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Wild *Lathyrus* species as a great source of resistance for introgression into cultivated grass pea (*Lathyrus sativus* L.) against broomrape weeds (*Orobanche crenata* Forsk. and *Orobanche foetida* Poir.)

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Abstract

Broomrape weeds (*Orobanche* spp.) are root holoparasitic plants that cause serious damage to a range of legume crops in the Mediterranean and sub-Saharan African regions. Grain yield of cultivated species of grass pea (*Lathyrus sativus* L.) is almost negligible at the highest infection severity of *Orobanche*. Crop wild relatives (CWRs) have emerged as a novel source for many traits in diverse crops. *Lathyrus* is one of the largest genera with more than 160 species. In the present study, we screened 285 accessions representing 13 *Lathyrus* species for their reactions against two common broomrape species, *Orobanche crenata* Forsk. and *O. foetida* Poir, under field conditions. Screening at hot spots in Morocco and Tunisia resulted in the identification of resistant accessions of wild *Lathyrus* species against the parasitic weed. The level of resistance to *O. foetida* was higher among wild species compared with *O. crenata.* Field results showed complete resistance for *O. crenata* and *O. foetida* by *L. articulatus* L. and moderate resistance by *L. aphaca* L. and *L. ochrus* (L.) DC. Resistance to *O. crenata* in *L. sativus* accessions was validated in a pot experiment under controlled conditions. Two accessions—namely, IG64782 and IG65197—showed complete resistance to *O. crenata*. A moderately resistant accession, IG116989, that revealed low infestation in the field showed high susceptibility in pot experiment. The results indicated that the resistance against *O. crenata* and *O. foetida* was associated with slow development of the established tubercles and low induction of parasite germination.

Abbreviations: β-ODAP, β-N-oxalyl-l-α,β diamino propionic acid; CWR, crop wild relative; EODW, dry weight of emerged *Orobanche* per plant; EON, emerged *Orobanche* spikes per plant; ICARDA, International Center for Agricultural Research in the Dry Areas; PI, parasitism index; MR, moderately resistant.

1 | INTRODUCTION

Grass pea (*Lathyrus sativus* L.) is a climate-resilient, nutrient-rich legume crop grown mainly in fragile agroecosystems since its domestication in the Balkan Peninsula (Kumar et al., 2013). The crop holds immense value in human food, animal feed, and ecosystem services in South Asia (Kumar, Bejiga, Ahmed, Nakkoul, & Sarker, 2011), sub-Saharan Africa (Girma & Korbu, 2012), and the Mediterranean region (Vaz Patto et al., 2006). It is a promising crop for adaptation under climate change and variability because of its tolerance to drought, waterlogging, and salinity (Jiang et al., 2013; Kumar et al., 2011; Lambein, Travella, Kuo, Van Montagu, & Heijde, 2019). With emphasis on plant-based protein diets and adaptation to climate change, grass pea has emerged as a focused crop for research, as well as for cultivation in difficult regions, in recent years (Sarkar et al., 2019). Despite the presence of a plant toxin called β-N-oxalyl-l-α,β diamino propionic acid (β-ODAP), the potential of grass pea as a health-promoting nutraceutical has recently been recognized (Lambein et al., 2019). The renewed interest in grass pea is also due to emphasis on animal feed and fodder, and diversification of cereal-based cropping systems, which occupy large areas under cultivation globally (Dixit, Parihar, Bohra, & Singh, 2016). The crop is almost free from major diseases and insect pests except some occasional appearance under favorable environmental conditions (Kumar et al., 2011). However, in the Mediterranean region of southern Europe and North Africa, the crop encounters the infestation of parasitic broomrape weeds, mainly *Orobanche crenata*, causing severe yield and biomass losses (Fernández-Aparicio, Flores, & Rubiales, 2016; Parker, 2009).

Broomrape weeds are root holoparasitic plants that attack a range of legume crops (Fernández-Aparicio et al., 2016; Rubiales et al., 2009; Trabelsi, Abbes, Amri, & Kharrat, 2015). Two species of broomrapes, *Orobanche crenata* Forsk. and *O. foetida* Poir., are reported to cause serious damage to grass pea crop (Fernández-Aparicio et al., 2016; Vaz Patto & Rubiales, 2009). Although the infestation of *O. foetida* is confined to Tunisia, *O. crenata* is a serious production constraint across the Mediterranean countries (Fernández-Aparicio et al., 2016). These parasitic weeds are completely dependent on the host for water and nutrients (Abbes, Kharrat, Delavault, Chaïbi, & Simier, 2009; Trabelsi et al., 2015). The germination of *Orobanche* seed occurs at the host roots in response to specific chemical compounds or germination stimulants released by the host plant (Abbes, Trabelsi, Kharrat, & Amri, 2019; Fernández-Aparicio et al., 2016; Trabelsi et al., 2015). Severe effects of *O. crenata* parasitism in the host crop, and high persistence of parasitic seedbank in agricultural soils, have led to abandonment of legume cultivation in major legume growing areas (Rubiales et al., 2009). The detrimental effect of broomrape parasitism in crop yield can reach up to 100% depending on infection severity and the broomrape–crop association (Fernández-Aparicio et al., 2016). In grass pea, reduction in aboveground biomass in both vegetative and reproductive organs was observed starting even at low infection severity, and half maximal inhibitory performance was predicted as 1.5 parasites per grass pea plant with almost zero grain yield at severities higher than four parasites per plant (Fernández-Aparicio et al., 2016).

Core Ideas

- Crop wild relatives are great source of novel traits/alleles
- Complete resistance to parasitic weeds Orobanche exists in wild relatives of grass pea
- Underground Orobanche attachments needs to be included inthe screening for Orobanche resistance

Several options including physical, mechanical, chemical, biological, and cultural practices have been suggested and tested to control *Orobanche* but none of them proved effective due to technical challenges, economic constraints, and the complexity of host–parasite interactions (Grenz, Manschadi, DeVoil, Meinke, & Sauerborn, 2005; Rubiales et al., 2009). Moderate and incomplete resistance has been reported in the cultivated species *L. sativus* (Fernández-Aparicio & Rubiales, 2010; Fernández-Aparicio, Flores, & Rubiales, 2012). Limited screening of crop wild relatives (CWRs) of grass pea, including *Lathyrus ochrus* (L.) DC. and *L. clymenum* L. (Sillero, Cubero, Fernández-Aparicio, & Rubiales, 2005), and *L. cicera* L. (Fernández-Aparicio & Rubiales, 2010; Fernández-Aparicio, Flores, & Rubiales, 2009), has shown some resistance to broomrape, indicating scope for introgression breeding. *Lathyrus* is a large genus containing >160 species (Lewis, Schrire, Mackinder, & Lock, 2005). Its center of diversity is located mainly in the Mediterranean and Irano-Turanian regions (Kupicha, 1983). The International Center for Agricultural Research in the Dry Areas (ICARDA) genebank holds 4,457 accessions of 45 *Lathyrus* species (Shehadeh, Amri, & Maxted, 2013). This collection also includes 1,555 accessions of wild species, which are recognized as an excellent source of novel traits or alleles due to their historical record of adaptation to a diverse range of habitats. This collection is unique because 35 and 64% of the accessions are respectively wild relatives and landraces, mainly of *L. sativus*, followed by *L. cicera* and *L. ochrus* (Kumar et al., 2013). Screening of this wild gene pool has emerged as a rich reservoir for traits of breeders' interest such as β-ODAP content, disease resistance, and so on (Aletor, El-Moneim, & Goodchild, 1994; Kumar et al., 2013; Patto et al., 2011). Therefore, efforts have been made to evaluate wild relatives to identify zero ODAP germplasm. Assessment of ODAP in wild relatives indicated that none of the species is free from ODAP. Under the Crop Trust-funded project on enhancing prebreeding in barley (*Hordeum vulgare* L.) and grass pea (GS16005), the present study was undertaken to screen 285 accessions representing 13 *Lathyrus* species against *O.*

TABLE 1 *Lathyrus* species, number of accessions, and their origin screened for *Orobanche crenata* and *O. foetida* in field experiment during the 2017–2018 cropping season

Species	No. of accessions	Origin
L. annuus	2	Syria
L. aphaca	1	
L. articulatus	7	Bulgaria, Czech Republic, Morocco, Portugal, Syria
L. blepharicarpus	1	
L. cassius	1	
L. cicera	54	Australia, Greece, India, Norway, Syria, Turkey
L. gorgoni	5	Syria, Turkey
L. hierosolymitanus	2	Syria, Turkey
L. inconspicuus	4	
L. ochrus	44	Cyprus, Czech Republic, Germany, Greece, India, Italy, Russia, Syria
L. pseudocicera	2	
L. sativus	161	Afghanistan, Bulgaria, Canada, Cyprus, Ethiopia, Germany, Greece, Iran, Moldova, Turkey
L. tingitanus	1	Bangladesh

crenata and *O. foetida* under highly infested field conditions to identify potential sources of resistance for their use in breeding programs.

