

Host-driven morphological variability in *Orobanche crenata* (Orobanchaceae)

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Abstract: Studies on interactions between *Orobanche* species and their hosts are mainly focused on resistance, radical interactions, and haustorium development. The influence of the host plant on morphology of the parasite under environmental controlled conditions is not reported in the literature. With the aim of filling this gap, the results of cultivation experiments of *Orobanche crenata* on *Vicia faba*, *V. sativa*, *Pisum sativum*, *Cicer arietinum*, and *Lathyrus clymenum* are presented. The tested population of *O. crenata* infected all the studied hosts but showed preferences toward *Vicia* and *Pisum* and, in particular, toward a foreign *V. sativa* cv. The higher resistance of the evaluated local cv. could be due to coevolution between host and parasite. There was little variation in times of emergence: about 110 days on *V. faba*, while around 125 on *P. sativum*, *C. arietinum*, and *V. sativa*. The shape and size of flowers of *O. crenata* were influenced by its hosts. The more flourishing the host, the more vigorous the parasite with respect to overall size, number of flowers, and density of the inflorescence. However, significant variations were also observed in the shape of the calyx and the colour of the corolla and stigma. These observations suggest that other taxa of *Orobanche* that grow in the wild, which are considered to be different species, could be morphotypes of the same taxon, although a process of speciation may be in progress.


Key words: Host-specificity, resistance, host-parasite coevolution, broomrape, morphometry, weed biology

1. Introduction

Orobanche L. (including *Phelipanche* Pomel) consists of holoparasitic taxa of worldwide distribution with greatly reduced vegetative organs. Parasitism has allowed simplification in shoot morphology of the holoparasites, including a reduction in features that are commonly used in plant taxonomy (Musselman, 1994).  Furthermore, several morphological characters undergo variation when drying in exsiccata preparation. Such differences result in difficulties in taxonomic identification.

The indication of the host plants has always been used as an additional attribute to support the morphological features in species description and identification (Piwowarczyk, 2015). Some species are reported to be species-specific, e.g., *O. salviae* F.W.Schultz is exclusive to *Salvia glutinosa* L. However, most parasitise several closely related species, e.g., *O. alba* Willd. on Lamiaceae, while others are more generalist, e.g., *O. minor* Sm. on Apiaceae, Asteraceae and Fabaceae (Beck-Mannagetta, 1930; Schneeweiss 2007), although races specifically linked to particular hosts have also evolved in generalist species (Thorogood et al., 2009; Schneider et al., 2016). The wide morphological variability observed in the field led to the description of several taxa not always unanimously accepted by the scientific community. For

instance, *O. cumana* Wallr. on the cultivated sunflower is often considered a variety of *O. cernua* Loefl. that grows on wild Asteraceae (Pujadas-Salvà and Velasco, 2000). In contrast, some infraspecific taxa have been described by their morphological variation but with explicit reference to the host (e.g., *O. minor* var. *compositarum* Pugsley).

The genus *Orobanche* includes several serious agricultural pests that cause major crop losses throughout the world (Parker and Riches, 1993; Joel et al., 2007). For instance, the virulence of *O. crenata* Forssk. and the consequent economic losses have led, in the last decades, to the abandonment of the cultivation of *Vicia faba* in large areas in the Mediterranean basin (Domina and Scibetta, 2006).  Hence, it is important to better understand the interactions between host and parasite as a starting point for future experiments of basic biology but also applied research on agriculture.

Studies on interactions between *Orobanche* species and their hosts are mainly focused on resistance, radical interactions, and haustorium development (e.g., Eizenberg et al., 2003; Pérez-de-Luque et al., 2005). The influence of the host plant on morphology of the parasite was reported by Musselman and Parker (1982), who recorded that *Orobanche* species found on different hosts show differences in morphology and vigour. Thorogood

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et al. (2008) sampled host-driven variation in wild populations of *O. minor* Sm. In both these studies there was no environmental control. Thus, the influence of environmental variables on the morphological diversity assessed cannot be appreciated.

The aim of this study was to assess possible morphological variations induced by host interactions on *O. crenata* morphology under fixed environmental conditions.

