10.1071/AR9780897.

Flores, F., Nadal, S., Solis, I., Winkler, J., Sass, O., Stoddard, F.L., Link, W., Raffiot, B., Muel, F., Rubiales, D., 2012. Faba bean adaptation to autumn sowing under European climates. Agron. Sustain. Dev. 32, 727–734. https://doi.org/10.1007/s13593-012-0082-0.

Fondevilla, S., Cubero, J.I., Rubiales, D., 2011. Confirmation that the *Er3* gene, conferring resistance to *Erysiphe pisi* in pea, is a different gene from *er1* and *er2* genes. Plant Breed. 130 (2), 281–282. https://doi.org/10.1111/j.1439-0523.2010.01769.x.

Fondevilla, S., Fernández-Aparicio, M., Satovic, Z., Emeran, A.A., Torres, A.M., Rubiales, D., 2010. Identification of quantitative trait loci for specific mechanisms of resistance to *Orobanche crenata* Forsk. in pea (*Pisum sativum* L.). Mol. Breed. 25, 259–272. https://doi.org/10.1007/s11032-009-9330-7.

Fondevilla, S., Flores, F., Emeran, A.A., Kharrat, M., Rubiales, D., 2017. High productivity of dry pea genotypes resistant to crenate broomrape in Mediterranean environments. Agron. Sustain. Dev. 37, 61. https://doi.org/10.1007/s13593-017-0470-6.

Fondevilla, S., Rubiales, D., 2012. Powdery mildew control in pea: A review. Agron. Sustain. Dev. 32, 401–409. https://doi.org/10.1007/s13593-011-0033-1.

Fondevilla, S., Satovic, Z., Rubiales, D., Torres, A.M., Cubero, J.I., 2008. Mapping of quantitative trait loci for resistance to *Mycosphaerella pinodes* in *Pisum sativum* subsp. *syriacum*. Mol. Breed. 21, 439–454. https://doi.org/10.1007/s11032-007-9144-4.

Fondevilla, S., Torres, A.M., Moreno, M.T., Rubiales, D., 2007. Identification of a new gene for resistance to powdery mildew in *Pisum fulvum*, a wild relative of pea. Breed. Sci. 57 (2), 181–184. https://doi.org/10.1270/jsbbs.57.181.

Gavuzzi, P., Rizza, F., Palumbo, M., Campanile, R.G., Ricciardi, G.L., Borghi, B., 1997. Evaluation of field and laboratory predictors of drought and heat tolerance in winter cereals. Can. J. Plant Sci. 77 (4), 523–531. https://doi.org/10.4141/P96-130.

Henderson, C.R., 1975. Best Linear Unbiased Estimation and Prediction under a Selection Model. Biometrics 31, 423–447. https://doi.org/10.2307/2529430.

Instituto de Investigación y Formación Agraria y Pesquera (IFAPA), n.d. Red de Información Agroclimática de Andalucía (RIA). Junta de Andalucía. ⟨https://www.juntadeandalucia.es/agriculturaypesca/ifapa/riaweb/web/⟩ (accessed 5 March 2025).

Joel, D.M., Hershenhorn, J., Eizenberg, H., Aly, R., Ejeta, G., Rich, P.J., Ransom, J.K., Sauerborn, J., Rubiales, D., 2007. Biology and management of weedy root parasites.

In: Janick, J. (Ed.), Horticultural Reviews, 33. Wiley, Hoboken, pp. 267–349. https://doi.org/10.1002/9780470168011.ch4.

Kang, Y., Ozdogan, M., Zhu, X., Ye, Z., Hain, C., Anderson, M., 2020. Comparative Assessment of Environmental Variables and Machine Learning Algorithms for Maize Yield Prediction in the US Midwest. Environ. Res. Lett. 15, 064005. https://doi.org/10.1088/1748-9326/ab7df9.

Kassambara, A., 2025. ggcorrplot: Visualization of a correlation matrix using 'ggplot2'. R package version 0.1.4.1. ⟨https://CRAN.R-project.org/package=ggcorrplot⟩.

Khan, M.F.R., Role, E., Fondevilla, S., Rubiales, D., 2013. *Didymella pinodes* and its management in field pea: Challenges and approaches. Field Crops Res. 148, 61–69. https://doi.org/10.1016/j.fcr.2013.04.003.