2 | MATERIALS AND METHODS

2.1 | Plant material

A total of 285 accessions representing 13 *Lathyrus* species were obtained from the ICARDA genebank and purified under cages during the preliminary screening in the 2016–2017 crop season. Single plant derived seeds of *L. annuus* L. (2), *L. aphaca* L. (1), *L. articulatus* L. (7), *L. blepharicarpus* Boiss. (1), *L. cassius* Boiss. (1), *L. cicera* L. (54), *L. gorgoni* Parl. (5), *L. hierosolymitanus* Boiss. (2), *L. inconspicuus* L. (4), *L. ochrus* (44), *L. pseudocicera* Pamp. (2), *L. sativus* (161), *and L. tingitanus* L. (1) were evaluated for resistance to *O. crenata* and *O. foetida* under field conditions. These accessions are originated from different geographical regions (Table 1).

2.2 | Experimental details and site description

Field experiments were carried out following an augmented design with repeated susceptible checks of the faba bean (*Vicia faba* L.) cultivar 'Aguadulce' and grass pea (IG90174, IG147607, and IG147655) at two locations: Marchouch (33.56˚ N, 6.63˚ W; 392 m asl) in Morocco and Oued-Beja (36.44˚ N, 9.13˚ E; 150 m asl) in Tunisia during the 2017–2018 cropping season. The Marchouch experimental station of ICARDA represents a Mediterranean semiarid environment with ∼400 mm annual rainfall (El-haddad et al., 2020). The Beja agricultural experimental station located in northwest Tunisia is characterized by a subhumid climate with moderate winters and ∼600 mm average annual rainfall (Trabelsi et al., 2015). Field screening was taken up in a field plot with a known history of a high and homogeneous infestation of *O. crenata* at Marchouch, Morocco, and of *O. foetida* at Beja, Tunisia. There were 19 blocks, each consisting 15 plots of test entries, three plots of faba bean, and one plot each of three grass pea checks. Each accession was planted in a 1-m single-row plot, with 60-cm distance between rows. In each row, 20 seeds were sown by hand at a 5-cm depth maintaining a 5-cm space between plants. Every tenth row in each block was planted with highly susceptible faba bean cultivar Aguadulce. Our previous studies indicated that faba bean served as a good indicator on *Orobanche* infestation and homogeneity within a sick plot and a good facilitator of *Orobanche* infestation on companion crops (Ennami et al., 2017, 2020). In fact, among all the cool-season legume crops, faba bean is considered as the most susceptible crop to broomrapes and was used in our trial in order to monitor the uniformity of *Orobanche* infestation. To increase the infestation, early planting in the first week of December was conducted. Care was taken to raise a successful crop with recommended doses of fertilizers, and need-based irrigation using a sprinkler system. The field was kept weed free by manual uprooting of weeds other than broomrape, and no herbicide was applied to prevent interference with broomrape development.

2.3 | Weather conditions

Daily minimum and maximum temperatures (˚C), precipitation (mm), and relative humidity (%) were recorded throughout the crop season at the experimental sites. A daily mean temperature between 10 and 28 ˚C was recorded at Marchouch and Beja research stations during the crop season (Figure 1). At Marchouch and Beja stations, the crop received 504 and 495 mm of well-distributed rainfall, about 106 mm more water than the average, which augured well for a uniformly high infestation of *Orobanche*.

2.4 | Data recording

Observations were recorded on days to 50% flowering, maturity, and appearance of the first *Orobanche* shoot on a plot

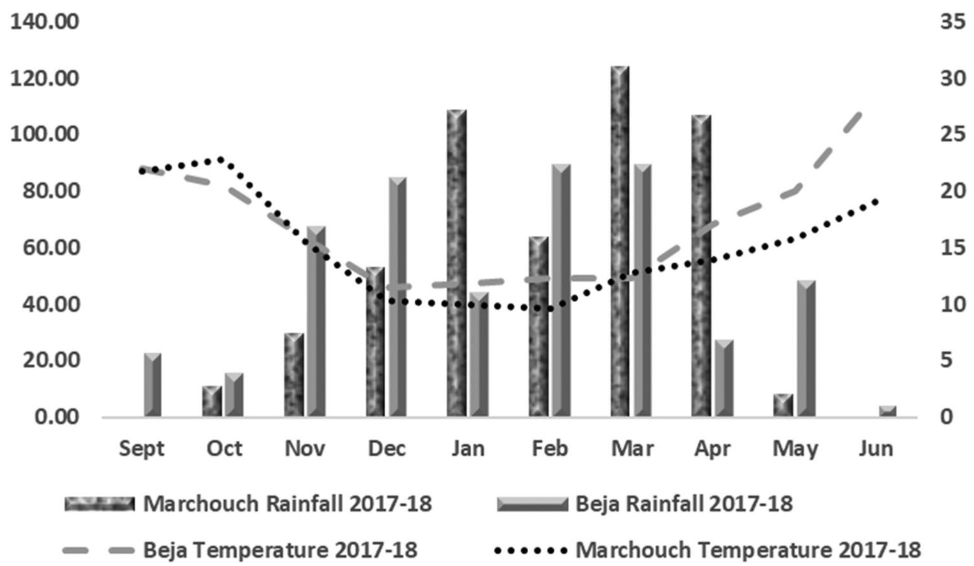

FIGURE 1 Rainfall (mm) and monthly air temperature (˚C) at Marchouch experimental station, Morocco, and Beja research station, Tunisia, during the 2017–2018 cropping season

TABLE 2 Incidence, severity, and parasitism index (PI) of different *Lathyrus* species tested against *O. crenata*- and *O. foetida*-infested plots in Morocco and Tunisia during the 2017–2018 cropping season

	O. crenata			***O. foetida***		
***Lathyrus* species**	**Incidence**	**Severity**	**PI**	**Incidence**	**Severity**	**PI**
	%	0–9 scale		%	0–9 scale	
L. annuus	95.00	6.00	5.85	0.00	1.00	0.00
L. aphaca	60.00	1.00	0.60	0.00	1.00	0.00
L. articulatus	0.00	1.00	0.00	0.00	1.00	0.00
L. blepharicarpus	30.00	1.00	0.30	0.00	1.00	0.00
L. cassius	15.00	1.00	0.15	0.00	1.00	0.00
L. cicera	74.70	1.64	1.19	0.19	1.02	0.00
L. gorgoni	35.00	3.67	1.81	0.00	1.00	0.00
L. hierosolymitanus	100.00	9.00	9.00	0.00	1.00	0.00
L. inconspicuus	85.00	5.00	4.85	0.00	1.00	0.00
L. ochrus	2.39	6.64	0.20	0.00	1.00	0.00
L. pseudocicera	75.00	1.00	0.75	0.00	1.00	0.00
L. sativus	54.88	8.21	4.48	0.47	1.09	0.01
L. tingitanus	100.00	9.00	9.00	5.00	2.00	0.10
Checks	77.28	8.89	6.75	50.88	5.09	4.52

basis. In addition, plants were harvested at maturity for recording biological and grain yield. *Orobanche* infestation level was estimated on each accession by counting the number of emerged *Orobanche* spikes per plant (EON) and by measuring the dry weight (EODW) (Amri, Trabelsi, Abbes, & Kharrat, 2019). This was done by dividing the number of emerged broomrapes by the number of host plants per row. The incidence (percentage of host plants showing emerged spikes on a 0–100% scale), severity on a 1–9 scale, and parasitism index (incidence × severity/100) were measured following the standard procedures suggested by Abbes, Kharrat, Delavault, Simier, and Chaïbi (2007).