2. Materials and methods

The experiment consisted in the cultivation in pots, under the same environmental conditions, of *Orobanche crenata* host of different plants. *O. crenata* was chosen for this study because it is a well-characterised taxon from the morphological perspective and is universally known to be capable of infesting different legume species. It is widely spread through the Mediterranean basin, and remains, to date, the most important threat to legume crops in the area (Domina and Scibetta, 2006). The seeds of *O. crenata* were collected in April 2014 from a single capsule of a plant growing in an agricultural environment, growing on cultivated *V. faba* var. *major* Harz. The sampled population was isolated more than 4 km from other populations of *O. crenata* and showed limited intrapopulation morphological variability. A voucher specimen of the parasite collected in the wild was deposited in the *Herbarium Mediterraneum Panormitanum* (PAL).

The cultivation experiments were conducted in open air in the Botanical Garden of Palermo (38°06'29.03" N, 13°22'13.00" E, 10 m a.s.l.). On 12 December 2016, a total of 210 polyethylene pots (18 cm diameter) were filled with new compost prepared with pruning residues, then presumptively clean of broomrape seeds. The host plants tested were both crops and spontaneous. Among the former were *V. faba* var. *major* 'Castelnuovo', *V. faba* var. *major* 'Aguadulce', *Pisum sativum* L. 'Senatore', and *Cicer arietinum* L. 'Calia', while amid the latter were *Lathyrus clymenum* L. and *V. sativa* subsp. *nigra* (L.) Ehrh. collected in the wild in Godrano (North Sicily). Thirty pots were prepared per host. The host seeds were sown together with about 30 *O. crenata* seeds, at a depth of 3 cm. In addition, 30 control pots without broomrape seeds were prepared. The pots were regularly watered whenever atmospheric precipitation was insufficient, until the development of fruits and parasites in late April 2017.

To assess if the individuals of *O. crenata* grown in pots showed differences compared to those in the wild, at the time of the seed harvest, in April 2014, measurements were taken on 30 clumps picked randomly from the centre of the collecting area. Measurements and observations on the plants cultivated in pots were done in April 2017. Character states were measured from all the individuals

in each pot and the mean was used for statistical analysis. Measurements were taken on dry specimens, using an electronic calliper. The hairs at the base of stamens were counted with 40× magnification. Colours were noted from captured photos of the fresh plants. Colour intensity was calculated on grey scale photographs, with photo-editing software, assigning 255 to white and 0 to black. On the whole, 15 quantitative characters, 9 continuous and 6 discrete, were considered: #1 Number of parasites per pot (or per clump in the field); #2 Total plant length (cm); #3 Spike length (cm); #4 Spike density (number of flowers per 2 cm); #5 Stem colour intensity; #6 Flower bract length (mm); #7 Flower bract width at its broadest (mm); #8 Calyx length (mm); #9 Calyx width at its broadest (mm); #10 Calyx tube length (mm); #11 Corolla length (mm); #12 Corolla width (mm); #13 Number of purple veins on the side view of the corolla; #14 Stigma colour intensity, and #15 Hairiness at the base of stamens (Figure 1). The data matrix used for statistics is presented in Supplementary Information 1. The number of parasites recorded per pot in different hosts is presented in Supplementary Information 2.

Measures on the broomrapes infesting *L. clymenum* and *C. arietinum* are not included in Supplementary Information 1 and were not used for statistical analysis because the number of sprouted shots was too low to be statistically relevant (Table). We performed multivariate analysis of the data in two steps: the first considering the wild population and the second excluding it. In this way it was possible to show with the first step the differences between the parasites in the wild and in cultivation, while with the second step was possible to emphasise the variability of parasites in pots with different hosts. Principal component analysis (PCA) and discriminant analyses (DAs) were performed, according to Giovino et al. (2015) and Domina et al. (2017a, 2017b), with the individuals a priori assigned to 5 groups, step 1 (A#: wild population on *V. faba* var. *major*; B#: cultivated on *V. faba* var. *major* 'Castelnuovo'; C#: cultivated on *V. faba* var. *major* 'Aguadulce'; D#: cultivated on *V. sativa* subsp. *nigra*; E#: cultivated on *P. sativum* 'Senatore') or 4 groups, step 2 (excluding the wild population, to avoid conflating variation caused by different hosts with that resulting from genetic variability). The scatter plots of the measures along the first two canonical axes are shown. Each character was also subjected to univariate analysis (ANOVA or Kruskal-Wallis test, with corrections for multiple comparisons, Pearson's correlation coefficients, Tukey HSD test and Bonferroni, respectively), using PAST version 3.15 (Hammer et al., 2001; Hammer, 2017). The range of each continuous character of the cultivated plants is represented using box-and-whisker plots. The wild population is not shown in these plots to better highlight the differences