Madden, L.V., Ojiambo, P.S., 2024. The value of generalized linear mixed models for data analysis in the plant sciences. Front. Hortic. 3, 1423462. https://doi.org/10.3389/fhort.2024.1423462.

Magrini, M.-B., Anton, M., Cholez, C., Corre-Hellou, G., Duc, G., Jeuffroy, M.-H., Meynard, J.-M., Pelzer, E., Voisin, A.-S., Walrand, S., 2016. Why are grain-legumes rarely present in cropping systems despite their environmental and nutritional benefits? Analyzing lock-in in the French agrifood system. Ecol. Econ. 126, 152–162. https://doi.org/10.1016/j.ecolecon.2016.03.024v.

Martin-Sanz, A., Caminero, C., Jing, R., Flavell, A.J., Pérez de la Vega, M., 2011. Genetic diversity among Spanish pea (*Pisum sativum* L.) landraces, pea cultivars and the World *Pisum* sp. core collection assessed by retrotransposon based insertion polymorphisms (RBIPs). Span. J. Agric. Res. 9 (1), 166–178. https://doi.org/10.5424/sjar/20110901-214-10.

Ministerio de Agricultura, Pesca y Alimentación (MAPA), 2023. Encuesta sobre superficies y rendimientos de cultivos (ESYRCE) 2023: Boletín monográfico 1. Secretaría General Técnica, Gobierno de España. ⟨https://www.mapa.gob.es/es/estadistica/temas/estadisticas-agrarias/agricultura/esyrce⟩ (accessed 12 June 2025).

Moussart, A., Tivoli, B., Lemarchand, E., Deneufbourg, F., 1998. Role of seed infection by the Ascochyta blight pathogen of dried pea (*Mycosphaerella pinodes*) in seedling emergence, early disease development and transmission of the disease to aerial plant parts. Eur. J. Plant Pathol. 104, 93–102. https://doi.org/10.1023/A:1008673914537.

Mrabet, R., Savé, R., Toreti, A., Caiola, N., Chentouf, M., Llasat, M.C., Mohamed, A.A.A., Santeramo, F.G., Sanz-Cobena, A., Tsikliras, A., 2020. Food. In: Climate and Environmental Change in the Mediterranean Basin – Current Situation and Risks for the Future. First Mediterranean Assessment Report. In: Cramer, W., Guiot, J., Marini, K. (Eds.), Union for the Mediterranean, Plan Bleu. UNEP/MAP, Marseille, pp. 237–264. https://doi.org/10.5281/zenodo.7101080.

Olivier, F.C., Annandale, J.G., 1998. Thermal time requirements for the development of green pea (*Pisum sativum* L.). Field Crops Res. 56 (3), 301–307. https://doi.org/10.1016/S0378-4290(97)00097-X.

Olivoto, T., Lúcio, A.D.C., 2020. metan: An R package for multi-environment trial analysis. Methods Ecol. Evol. 11, 783–789. https://doi.org/10.1111/2041-210X.13384.

Olivoto, T., Lúcio, A.D.C., da Silva, J.A.G., Marchioro, V.S., de Souza, V.Q., Jost, E., 2019. Mean Performance and Stability in Multi-Environment Trials I: Combining Features of AMMI an BLUP Techniques. Agron. J. 111 (6), 2949–2960. https://doi.org/10.2134/agronj2019.03.0220.

Olivoto, T., Nardino, M., 2021. MGIDI: Toward an effective multivariate selection in biological experiments. Bioinformatics 37 (10), 1383–1389. https://doi.org/10.1093/bioinformatics/btaa981.

Perea-Torres, F., Castilla Bonete, A., Sillero Sánchez de la Puerta, J., Pasadas González, R., Canseco Merino, E., Basallote Serrano, E., 2021. Resultados de ensayos de variedades de guisantes proteaginosos en Andalucía, campaña 2020/21. Instituto de Formación Agraria y Pesquera(IFAPA) 1–21. ⟨https://www.juntadeandalucia.es/agriculturaypesca/ifapa/web/servifapa⟩.

Pérez-de-Luque, A., Flores, F., Rubiales, D., 2016. Differences in crenate broomrape parasitism dynamics on three legume crops using a thermal time model. Front. Plant Sci. 7, 1910. https://doi.org/10.3389/fpls.2016.01910.