2.5 | Pot experiment

Based on the field results of 2017–2018, eight accessions of *L. sativus* selected for their resistance to both *O. foetida* and *O.*

TABLE 3 Number (EON) and dry weight (EODW) of emerged Orobanche per plant along with seed yield of different *Lathyrus* species in field uniformly infested with *O. crenata* in Morocco and *O. foetida* in Tunisia during the 2017–2018 cropping season

	O. crenata			*O. foetida*		
Species	**EON**	**EODW**	**Seed yield**	**EON**	**EODW**	**Seed yield**
		———g———			———g———	
L. annuus	2.74	0.38	3.13	0.03	0.13	6.86
L. aphaca	0.38	0.15	21.14	0.00	0.00	0.50
L. articulatus	0.00	0.00	29.68	0.00	0.00	9.08
L. blepharicarpus	0.60	0.25	20.13	0.00	0.00	6.22
L. cassius	1.36	0.14	10.47	0.00	0.00	5.23
L. cicera	2.91	0.60	16.54	0.00	0.00	5.71
L. gorgoni	0.13	0.13	3.43	0.00	0.00	9.93
L. hierosolymitanus	2.83	0.44	0.00	0.00	0.00	1.35
L. inconspicuus	3.96	0.65	6.08	0.00	0.00	6.00
L. ochrus	0.07	0.00	31.17	0.00	0.00	5.72
L. pseudocicera	2.57	0.39	10.97	0.00	0.01	9.43
L. sativus	1.91	1.00	1.14	0.00	0.00	9.93
L. tingitanus	3.77	0.38	0.08	0.02	0.10	9.06
Susceptible checks	19.45	1.97	0.00	0.25	0.75	2.50

crenata were further evaluated along with two moderately and high susceptible checks, respectively, under controlled conditions in a glasshouse at ICARDA-Rabat facilities during 2018–2019. To evaluate the resistance level and the impact of the parasite on the host plant development, two treatments were applied: (a) infested and (b) noninfested plants or pots. The experimental design was a randomized complete block with three replications. Three pots per accession were used for each treatment. Pots were filled with soil–peat (2:3, v/v). Soil in infested pots was artificially inoculated with 20 mg of *O. crenata* seeds per kilogram of soil. Plants were watered when necessary, and at maturity, they were uprooted from soil and roots and were carefully washed with running tap water. Host plant parameters—namely, total attachment (TAN), underground (UON), and emerged (EON) *Orobanche* number per plant—were recorded. Root (RDW) and shoot (SDW) dry weight per plant, number of pods per plant (PDN), dry weight of emerged (EODW) and underground (UODW) *Orobanche* per plant were determined after drying in oven at 70 ˚C for 72 h. The broomrape attachments were classified according to the stage of development (S), following S1 to S5 stages, where S1 = small tubercle (1–3 mm), S2 = crown roots start to develop, S3 = bud ≤1 cm, S4 = first development of spike below ground surface, and S5 = emergence of spike (Labrousse, Arnaud, Serieys, Bervillé, & Thalouarn, 2001; Sillero et al., 2005).

2.6 | Statistical analysis

Statistical analysis was carried out with the R statistical software (RStudio Team, 2016). Analysis of variance (ANOVA) was conducted using a randomized complete block design, to test for the significance of differences among accessions for the host and parasite variables. Treatment means were compared by Duncan test. Pearson correlations were calculated among the host and parasite variables on the basis of mean values. The statistical model for pot experiments involved a completely randomized design with three replicates, in which the host genotype was the unique fixed factor. For shoot dry weight, root dry weight, and pod number, comparison includes the genotype with and without *Orobanche* infection. To get a genotypic variance component, a linear mixed model with genotypes considered to be random was performed for both designs. The Lme4 package (Bates, Mächler, Bolker, & Walker, 2015) in R was used for these analyses.

3 | RESULTS

3.1 | Identification of resistance sources

Field screening showed significant differences ($P \leq .05$) among *Lathyrus* species against *O. crenata*. However, no significant difference was observed against *O. foetida*. Among 13 *Lathyrus* species tested against *O. crenata*, the incidence of *Orobanche* infestation ranged from 0 to 100% and severity ranged from 1 to 9 as compared with 77.3% and 8.9 score in susceptible checks, respectively (Table 2). The incidence of *Orobanche* was zero in *L. articulatus* and 2.39% in *L. ochrus*, with a severity score of 1 in *L. aphaca*, *L. articulatus*, *L. blepharicarpus*, *L. cassius*, and *L. pseudocicera.* Based on the parasitism index (PI), *L. aphaca*, *L. articulatus*, *L.*

FIGURE 2 Infestation of *O. crenata* at Marchouch in Morocco ([a] resistant, [b] moderately resistant, and [c] susceptible) and (d, f) *O. foetida* at Beja in Tunisia in grass pea germplasm during the 2017–2018 cropping season

blepharicarpus, *L. cassius*, *L. pseudocicera*, and *L. ochrus* showed overall high resistance to *O. crenata* parasitism with <1 score as compared with a 6.75 score in susceptible checks. Two species, *L. cicera* and *L. gorgoni*, showed a moderately resistant (MR) reaction with PI score between 1 and 2 while cultivated species *L. sativus* and *L. inconspicuous* recorded PI score between 4 and 5, suggesting their moderate susceptibility to *O. crenata.* The remaining three species (*L. annuus*, *L. hierosolymitanus,* and *L. tingitanus*) recorded >5 PI score, showing high susceptibility to *O. crenata*. All wild species including cultivated one showed less than 1 PI score as compared with 4.5 PI of susceptible checks, indicating high resistance to *O. foetida*.

Table 3 presents the number (EON) and dry weight (EODW) of emerged *Orobanche* spikes per host plant along with seed yield per plant to assess the performance of wild species under *Orobanche* infestation. Among the 13 *Lathyrus* species, the number of emerged *Orobanche* spikes (EON) varied from 0 to 19.45 for *O. crenata* and from 0 to 0.25 for *O. foetida.* Four species—namely, *L. articulatus* (0), *L. ochrus* (0.07), L. gorgoni (0.13), *L. blepharicarpus* (0.6), and *L. aphaca* (0.38)—were compared with 19.45 EON for checks (Figure 2). Dry weight of emerged *O. crenata* (EODW) on these species was <0.25 g as compared with 1.97 g on checks. For *O. foetida,* only three species (*L. annuus*, *L. tingitanus*, and *L. pseudocicera*) showed very low EON and EODW. Seed