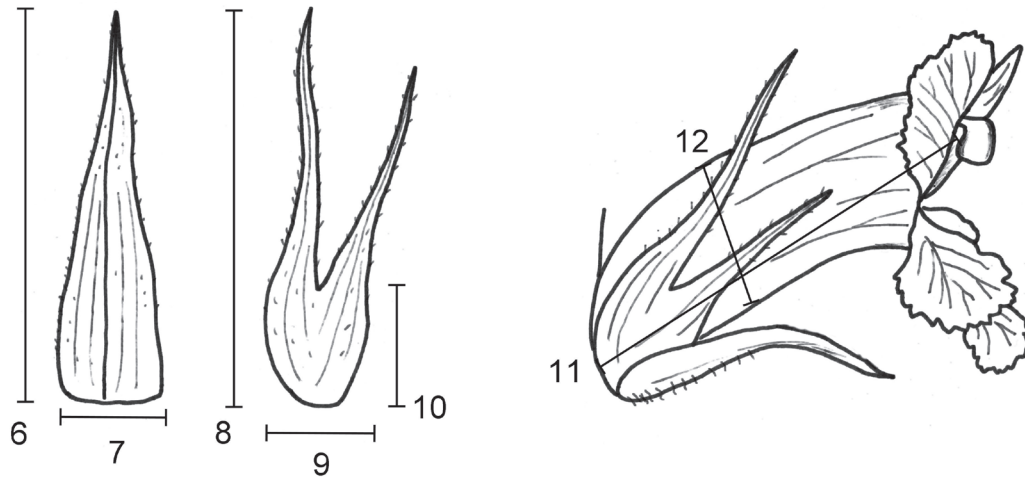


Figure 1. Characters scored for floral morphology analysis: #6 Flower bract length (mm); #7 Flower bract width (mm); #8 Calyx length (mm); #9 Calyx width at its broadest (mm); #10 Calyx tube length (mm); #11 Corolla length (mm); #12 Corolla width (mm).

Table. Synoptic table of pot infestation. Host: host plant; emergence time: number of days before the first emergences; infestation: number of infested pots out of 30; parasites per pot: average number of parasites per pot. Mean, median, standard deviation, asymmetry, and kurtosis of the number of parasites per pot.

Host	Emergence time	Infestation	Parasites	Mean ¹	Median	St. dev.	Asymmetry	Kurtosis
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	109	27	5	5.33 B	5	1.33	-0.25	-0.52
<i>V. faba</i> var. <i>major</i> 'Aguadulce'	108	30	8	8.47 C	8	1.94	1,4	2.82
<i>V. sativa</i> subsp. <i>nigra</i>	123	20	4	4.15 A	4	0.99	0,4	-0.77
<i>Pisum sativum</i> 'Senatore'	123	25	4	4.36 A	4	1.25	-0,48	-0.44
<i>Cicer arietinum</i> 'Calia'	128	3	2	-	-	-	-	-
<i>Lathyrus clymenum</i>	128	6	2	-	-	-	-	-
Control pots with <i>Vicia faba</i> var. <i>major</i> 'Castelnuovo' not inoculated	-	0	0	-	-	-	-	-

¹Letters indicate statistically significant difference to that particular group by the Student–Newman–Keuls test ($P < 0.01$).

between parasites of the different species cultivated in pots that otherwise would have been less readable due to the great difference between the parasites in the wild and in cultivation.