Pérez-de-Luque, A., Jorrín-Novo, J.I., Cubero, J.I., Rubiales, D., 2005. *Orobanche crenata* resistance and avoidance in pea (*Pisum* spp.) operate at different developmental stages of the parasite. Weed Res. 45 (5), 379–387. https://doi.org/10.1111/j.1365-3180.2005.00464.x.

Pérez-de-Luque, A., Sillero, J.C., Cubero, J.I., Rubiales, D., 2004. Effect of sowing date and host resistance on the establishment and development of *Orobanche crenata* on faba bean and common vetch. Weed Res. 44 (3), 282–288. https://doi.org/10.1111/j.1365-3180.2004.00401.x.

Pesic, V., Djordjevic, R., Kadhum, E., Jankovic, P., Misic, D., 2013. Influence of the afila gene on grain yield in pea (*Pisum sativum* L.). Bulg. J. Agric. Sci. 19 (2), 186–191.

Pheirim, R., Singh, N.K., Mahanta, M., 2022. Molecular markers for powdery mildew in pea (*Pisum sativum* L.): A review. Legume Res. 45 (4), 399–409. https://doi.org/10.18805/LR-4740.

R Core Team, 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Robinson, G.K., 1991. That BLUP Is a Good Thing: The Estimation of Random Effects, 15–3 Stat. Sci. 6. https://doi.org/10.1214/ss/1177011926.

Roger, C., Tivoli, B., Huber, L., 1999. Effects of temperature and moisture on disease and fruit-body development of *Mycosphaerella pinodes* on pea (*Pisum sativum*). Plant Pathol. 48 (1), 1–9. https://doi.org/10.1046/j.1365-3059.1999.00312.x.

Roger, C., Tivoli, B., 1996. Spatio temporal development of pycnidia and perithecia and dissemination of spores of *Mycosphaerella pinodes* on pea (*Pisum sativum*). Plant Pathol. 45 (3), 518–528. https://doi.org/10.1046/j.1365-3059.1996.d01-139.x.

Rosielle, A.A., Hamblin, J., 1981. Theoretical aspects of selection for yield in stress and non-stress environments. Crop Sci. 21 (6), 943–946. https://doi.org/10.2135/cropsci1981.0011183X002100060033x.

Rubiales, D., 2018. Can we breed for durable resistance to broomrapes? Phytopathol. Mediterr. 57 (1), 170–185. https://doi.org/10.14601/Phytopathol_Mediterr-22543.

Rubiales, D., 2023. Managing Root Parasitic Weeds to Facilitate Legume Reintroduction into Mediterranean Rain-fed Farming Systems. Soil Syst. 7 (4), 99. https://doi.org/10.3390/soilsystems7040099.

Rubiales, D., Barilli, E., Rispail, N., 2023. Breeding for biotic stress resistance in pea. Agriculture 13 (9), 1825. https://doi.org/10.3390/agriculture13091825.

Rubiales, D., Fernández-Aparicio, M., Moral, A., Barilli, E., Sillero, J.C., Fondevilla, S., 2009. Disease resistance in pea (*Pisum sativum* L.) types for autumn sowings in Mediterranean environments. Czech J. Genet. Plant Breed. 45, 135–142. https://doi.org/10.17221/75/2009-CJGPB.

Rubiales, D., Fernández-Aparicio, M., Pérez-de-Luque, A., Prats, E., Castillejo, M.A., Sillero, J., Rispail, N., Fondevilla, S., 2009. Breeding approaches for crenate broomrape (*Orobanche crenata* Forsk.) management in pea (*Pisum sativum* L.). Pest Manag. Sci. 65, 553–559. https://doi.org/10.1002/ps.1740.

Rubiales, D., Fondevilla, S., Fernández-Aparicio, M., 2021. Development of pea breeding lines with resistance to *Orobanche crenata* derived from pea landraces and wild *Pisum* spp. Agronomy 11 (1), 36. https://doi.org/10.3390/agronomy11010036.

Rubiales, D., González-Bernal, M.J., Warkentin, T., Bueckert, R., Vaz Patto, McPhee, K., McGee, R., Smýkal, P., 2019. Advances in pea breeding. En. In: Hochmuth, G. (Ed.), *Achieving sustainable cultivation of vegetables*. Burleigh Dodds Science Publishing, pp. 575–606. https://doi.org/10.19103/AS.2019.0045.28.