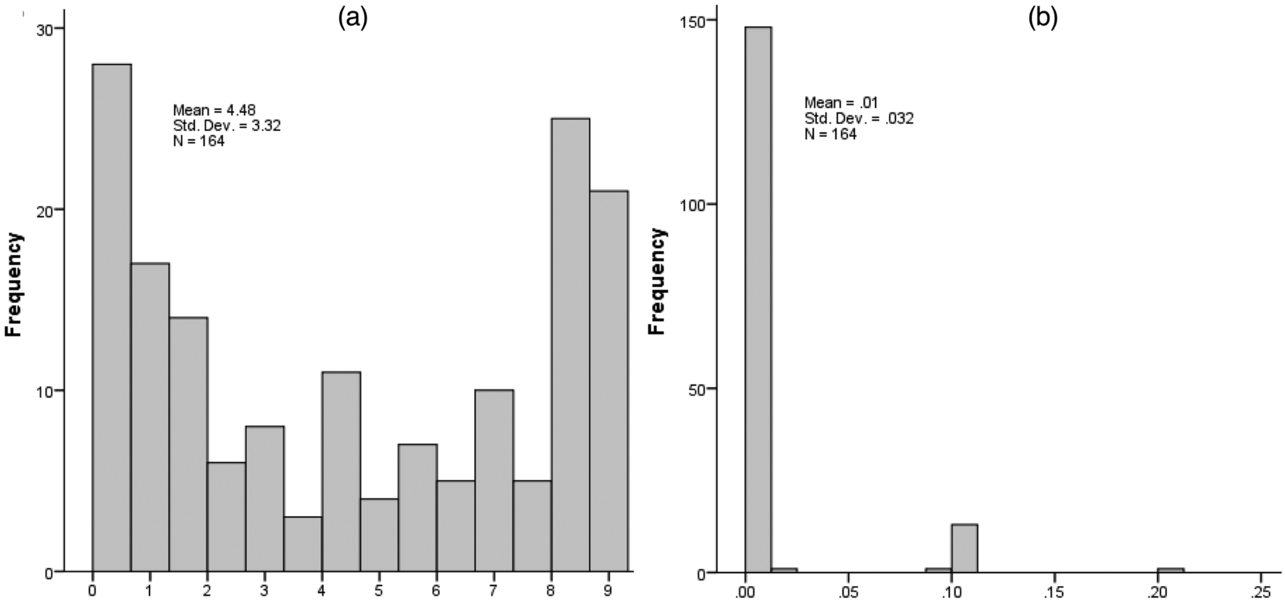

FIGURE 3 Frequency distribution of 162 *L. sativus* accessions based to the parasitism index for (a) *O. crenata* tested in Morocco and (b) *O. foetida* in Tunisia

yield per plant was significantly higher in *Lathyrus* species in Morocco as compared with Tunisia. The highest seed yield was recorded in *L. ochrus* (31.17 g), *L. articulatus* (29.68 g), *L. aphaca* (21.14 g), *L. blepharicarpus* (20.13 g), *L. cicera* (16.54 g), *L. pseudocicera* (10.97 g), and *L. cassius* (10.47 g) as compared with no seed yield in susceptible checks. In Tunisia, the highest seed yield was recorded in *L. gorgoni*, *L. sativus*, and *L. pseudocicera*. Based on the low score of EON and EODW and high seed yield, four species—namely, *L. aphaca, L. articulatus, L. blepharicarpus*, and *L. ochrus*—qualified as highly resistant against *O. crenata* in the present study. The frequency distribution of 162 cultivated accessions showed significant variation for PI ranging from 1 to 10 (Figure 3). Based on low PI and performance, one accession each of *L. aphaca* (IG65053) and *L. gorgoni* (IG65375), four accessions of *L. cicera* (IG64844, IG64867, IG64873, and IG 64864), seven of *L. articulatus* (IG64733, IG64735, IG64786, IG64787, IG64795, IG64798, and IG64800), and 13 of *L. ochrus* (IG62140, IG64731, IG64801, IG64804, IG64807, IG64808, IG64809, IG64810, IG64812, IG64813, IG64814, IG64816, and IG64823), and 10 of *L. sativus* (IG64782, IG64875, IG65187, IG65197, IG116989, IG65204, IG64951, IG116997, IG117544, and IG65149) were identified as resistant against *O. crenata* and *O. foetida* (Table 4). These results were validated in the same field at Marchouch in Morocco during the 2018–2019 cropping season.

3.2 | Result validation

Resistance to *O. crenata* in *L. sativus* accessions was validated in pot experiment during 2018–2019 using 10 grass pea accessions representing resistant, MR, and susceptible reactions in field screening at Marchouch in Morocco during 2017–2018.

The ANOVA (Table 5) showed significant differences among the selected accessions for emerged Orobanche number per plant (EON), emerged Orobanche dry weight per plant (EODW), underground *Orobanche* number per plant (UON), and underground Orobanche dry weight per plant (UODW). The results showed no significant differences between the studied accessions for the average attachments per plant, which varied from 0 to 16.67 in *O. crenata*-inoculated pots (Table 6). Significant differences were observed for the average of emerged and underground *Orobanche* number and dry weight per plant. The results showed that *O. crenata* parasitized only eight accessions. Two accessions—namely, IG64782 and IG65197—confirmed their complete resistance to *O. crenata* in the pot experiment. Among the six accessions with MR reaction in the field experiment, four accessions—namely, IG65204, IG64875, IG64951, and IG65187—confirmed their MR reaction in pot experiments. The remaining two accessions (IG116989 and IG116997) that showed low infestation in field experiment revealed high susceptibility in the pot experiment. The numbers of underground *Orobanche* in IG116989 (13.3) and IG116997 (9.3) were higher than the number of emerged ones (3), resulting in the susceptible reaction in the pot experiment. In addition, dry weights of emerged and underground *Orobanche* were significantly higher in two MR lines (IG64951 and IG116997) in the pot experiment. These accessions were more susceptible than the checks because the underground *Orobanche* number per plant were not counted in the field experiment, followed by the susceptible check IG65042 (11.33). The low number of underground *O. crenata* per plant were recorded for MR line IG65187 (1.33) and susceptible check IG64908 (3.00).

TABLE 4 Germplasm accessions of 13 *Lathyrus* species tested and their reactions to *Orobanche crenata* and *O. foetida* in field experiment during the 2017–2018 cropping season

Species	IG name
L. annuus	65353, 65463
L. aphaca	65053
L. articulatus	**64733, 64735, 64786, 64787, 64795, 64798, 64800**
L. blepharicarpus	64865
L. cassius	65277
L. cicera	64831, 64832, 64833, 64836, 64837, 64838, 64839, 64842, **64844**, 64845, 64846, 64848, 64849, 64851, 64855, 64857, 64858, 64859, 64861, 64862, 64863, 64866, **64867**, 64868, 64869, 64870, 64872, **64873**, 64876, 64878, 65103, 65281, 65823, 64843, 64734, 64841, 64745, 64830, 64834, 64840, 64853, 65046, 64879, 64977, 64852, 64856, **64864**, 64854, 64860, 65252, 65820, 64847, 65074, 65949
L. gorgoni	65330, **65375**, 65750, 63034, 64989
L. hierosolymitanus	65735, 65494
L. inconspicuus	65279, 65519, 64983, 65500
L. ochrus	**62140, 64731, 64801, 64804, 64807, 64808, 64809, 64810, 64812, 64813, 64814, 64816,** 64817, 64818, 64819, 64820, 64821, 64822, **64823**, 64824, 64825, 64827, 64828, 64850, 64950, 65075, 65221, 65222, 65224, 65225, 65226, 65227, 65228, 65229, 65230, 65237, 65242, 65310, 65340, 65373, 65376, 65390, 117945,65235
L. pseudocicera	65065, 65543
L. sativus	**64782**, **64875**, 64882, 64886, 64900, 64908, 64909, 64915, 64918, 65136, 65184, **65187,** 65195, **65197**, 65210, 65211, 65212, 65213, 65223, 116890, 64935, 65186, 116889, 117496, 65040, 65179, 117178, 65178, 65183, 65189, 65194, 65200, 116893, 117117, 65039, 117003, 117333, 65017, 65112, 65192, 117121, 117122, 117331, 117493, **116989**, 65108, 65201, 117065, 117369, 117548, 117551, 117553, 64975, 64993, 117113, 117504, 117528, 117022, 65176, 65232, 65240, 65248, 116992, 117012, 117018, 117034, 117047, 117053, 117064, 117110, 117115, 117119, 117175, 65143, 65174, 65175, 65162, 117365, 117598, **65204**, 64723, 65104, 65231, 65244, 116913, 117171, 117224, 117511, 117531, 117543, 64970, 65157, 117352, 64961, 117515, 117535, 117546, 65147, **64951,** 64958, 64960, 64962, 64963, 64968, 65042, 65153, 65154, 65156, 65160, 65163, 65170, 65171, 65173, 65193, 65205, 65233, 65234, 65236, 65245, 65246, 65247, 116818, **116997**, 117004, 117060, 117095, 117182, 117196, 117222, 117225, 117229, 117255, 117277, 117283, 117328, 117332, 117334, 117358, 117368, 117373, 117506, 117507, 117509, 117530, 117533, **117544,** 117604, **65149**, 117118, 117197, 117220, 117223, 117279, 117336, 117540, 64964, 116949, 117204, 117211, 117510, 117526
L. tingitanus	116891

Note. IG numbers in **bold** are highly resistant accessions against *O. crenata* and *O. foetida*.