3. Results

There was a small variation in emergence times, regarding hosts and parasites. On *V. faba*, the parasites emerged in

about 110 days, while on *P. sativum*, *C. arietinum*, and *V. sativa* it took around 125 days. In any case, the parasite always developed in conjunction with the host fruiting

The Table summarises the infestation of the host p tested (full data available in Supplementary Information 2). The data were normally distributed. The population of *O. crenata*, collected in North Sicily and parasite of *V. faba*, used to inoculate the pots, showed a certain preference

toward the genera *Vicia* and *Pisum* and displayed a limited capability to infect *Lathyrus clymenum* and *Cicer arietinum*. Moreover, it could be argued that the local cultivar of *V. faba* var. *major* ‘Castelnuovo’ registered a higher resistance to the parasite compared to the Spanish cv. ‘Aguadulce’. The Student–Newman–Keuls test revealed a significant difference between the means observed ($P < 0.01$) (Hammer, 2017). Likewise, a significant difference was evident when Student’s t-test was applied to the data for *V. faba* var. *major* ‘Castelnuovo’ and *V. faba* var. *major* ‘Aguadulce’ ($P < 0.01$). This result indicates that cv. ‘Castelnuovo’ was statistically more resistant to the tested population of *O. crenata* than cv. ‘Aguadulce’.

The measures done (Supplementary Information 1) reveal a higher morphological variability of the parasite in the wild than in cultivation. This finding was expected because all the seeds for the cultivation experiment were collected from a single capsule, to ensure reduced genetic variability.

The total size of the parasite varied with the vigour of the host. The host plants of *V. faba* in the field were more developed and florid than the ones in the pots (about 90–100 vs. 40–50 cm), and their parasites showed a larger overall size, more flowers, and denser inflorescences than in the cultivated plants. The host plant influenced the colour, size, and shape of the parasite. This behaviour is evident when comparing the broomrapes developed with

different hosts. On *V. faba*, independently from the cultivar, denser and longer inflorescences, larger corollas than in other hosts, with several purple veins, and a purple stem and stigma were recorded. On *V. sativa*, fewer and shorter inflorescences, a different calyx shape (between total length, total width, and tube length), smaller corollas with fewer purple veins than in *V. faba*, a yellowish stem, and pinkish or whitish stigma were identified. On *P. sativum*, fewer and shorter inflorescences, a different shape of the calyx (between total length, total width, and tube length), smaller corollas with few purple veins, a yellowish stem, and yellowish or whitish stigma were noted.

3.1. Step 1 (including the plants in the wild and the plants in pots)

PCA (Figure 2) discriminated the *Orobanchae* in cultivation from wild ones but presented an overlap between the plants growing on different hosts (Figures 2 and 3). The DAs (Figures 4 and 5) showed three well-differentiated groups, whereby one included the population in the wild (Figure 4), another with the cultivated broomrapes growing on *V. faba*, and the other with the cultivated broomrapes growing on *V. sativa* and *P. sativum* (Figures 4 and 5). The same results were obtained with standardised logarithmic data.

The initial hypothesis that the host influences the parasite’s morphology was confirmed. Of the individuals, 93.94% were correctly classified by the first DA to their five