Rubiales, D., Moreno, M.T., Sillero, J.C., 2005. Search for resistance to crenate broomrape (*Orobanche crenata* Forsk.) in pea germplasm. Genet. Resour. Crop Evol. 52 (8), 853–861. https://doi.org/10.1007/s10722-003-6116-3.

Rubiales, D., Osuna-Caballero, S., González-Bernal, M.J., Cobos, M.J., Flores, F., 2021. Pea breeding lines adapted to autumn sowings in broomrape prone Mediterranean environments. Agronomy 11 (4), 769. https://doi.org/10.3390/agronomy11040769.

Rubiales, D., Pérez-de-Luque, A., Cubero, J.I., Sillero, J.C., 2003. Crenate broomrape (*Orobanche crenata*) infection in field pea cultivars. Crop Prot. 22 (6), 865–872. https://doi.org/10.1016/S0261-2194(03)00070-X.

Schneider, K.A., Rosales-Serna, R., Ibarra-Perez, F., Cazares-Enriquez, B., Acosta-Gallegos, J.A., Ramirez-Vallejo, P., Wassimi, N., Kelly, J.D., 1997. Improving common bean performance under drought stress. Crop Sci. 37 (1), 43–50. https://doi.org/10.2135/cropsci1997.0011183X003700010007x.

Searle, S.R., Casella, G., McCulloch, C.E., 2006. Variance Components, second ed. Wiley, Hoboken. https://doi.org/10.1002/9780470316856.

Sinclair, T.R., Vadez, V., 2012. The future of grain legumes in cropping systems. Crop Pasture Sci. 63 (6), 501–512. https://doi.org/10.1071/CP12128.

Stagnari, F., Maggio, A., Galieni, A., Pisante, M., 2017. Multiple benefits of legumes for agriculture sustainability: An overview. Chem. Biol. Technol. Agric. 4 (1), 2. https://doi.org/10.1186/s40538-016-0085-1.

Tafesse, E.G., Gali, K.K., Lachagari, V.B.R., Bueckert, R., Warkentin, T.D., 2021. Genome-Wide Association Mapping for Heat and Drought Adaptive Traits in Pea. Genes 12 (12), 1897. https://doi.org/10.3390/genes12121897.

Talbot, M., Milner, A.D., Nutkins, M.A.E., Law, J.R., 1995. Effect of interference between plots on yield performance in crop variety trials. J. Agric. Sci. 124 (3), 335–342. https://doi.org/10.1017/S0021859600073299.

Tivoli, B., Banniza, S., 2007. Comparison of the epidemiology of ascochyta blights on grain legumes. Eur. J. Plant Pathol. 119 (1), 59–76. https://doi.org/10.1007/s10658-007-9117-9.

Tivoli, B., Béasse, C., Lemarchand, E., Masson, E., 1996. Effect of ascochyta blight (*Mycosphaerella pinodes*) on yield components of single pea (*Pisum sativum*) plants under field conditions. Ann. Appl. Biol. 129 (2), 207–216. https://doi.org/10.1111/j.1744-7348.1996.tb05745.x.

Urdiales-Flores, D., Zittis, G., Hadjinicolaou, P., Osipov, S., Klingmüller, K., Mihalopoulos, N., Kanakidou, M., Economou, T., Lelieveld, J., 2023. Drivers of accelerated warming in Mediterranean climate-type regions. npj Clim. Atmos. Sci. 6 (1), 97. https://doi.org/10.1038/s41612-023-00423-1.

Valderrama, M.R., Román, B., Satović, Z., Rubiales, D., Cubero, J.I., Torres, A.M., 2004. Locating quantitative trait loci associated with *Orobanche crenata* resistance in pea (*Pisum sativum*). Weed Res. 44 (4), 323–328. https://doi.org/10.1111/j.1365-3180.2004.00406.x.

van Loon, M.P., Alimagham, S., Pronk, A., Fodor, N., Ion, V., Kryvoshein, O., Kryvobok, O., Marrou, H., Mihail, R., Mínguez, M.I., Pulina, A., Reckling, M., Rittler, L., Roggero, P.P., Stoddard, F.L., Topp, C.F.E., van der Wel, J., Watson, C., van Ittersum, M.K., 2023. Grain legume production in Europe for food, feed and meat-substitution. Glob. Food Secur. 39, 100723. https://doi.org/10.1016/j.gfs.2023.100723.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, fourth ed. Springer, New York. https://doi.org/10.1007/978-0-387-21706-2.