TABLE 5 Mean squares for five infestation parameters recorded in the pot experiment

Source	df	TAN	EON	EODW	UON	UODW
				g		g
Corrected model	7	51.18ns[a]	14.90*	75.43*	3.95*	30.47*
Genotypes	7	51.18ns	14.90*	75.43*	3.95*	30.47*
Error	12	44.56	7.56	34.5	1.86	24.22

Note. TAN, total attachment number per plant; EON, emerged *Orobanche* number per plant; EODW, emerged *Orobanche* dry weight per plant; UON, underground *Orobanche* number per plant; UODW, underground *Orobanche* dry weight per plant.

[a]ns, nonsignificant.

*Significant at the .05 probability level.

However, dry weight of underground *Orobanche* per plant was highest in MR accession IG116997 (9.73 g), with IG64875 having the lowest value (0.5 g).

Root and shoot dry weight and pod number per plant of tested grass pea germplasm were determined in infested and noninfested pots (Figure 4). The ANOVA analysis showed significant differences among the tested germplasm accessions for shoot dry weight, root dry weight, and pod number per plant under both treatments (Table 7). Performance of the test entries differed significantly under infested vs. noninfested conditions with significant interaction effects. The root dry weight of host plants was higher in infested than noninfested pots (Table 8), whereas the opposite holds true for shoot dry weight and pod numbers. High shoot dry weight per plant in infested pots were observed in resistant accessions IG64782 (20.6 g) and IG65197 (10.7 g), whereas low values were recorded for IG116989 (1.17 g) and susceptible check IG64908 (1.43 g). No pod development was observed on two MR accessions (IG64951 and IG116989) and susceptible accessions (IG65042 and IG64908) in infested pots, whereas

TABLE 6 Total attachment number (TAN), and number (EON, UON) and dry weight (EODW, UODW) of emerged and underground *Orobanche crenata* per plant in selected grass pea accessions in the pot experiment under controlled conditions during 2018–2019

Accession	Reaction against *O. crenata* in 2017–2018 test	TAN S1–S5	Emerged *Orobanche* per plant EON S5	Emerged *Orobanche* per plant EODW S5	Underground *Orobanche* per plant UON S5	Underground *Orobanche* per plant UODW S5
				g		g
IG65197	Resistant	0.00a	0.00b	0.00d	0.00c	0.00b
IG64782	Resistant	0.00a	0.00b	0.00d	0.00c	0.00b
IG65204	Moderate R	5.67a	0.33b	0.10cd	5.33abc	0.83b
IG64875	Moderate R	11.67a	7.67a	2.30bc	4.00abc	0.50b
IG64951	Moderate R	10.00a	7.67a	4.57a	2.33bc	1.07b
IG65187	Moderate R	10.00a	5.33a	1.93bcd	1.33bc	0.60b
IG116989	Moderate R	16.67a	3.33ab	1.07bcd	13.33a	1.47b
IG116997	Moderate R	12.33a	3.00ab	3.27ab	9.33abc	9.73a
IG65042	Susceptible	14.67a	3.33ab	1.80bcd	11.33ab	3.73ab
IG64908	Susceptible	6.67a	3.67ab	2.57ab	3.00abc	0.73b
Mean over all accessions		11.00	3.43	1.76	5.00	1.87

Note. Values with a common letter per column are not significantly different according to Duncan's test ($p = .05$). R, resistant; MR, moderately resistant; S, susceptible.

these lines showed 8–16 pods per plant in non-infested pots. These results indicate that the resistance against *O. crenata* and *O. foetida* could be associated with a low induction of parasite seed germination and/or a slowed development of the established tubercles on host root system.

3.3 | Correlations among parasitism parameters

Correlation coefficients between different parameters of *Orobanche* infestation are presented in Table 9. No correlation was observed between the number of emerged *Orobanche* spikes and the pod number per plant with all the other recorded parameters. The number of emerged *Orobanche* spikes reflects the level of infestation and could be used as a good indicator of resistance but should be used with the number of underground tubercles. The number of pods per plant is one of the determinant yield attributes that can provide a good information on the resistance level against broomrapes. Results also showed a significant positive correlation between total attachment number and underground *Orobanche* number. This positive correlation indicates that number of underground Orobanche is very important parameter to measure during screening.

4 | DISCUSSION

Grass pea cultivation in the Mediterranean region of southern Europe, North Africa, and West Asia has almost been abandoned because of high incidence of *Orobanche* in the region, high susceptibility of existing grass pea varieties, and favorable environments for growth and development of parasitic weeds (Vaz Patto et al., 2006, 2008). Area under grass pea cultivation could be regained in cereal–livestock systems if *Orobanche* resistant varieties with low ODAP content are developed and popularized in these regions. Past efforts in the screening of limited germplasm showed moderate and incomplete resistance in cultivated (Fernández-Aparicio & Rubiales, 2010; Fernández-Aparicio et al., 2012) and wild (Fernández-Aparicio & Rubiales, 2010; Fernández-Aparicio et al., 2009; Sillero et al., 2005) species of grass pea. The present study screened 13 *Lathyrus* wild species against *O. crenata* and *O. foetida* under most congenial environments in Morocco and Tunisia, as indicated by high PI on susceptible check across the blocks.

In the present study, we used number and dry weight of emerged *Orobanche* shoots per plant, seed yield, *Orobanche* incidence (%), severity score, and PI in field trials to assess *Orobanche* infestation in test entries. The number of emerged *Orobanche* shoots per host plant is generally considered the principal parasitism parameter. Nevertheless, because of technical constraints, field trials do not often consider the number and dry weight of underground *Orobanche* tubercles, which could be important under high infested fields and the results solely derived from the emerged shoots could overestimate the resistance level and might lead to wrong inference (Fernández-Aparicio, Flores, & Rubiales, 2012). This was evident in the present study when some of the MR accessions showed highly susceptible reaction in pot experiment under controlled conditions where both emerged and underground shoots were considered for assessing the