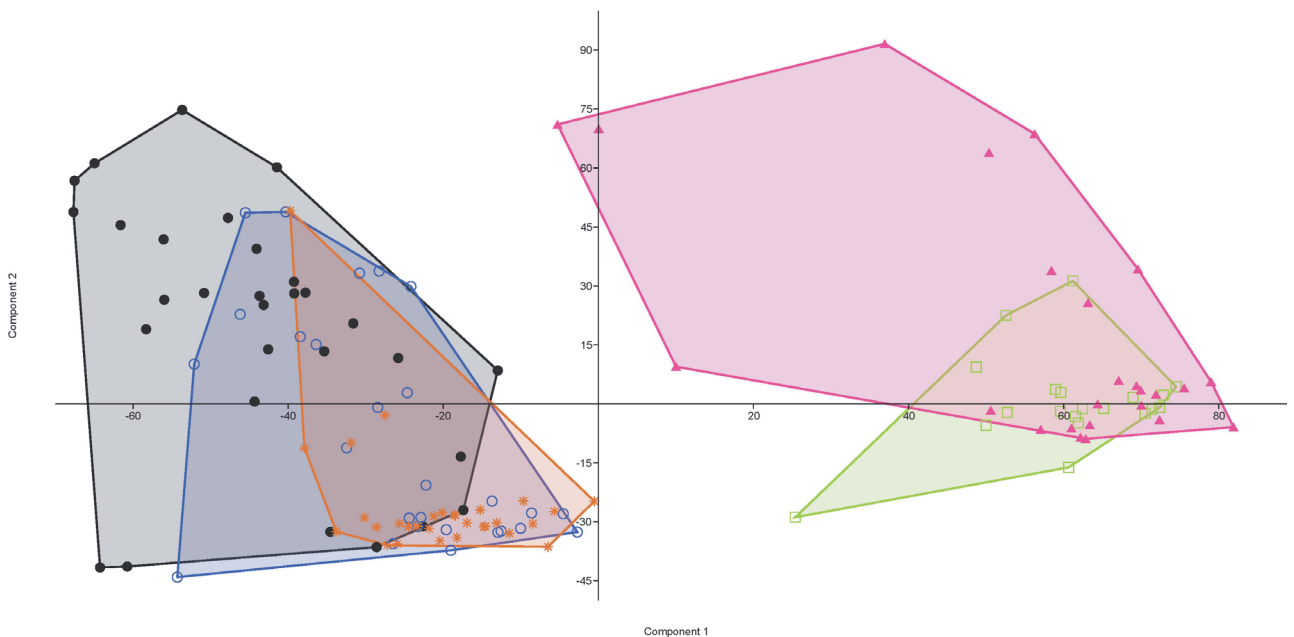


Figure 2. Principal components analysis based on the 15 considered morphological characters, with 5 a priori defined groups based on different hosts. PC1 Eigenvalue 2074.31, % variance 62.62, PC2 Eigenvalue 959.158, % variance 28.955. Black dot: wild population on *Vicia faba* var. *major*; blue circle: cultivated on *V. faba* var. *major* ‘Castelnuovo’; orange star: cultivated on *V. faba* var. *major* ‘Aguadulce’; pink triangle: cultivated on *V. sativa* subsp. *nigra*; green square: cultivated on *Pisum sativum* ‘Senatore’.