Wang, K., Zhou, H., Wang, B., Jian, Z., Wang, F., Huang, J., Nie, L., Cui, K., Peng, S., 2013. Quantification of border effect on grain yield measurement of hybrid rice. Field Crops Res. 141, 47–54. https://doi.org/10.1016/j.fcr.2012.11.012.

Wohor, O.Z., Rispail, N., Rubiales, D., 2025. Genome wide association study unveils the genetic basis of *Orobanche crenata* resistance in pea. Theor. Appl. Genet. 138 (11), 272. https://doi.org/10.1007/s00122-025-05051-2.

Glossary

Appearance: Subjective trait stablished throught discussions with participating farmers regarding the crop type they would visually select. It was scored on a 1–5 scale (1 = poorest appearance; 5 = best appearance). The score integrates visual traits such us erect growth habit, high vegetative density, high pod number per plant, and absence of chlorosis.

arcsin-DS: Disease severity values (%) for the corresponding disease, transformed using the arcsine square-root method to stabilise variance prior to statistical analysis.

BLUPs (Best linear unbaised predictors): Predictors derived from linear mixed models modelling. In this study, they were used to predict genotype performance for a given trait after adjusting for environmental and other model effects.

Check cultivars: Commercial cultivar included in the field trial as a reference genotype for comparison with the breeding lines.

E, G, G×E: Relative contribution to total trait variance of environmental effects (E), genetic effects (G), and Genotype×Environment interaction (G×E).

Flowering: Phenological stage extending from sowing date to flowering onset within the plot.

Flower–pod: Phenological transition period from flowering onset to pod-filling onset.

GDD (growing degree days): Thermal accumulation calculated over a specific phenological window.

GY (grain yield): Dry seed yield extrapolated to kg ha^{-1}.

HI (harvest index): Ratio of dry grain yield to total dry biomass of the plot, expressed as a percentage.

Hmax / Hmin: Maximum and minimum relative humidity values summarised over the whole crop cycle.

IAS-CSIC: Institute for Sustainable Agriculture (IAS) of the Spanish National Research Council (CSIC). Research centre responsible for the development of the breeding lines tested in this study.

LMMs (Linear mixed models): Statistical models that account for both fixed and random effects. In this study, they were used to estimate or predict genotype performance across environments.

Lodging: Degree of stem leaning, scored on a 1–10 scale, from completely erect (1) to fully lodged (10).

MGIDI (multi-trait genotype–ideotype distance index): Multivariate index used to rank genotypes according to their distance from an ideotype that optimises yield and selected agronomic traits.

NDT>X: Number of consecutive days during which maximum temperature (*Tmax*) exceeds a threshold value X°C within a specific crop stage (in this study, X = 25 °C for Flower–pod and X = 30 °C for Pod-filling).

Oc: *Orobanche crenata* Forsk., a parasitic weed causing severe yield reductions in pea crops in the Mediterranean Basin.

Oc-free: Experimental environments without natural *Orobanche crenata* infestation.

Oc-infested: Experimental environments with natural *Orobanche crenata* infestation.

Plot height: Maximum vertical canopy height (cm), measured within each plot at the beginning of pod filling.

Pod-filling: Phenological stage extending from pod-filling onset to plot senescence.

Rainfall: Accumulated precipitation (mm) over the crop cycle or a specific phenological window, within an experimental environment.

SMLR (stepwise multiple linear regression): Regression approach used to identify key climatic, agronomic and stress-related predictors of yield. In this study, variables were iteratively added to or removed from the model according to their contribution to the Akaike information criterion (AIC).

Tmax, Tmin: Mean daily maximum and minimum air temperatures summarised for a specific phenological window, within an experimental environment.

WAASB: Weighted average of absolute scores from the singular value decomposition of the G×E interaction matrix of BLUPs. Stability index derived from the singular value decomposition of the BLUPs-based G×E interaction matrix. Lower WAASB values indicate greater stability across environments.

Yp: Grain yield of a given genotype in the favourable reference environment (SJ-NOV21 in this study) used to compute abiotic stress-tolerance indices.

Ys: Grain yield of a given genotype in the stress-prone reference environment (SJ-22 in this study) used to compute abiotic stress-tolerance indices.