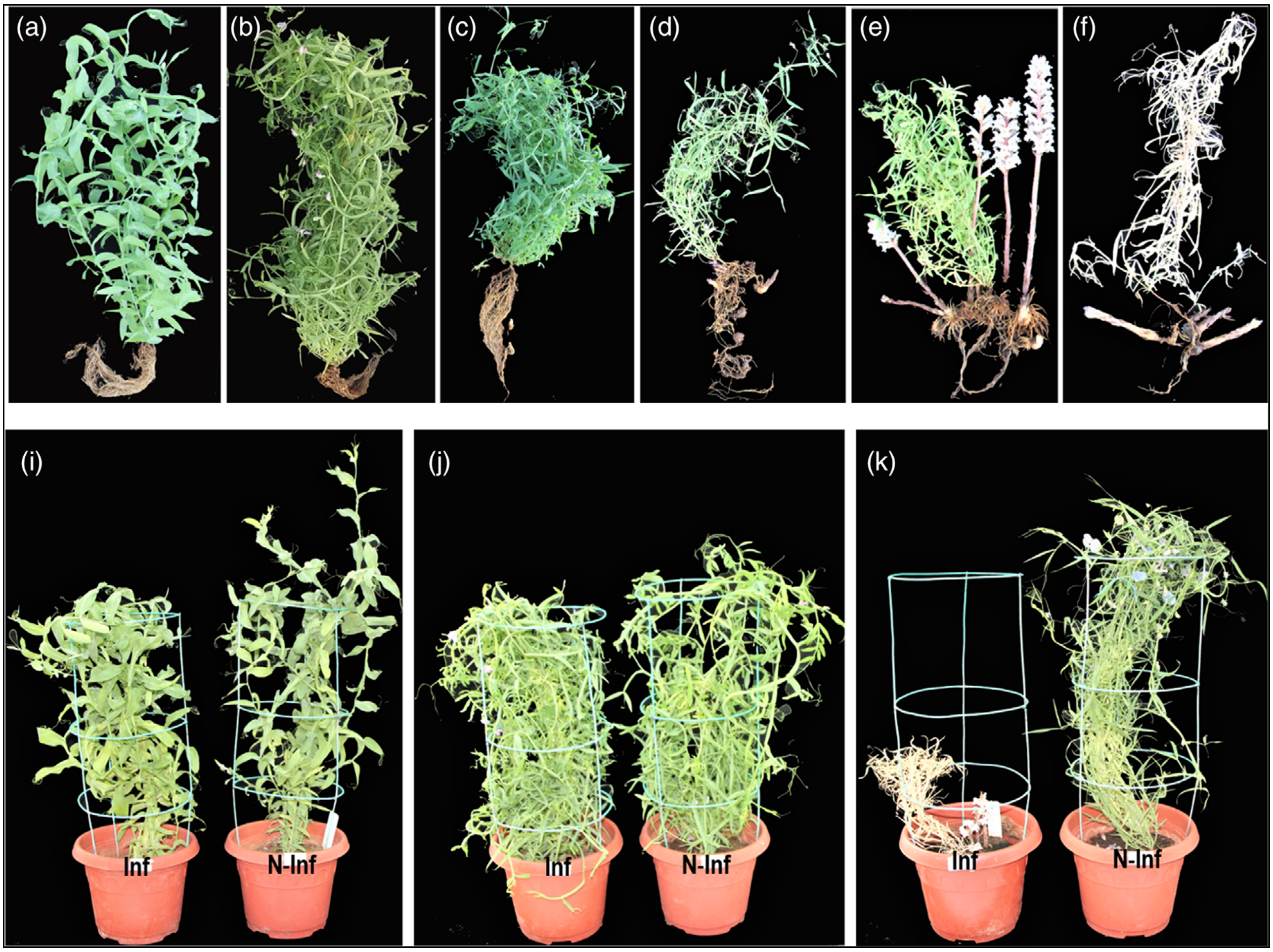

FIGURE 4 Validation of the reaction of *Lathyrus sativus* accessions tested on *Orobanche crenata*-infested and noninfested soils in the pot experiment. Reaction of resistant ([a] IG65197 and [b] IG64782), moderately resistant ([c] IG65204, [d] IG116989, and [e] IG64951), and susceptible ([f] IG64908) accessions in *O. crenata*-infested pots. Comparison of performance of resistant ([i] IG65197 and [j] IG64782) and susceptible ([k] IG64908) plants in infested and noninfested pots

TABLE 7 Mean squares for three *Orobanche* infestation parameters recorded on 10 grass pea genotypes in infested and noninfested pot experiments under controlled conditions during 2018–2019

Source	df	RDW	SDW	PDN
Corrected model	15	25.09*	55.81**	73.60*
Treatment (T)	1	58.75*	26.16**	343.14*
Genotypes (G)	9	17.77*	69.29**	66.55**
T × G	5	33.65*	39.40*	29.95**
Error	23	0	0	0

Note. RDW, root dry weight per plan; SDW, shoot dry weight per plant; PDN, pod number per plant.
*Significant at the .05 probability level.
**Significant at the .01 probability level.

resistance level of test entries. The numbers of underground *Orobanche* shoots in IG116989 and IG116997 were much higher than the emerged ones, resulting in the susceptible reaction.

Field trials at hot spots revealed that *O. crenata* was much more parasitic on *Lathyrus* species than *O. foetida*. Similar results were observed for faba bean with regard to parasitism of *O. foetida* and *O. crenata* (Trabelsi et al., 2015) and chickpea (*Cicer arietinum* L.) and pea (*Pisum sativum* L.) (Abbes, Kharrat, & Chaibi, 2008). The present study identified six wild species—namely, *L. aphaca, L. articulatus, L. blepharicarpus, L. cassius*, *L. pseudocicera*, and *L. ochrus*—with <1 PI as compared with 6.75 in susceptible checks. These wild species with complete resistance against *O. crenata* parasitism offer scope for introgression breeding. In earlier studies with a limited number of accessions, *L. ochrus* was identified as a source of resistance to *Orobanche crenata* by Sillero et al. (2005). In the past, only few attempts were made for interspecific hybridization among *Lathyrus* species (Davies, 1958; Hammett, Murray, Markham, Hallett, & Osterloh, 1996; Kearney, 1996; Khawaja, 1985, 1988; Trankovskij, 1962; Yamamoto, Fujiware, & Blumenreich, 1986; Yunus, 1990; Yunus & Jackson, 1991). Yunus (1990) crossed 11

TABLE 8 Root (RDW) and shoot (SDW) dry weight and pod number (PDN) of selected *Lathyrus sativus* accessions in *O. crenata*-infested and noninfested pots during 2018–2019

Accession	Reaction against *O. crenata* in 2017–2018 test	RDW		SDW		PDN	
		Infested	Noninfested	Infested	Noninfested	Infested	Noninfested
		g					
IG65197	Resistant	1.97b	1.47a	10.70b	7.37b	6.00b	3.50c
IG64782	Resistant	1.27b	1.67a	20.60a	16.80a	5.00ab	15.00ab
IG65204	Moderate R	0.93b	1.03b	5.30bc	12.40b	14.33a	21.00a
IG64875	Moderate R	2.80b	0.83b	2.00bc	11.53b	4.00ab	14.67ab
IG64951	Moderate R	5.63b	0.63b	1.53bc	8.20b	0.00ab	12.00abc
IG65187	Moderate R	2.63b	0.73b	3.50c	6.13b	9.50ab	15.67ab
IG116989	Moderate R	2.53b	0.73b	1.17bc	7.90b	0.00a	16.00ab
IG116997	Moderate R	13.00a	1.00b	2.60bc	9.83b	2.00ab	17.00ab
IG65042	Susceptible	5.53b	0.77b	1.43bc	8.87b	0.00ab	9.67bc
IG64908	Susceptible	3.30b	1.30ab	1.43b	11.17b	0.00ab	7.67bc
Mean over all accessions		3.96	1.02	5.03	10.02	7.73	13.5

Note. Data with a common letter per column are not significantly different according to Duncan's test ($p = .05$). R, resistant; MR, moderately resistant; S, susceptible.

TABLE 9 Pearson correlations between different parameter combinations of *Orobanche* infestation in the pot experiment

Parameter	EON	EODW	UON	UODW	RDW	SDW	PDN
TAN	.050ns	−.128ns	**.780****	.496ns	.220ns	−.183ns	.015ns
EON		.389ns	−.179ns	−.314ns	−.054ns	−.036ns	.038ns
EODR			.008ns	.373ns	.012ns	.012ns	.281ns
UON				.592ns	.466ns	.271ns	−.267ns
UODR					.109ns	−.233ns	−.060ns
RDW						.431ns	−.204ns

Note. TAN, total attachment number per plant, EON, emerged *Orobanche* number per plant; EODW, emerged *Orobanche* dry weight per plant; UON, underground *Orobanche* number per plant; UODW, underground *Orobanche* dry weight per plant; RDW, root dry weight per plant; SDW, shoot dry weight per plant; PDN, pod number per plant.

**Significant at the .01 probability level. †ns, nonsignificant.

wild species with *L. sativus* and found viable seeds only with *L. cicera* and *L. amphicarpus*. Under the Crop Trust-funded project on enhancing prebreeding in barley and grass pea (GS16005), we investigated crossability of *Lathyrus sativus* with six wild species resulting in viable F_1 plants only with *L. cicera* and to a lesser extent with *L. ochrus*, *L. inconspicuous*, *L. marmoratus* Boiss., and *L. heirosolymitanus* Boiss., but not with *L. articulatus*, indicating the prospects of transferring useful traits from the CWRs. Resistance in *L. articulatus* and *L. ochrus* accessions was due to low incidence, severity, and PI. This resistance acts as an early barrier to the establishment of broomrape, as none or few broomrape tubercles were recorded at early stage in these accessions. This low establishment is due to the low induction of germination of the broomrape seeds. Low levels of induction of germination have been described as a resistance mechanism in other legume species such as chickpea (Sillero et al., 2005).