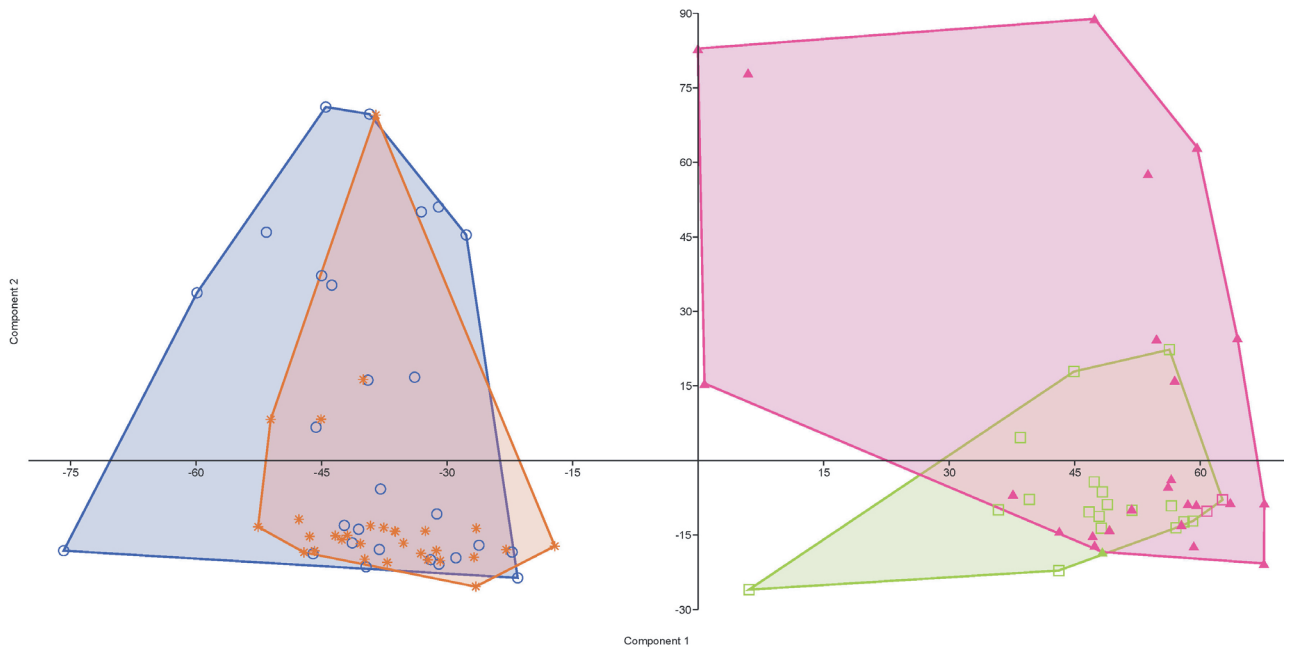


Figure 3. Principal components analysis based on the 15 considered morphological characters, with 4 a priori defined groups based on different hosts. PC1 Eigenvalue 2029.26, % variance 71.183, PC2 Eigenvalue 763.288, % variance 26.775. Blue circle: cultivated on *V. faba* var. *major* 'Castelnuovo'; orange star: cultivated on *V. faba* var. *major* 'Aguadulce'; pink triangle: cultivated on *V. sativa* subsp. *nigra*; green square: cultivated on *Pisum sativum* 'Senatore'.

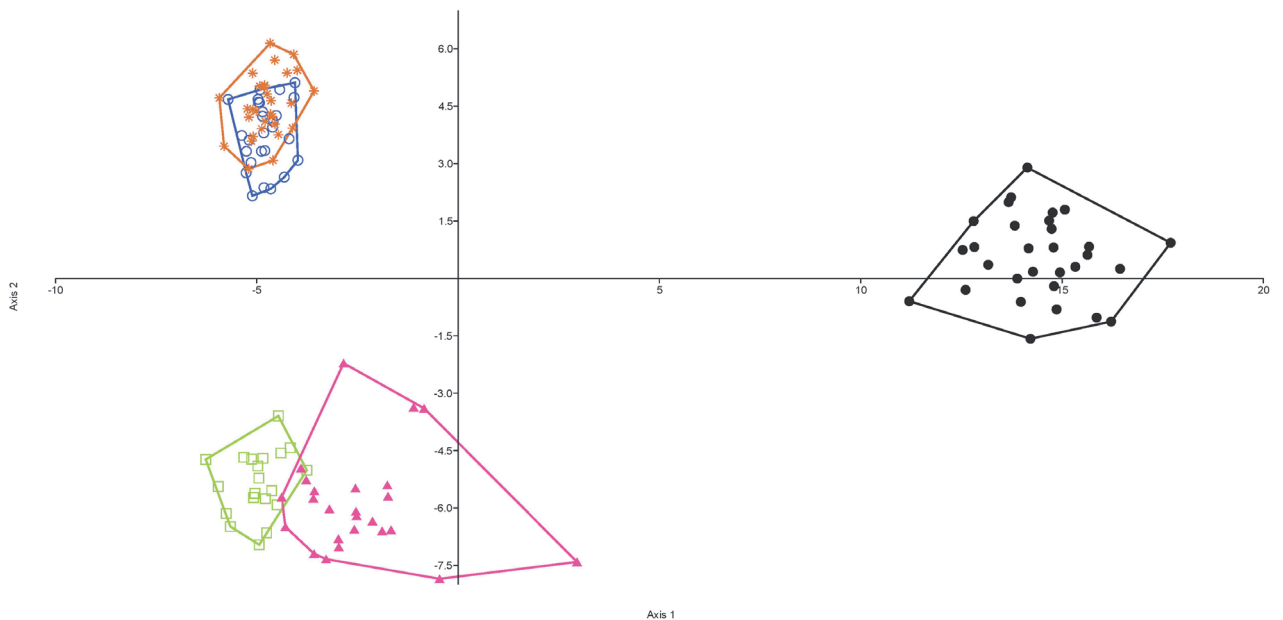


Figure 4. Discriminant analysis based on the 15 considered morphological characters, with 5 a priori defined groups based on different hosts. Axis 1: Eigenvalue 64.382, % variance 76.1; Axis 2: Eigenvalue 19.225, % variance 22.72. Black dot: wild population on *Vicia faba* var. *major*; blue circle: cultivated on *V. faba* var. *major* 'Castelnuovo'; orange star: cultivated on *V. faba* var. *major* 'Aguadulce'; pink triangle: cultivated on *V. sativa* subsp. *nigra*; green square: cultivated on *Pisum sativum* 'Senatore'.