Results with complete resistance observed for the two accessions IG64782 and IG65197 against *O. crenata* and *O. foetida* under open field conditions were confirmed and validated under controlled conditions in pot experiment. However, there were few mismatches in MR accessions, which showed a highly susceptible reaction in pot experiments. This includes the susceptible reaction of IG116989 with the highest number of emerged *Orobanche* in the pot experiment. This is due to the underground development of *Orobanche* shoots at the host plant root level. Effectively, it makes a false selection of resistant genotypes in field screening (Briache et al., 2019). Other studies showed that in a susceptible genotype, high infestation level could occur, leading to intense uptake of nutrients by *Orobanche* attachment to host plant roots. In such cases, the majority of underground *Orobanche* sprouts might not emerge, judging the test entry erroneously as resistant (Mbasani-Mansi, Ennami, et al., 2019; Rubiales et al., 2006). The number of emerged *Orobanche* shoots and pod number did not show any correlation with any of the parasitism parameters and, therefore, these two parameters, which are easy to measure, are not good selection criteria for evaluation of *Orobanche* resistance in grass pea. For this reason, the underground number of *Orobanche* shoots should always be considered for identification and classification of test entries correctly. Infestation by *O. crenata* showed low induction of growth and yield in some accessions with significant difference between them. Pod number per plant was more affected than root and shoot dry weights. It could be attributed to host nutrient losses caused by *O. crenata*, which limited the availability of nutrients to the host plant. The latter tends to maintain its vegetative biomass to offset nutrient losses, rather than to produce seeds. Previous studies reported higher reduction in yield than in growth parameters in faba bean (Briache et al., 2019), lentil (*Lens culinaris* Medikus; Mbasani-Mansi, Briache, et al., 2019) and grass pea (Fernández-Aparicio et al., 2016). Thus, resistance against broomrape is particularly a difficult task for evaluation. Thus, there is a need to find sources of true resistance in order to facilitate the development of resistant cultivars.

5 | CONCLUSION

A 2-yr study in field and controlled conditions showed wide variation among crop wild relatives of grass pea for resistance to broomrape species (*O. crenata* and *O. foetida*). Six wild species—namely, *L. aphaca, L. articulatus, L. blepharicarpus, L. cassius*, *L. pseudocicera*, and *L. ochrus*—with <1 PI against *O. crenata* offer scope to develop introgression lines for their use in mainstream grass pea breeding. Underground number and weight of the *Orobanche* shoot should always be considered as selection criteria for identification and classification of test entries correctly. The resistant accessions are included in the crossing block to strengthen prebreeding efforts in grass pea.

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AUTHOR CONTRIBUTIONS

F.A., S.K., A.A., and M.A. designed the research. F.A., S.K., R.M., R.K.M., K.H., and M.A. performed the experiments. F.A., S.K., A.A., Z.K., K.H., and M.A, contributed materials and analysis tools. F.A., S.K., M.A., and A.H. wrote the paper. R.M., Z.K., R.K.M., Z.E.T., and M.B. revised the paper. All authors approved the final manuscript.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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REFERENCES

Abbes, Z., Kharrat, M., & Chaibi, W. (2008). Seed germination and tubercle development of *Orobanche foetida* and *Orobanche crenata* in presence of different plant species. *Tunisian Journal of Plant Protection*, *3*, 101–110.

Abbes, Z., Kharrat, M., Delavault, P., Chaïbi, W., & Simier, P. (2009). Osmoregulation and nutritional relationships between *Orobanche foetida* and faba bean. *Plant Signaling & Behavior*, *4*, 336–338.

Abbes, Z., Kharrat, M., Delavault, P., Simier, P., & Chaïbi, W. (2007). Field evaluation of the resistance of some faba bean (*Vicia faba* L.) genotypes to the parasitic weed *Orobanche foetida* Poiret. *Crop Protection*, *26*, 1777–1784. https://doi.org/10.1016/j.cropro.2007.03.012

Abbes, Z., Trabelsi, I., Kharrat, M., & Amri, M. (2019). Intercropping with fenugreek (*Trigonella foenum-graecum*) enhanced seed yield and reduced *Orobanche foetida* infestation in faba bean (*Vicia faba*). *Biological Agriculture & Horticulture*, *35*, 238–247.

Aletor, V. A., El-Moneim, A. A., & Goodchild, A. V. (1994). Evaluation of the seeds of selected lines of three *Lathyrus* spp for β-*N*-oxalylamino-L-alanine (BOAA), tannins, trypsin inhibitor activity and certain in-vitro characteristics. *Journal of the Science of Food and Agriculture*, *65*, 143–151. https://doi.org/10.1002/jsfa.2740650204

Amri, M., Trabelsi, I., Abbes, Z., & Kharrat, M. (2019). Release of a new faba bean variety "Chourouk" resistant to the parasitic plants *Orobanche foetida* and *O. crenata* in Tunisia. *International Journal of Agriculture and Biology*, *21*, 499–505.

Bates, D. M., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Briache, F. Z., Ennami, M., Mbasani-Mansi, J., Gaboun, F., Abdelwahd, R., … Mentag, R. (2019). Field and controlled conditions screenings of some faba bean (*Vicia faba* L.) genotypes for resistance to the parasitic plant *Orobanche crenata* Forsk. and investigation of involved resistance mechanisms. *Journal of Plant Diseases and Protection*, *126*, 211–224. https://doi.org/10.1007/s41348-019-00207-x

Davies, A. J. S. (1958). A cytogenetic study in the genus Lathyrus. (Doctoral dissertation, University of Manchester).

Dixit, G. P., Parihar, A. K., Bohra, A., & Singh, N. P. (2016). Achievements and prospects of grass pea (*Lathyrus sativus* L.) improvement for sustainable food production. *Crop Journal*, *4*, 407–416. https://doi.org/10.1016/j.cj.2016.06.008

El-haddad, N., Rajendran, K., Smouni, A., Es-safi, N. E., Benbrahim, N., Mentag, R., … Kumar, S. (2020). Screening the FIGS set of lentil (*Lens culinaris* Medikus) germplasm for tolerance to terminal heat and combined drought-heat stress. *Agronomy*, *10*(1036). https://doi.org/10.3390/agronomy10071036

Ennami, M., Briache, F. Z., Gaboun, F., Abdelwahd, R., Ghaouti, L., Belqadi, L., … Mentag, R. (2017). Host differentiation and variability of *Orobanche crenata* populations from legume species in Morocco as revealed by cross-infestation and molecular analysis. *Pest Management Science*, *73*, 1753–1763. https://doi.org/10.1002/ps.4536

Ennami, M., Mbasani-mansi, J., Briache, F. Z., Oussible, N., Gaboun, F., Ghaouti, L., … Mentag, R. (2020). Growth-defense tradeoffs and source-sink relationship during both faba bean and lentil interactions with *Orobanche crenata* Forsk. *Crop Protection*, *127*. https://doi.org/10.1016/j.cropro.2019.104924

Fernández-Aparicio, M., Flores, F., & Rubiales, D. (2009). Field response of *Lathyrus cicera* germplasm to crenate broomrape (*Orobanche crenata*). *Field Crops Research*, *113*, 321–327.

Fernández-Aparicio, M., Flores, F., & Rubiales, D. (2012). Escape and true resistance to crenate broomrape (*Orobanche crenata* Forsk.) in grass pea (*Lathyrus sativus* L.) germplasm. *Field Crops Research*, *125*, 92–97. https://doi.org/10.1016/j.fcr.2011.09.003

Fernández-Aparicio, M., Flores, F., & Rubiales, D. (2016). The effect of *Orobanche crenata* infection severity in faba bean, field pea, and grass pea productivity. *Frontiers in Plant Science*, *7*. https://doi.org/10.3389/fpls.2016.01409

Fernández-Aparicio, M., & Rubiales, D. (2010). Characterisation of resistance to crenate broomrape (*Orobanche crenata* Forsk.) in *Lathyrus cicera* L. *Euphytica*, *173*, 77–84. https://doi.org/10.1007/s10681-009-0116-0

Girma, D., & Korbu, L. (2012). Genetic improvement of grass pea (*Lathyrus sativus*) in Ethiopia: An unfulfilled promise. *Plant Breeding*, *131*, 231–236. https://doi.org/10.1111/j.1439-0523.2011.01935.x

Grenz, J. H., Manschadi, A. M., DeVoil, P., Meinke, H., & Sauerborn, J. (2005). Assessing strategies for *Orobanche* sp. control using a combined seedbank and competition model. *Agronomy Journal*, *97*, 1551–1559. https://doi.org/10.2134/agronj2005.0061

Hammett, K. R. W., Murray, B. G., Markham, K. R., Hallett, I. C., & Osterloh, I. (1996). New interspecific hybrids in *Lathyrus* (Leguminosae): *Lathyrus annuus* × *L. hierosolymitanus*. *Botanical Journal of the Linnean Society*, *122*, 89–101. https://doi.org/10.1111/j.1095-8339.1996.tb02066.x

Jiang, J., Su, M., Chen, Y., Gao, N., Jiao, C., Sun, Z., … Wang, C. (2013). Correlation of drought resistance in grass pea (*Lathyrus sativus*) with reactive oxygen species scavenging and osmotic adjustment. *Biologia*, *68*, 231–240. https://doi.org/10.2478/s11756-013-0003-y

Kearney, J. P. (1996). Wild Lathyrus species as genetic resources for improvement of grasspea (Lathyrus sativus) (Doctoral dissertation, University of Southampton).

Khawaja, H. I. T. (1985). Cytogenetic studies in the genus Lathyrus. (Doctoral dissertation, University of London).

Khawaja, H. I. T. (1988). A new interspecific *Lathyrus* hybrid to introduce the yellow flower character into sweet pea. *Euphytica*, *37*, 69–75.

Kumar, S., Bejiga, G., Ahmed, S., Nakkoul, H., & Sarker, A. (2011). Genetic improvement of grass pea for low neurotoxin (β-ODAP) content. *Food and Chemical Toxicology*, *49*, 589–600. https://doi.org/10.1016/j.fct.2010.06.051

Kumar, S., Gupta, P., Barpete, S., Sarker, A., Amri, A., Mathur, P. N., & Baum, M. (2013). Grass pea. In M. Singh, H. D. Upadhyaya, & I. S. Bisht (Eds.), *Genetic and genomic resources of grain legume improvement* (pp. 269–292). Amsterdam: Elsevier. https://doi.org/10.1016/B978-0-12-397935-3.00011-6

Kupicha, F. K. (1983). Infrageneric structure of *Lathyrus*. *Notes-Royal Botanic Garde, Edinburgh*.

Labrousse, P., Arnaud, M. C., Serieys, H., Bervillé, A., & Thalouarn, P. (2001). Several mechanisms are involved in resistance of *Helianthus* to *Orobanche cumana* Wallr. *Annals of Botany*, *88*, 859–868. https://doi.org/10.1006/anbo.2001.1520

Lambein, F., Travella, S., Kuo, Y. H., Van Montagu, M., & Heijde, M. (2019). Grass pea (*Lathyrus sativus* L.): Orphan crop, nutraceutical or just plain food. *Planta*, *250*, 821–838. https://doi.org/10.1007/s00425-018-03084-0

Lewis, G., Schrire, B., Mackinder, B., & Lock, M. (2005). *Legumes of the world*. London: Royal Botanic Gardens, Kew.

Mbasani-Mansi, J., Briache, F. Z., Ennami, M., Gaboun, F., Benbrahim, N., Triqui, Z. E. A., & Mentag, R. (2019a). Resistance of Moroccan lentil genotypes to *Orobanche crenata* infestation. *Journal of Crop Improvement*, *33*, 306–326. https://doi.org/10.1080/15427528.2019.1581866

Mbasani-Mansi, J., Ennami, M., Briache, F. Z., Gaboun, F., Benbrahim, N., … Mentag, R. (2019b). Characterization of genetic diversity and population structure of Moroccan lentil cultivars and landraces using molecular markers. *Physiology and Molecular Biology of Plants*, *25*, 965–974. https://doi.org/10.1007/s12298-019-00673-5

Parker, C. (2009). Observations on the current status of Orobanche and Striga problems worldwide. *Pest Management Science*, *65*, 453–459.

Patto, M. C., Hanbury, C. D., Van Moorhem, M., Lam-Bein, F., Ochatt, S. & Rubiales, D. (2011). Grass pea. In M. Perez De La Vega, J. I. Cubero & A. M. Torres (Eds.), *Genetics, genomics and breeding of cool season grain legumes* (pp. 151–204). Boca Raton, FL: CRC Press.

RStudio Team. (2016). RStudio: Integrated development environment for R. Boston, MA: RStudio. Retrieved from http://www.rstudio.com/

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

Rubiales, D., Pérez-de-Luque, A., Fernández-Aparico, M., Sillero, J. C., Román, B., Kharrat, M., … Riches, C. (2006). Screening techniques and sources of resistance against parasitic weeds in grain legumes. *Euphytica*, *147*, 187–199. https://doi.org/10.1007/s10681-006-7399-1

Sarkar, A., Emmrich, P. M. F., Sarker, A., Zong, X., Martin, C. & Wang, T. L. (2019). Grass pea: Remodeling an ancient insurance crop for climate resilience. In C. Kole (Ed.), *Genomic designing of climate-smart pulse crops*. Cham, Switzerland: Springer. https://doi.org/10.1007/978-3-319-96932-9

Shehadeh, A., Amri, A., & Maxted, N. (2013). Ecogeographic survey and gap analysis of *Lathyrus* L. species. *Genetic Resources and Crop Evolution*, *60*, 2101–2113. https://doi.org/10.1007/s10722-013-9977-0

Sillero, J. C., Cubero, J. I., Fernández-Aparicio, M., & Rubiales, D. (2005). Search for resistance to crenate broomrape (*Orobanche crenata*) in *Lathyrus*. *Lathyrus Lathyrism Newsletter*, *4*, 7–9.

Trabelsi, I., Abbes, Z., Amri, M., & Kharrat, M. (2015). Performance of faba bean genotypes with *Orobanche foetida* Poir. and *Orobanche crenata* Forsk. infestation in Tunisia. *Chilean Journal of Agricultural Research*, *75*, 27–34. http://doi.org/10.4067/S0718-58392015000100004

Trankovskij, D. A. (1962). Interspecific hybridization in the genus *Lathyrus*. *Bulletin of Moscow, Nature and Biology Series*, *67*, 140–141.

Vaz Patto, M. C., Díaz-Ruiz, R., Satovic, Z., Román, B., Pujadas-Salvà, A. J., & Rubiales, D. (2008). Genetic diversity of Moroccan populations of *Orobanche foetida*: Evolving from parasitising wild hosts to crop plants. *Weed Research*, *48*, 179–186.

Vaz Patto, M. C., & Rubiales, D. (2009). Identification and characterization of partial resistance to rust in a germplasm collection of *Lathyrus sativus* L. *Plant Breeding*, *128*, 495–500. https://doi.org/10.1111/j.1439-0523.2008.01601.x

Vaz Patto, M. C., Skiba, B., Pang, E. C. K., Ochatt, S. J., Lambein, F., & Rubiales, D. (2006). Lathyrus improvement for resistance against biotic and abiotic stresses: From classical breeding to marker assisted selection. *Euphytica*, *147*, 133–147. https://doi.org/10.1007/s10681-006-3607-2

Yamamoto, K., Fujiware, T., & Blumenreich, I. D. (1986). Isozymic variation and interspecific crossability in annual species of the genus *Lathyrus* L. In A. K. Kaul & D. Combes (Eds.), *Lathyrus and Lathyrism* (pp. 118–121). New York: Third World Medical Research Foundation.

Yunus, A. G. (1990). Biosystematics of Lathyrus section Lathyrus with special reference to the grasspea, L. sativus L. (Doctoral dissertation, University of Birmingham).

Yunus, A. G., & Jackson, M. T. (1991). The gene pools of the grasspea (*Lathyrus sativus* L.). *Plant Breeding*, *106*, 319–328. https://doi.org/10.1111/j.1439-0523.1991.tb00517.x

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