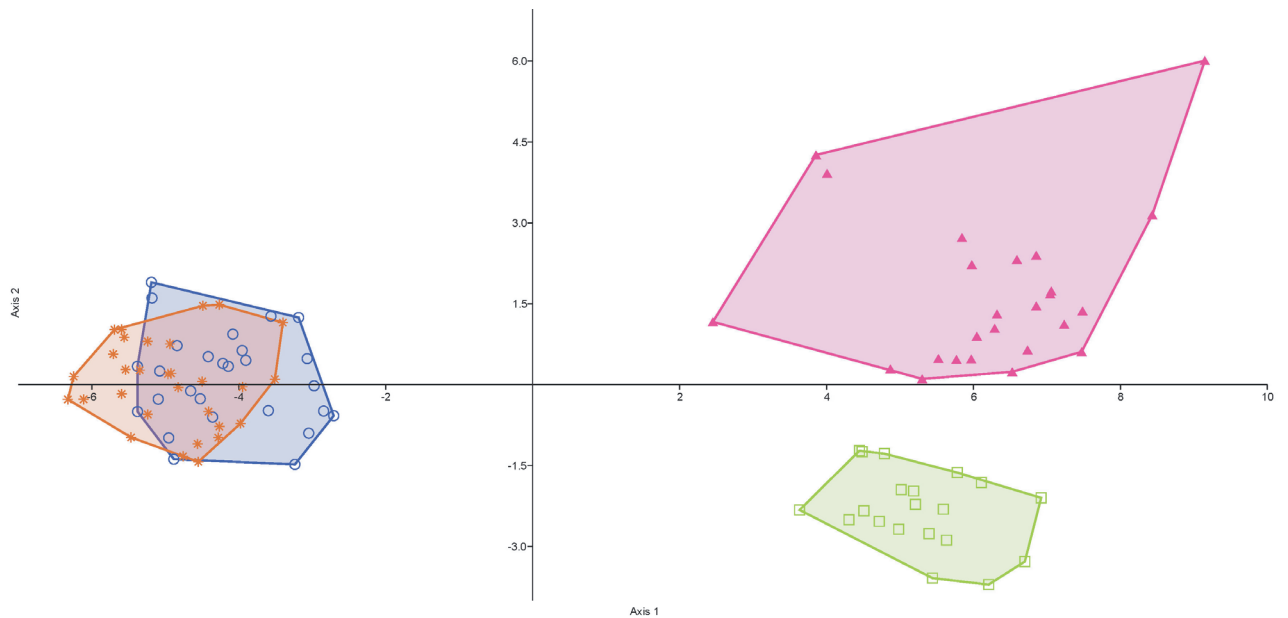


Figure 5. Discriminant analysis based on the 15 considered morphological characters, with 4 a priori defined groups based on different hosts. Axis 1: Eigenvalue 27.776, % variance 91.1; Axis 2: Eigenvalue 1.8234, % variance 5.98. Blue circle: cultivated on *V. faba* var. *major* 'Castelnuovo'; orange star: cultivated on *V. faba* var. *major* 'Aguadulce'; pink triangle: cultivated on *V. sativa* subsp. *nigra*; green square: cultivated on *Pisum sativum* 'Senatore'.

a priori assigned groups (or 89.39% with the jackknife method; see Osuji et al. (2013)).

3.2. Step 2 (including only the plants in pots)

The DA on the cultivated plants only (Figure 5) showed similar values of correct classification (95.1% and 87.25% with the jackknife method). Univariate analysis of all continuous morphological characters (Supplementary Information 1) showed a larger variation in size in the wild population of *O. crenata* than the cultivated ones. The intensity of stem colour distinguished between the broomrapes growing on *V. faba* and those growing on *V. sativa* and *P. sativum*. There were outlier values in the corolla length, corolla width, and the intensity of the colour of the stigma. The characters that showed the highest variation included the length of the flower bract, the total calyx length, and the calyx tube length (Figure 6).

4. Discussion

From this study, it can be confirmed that the tested population of *O. crenata* can parasitise different legumes but has some preferences, supposedly due to a local coevolution between the host plant and the parasite. The Sicilian cv. 'Castelnuovo' of *V. faba* demonstrated more resistance to the tested population of *O. crenata* than the Spanish cv. 'Aguadulce'. This behaviour could be explained by a pluri-generational selection of the local variety to

that specific parasite. The same phenomenon has been shown in other broomrapes, e.g., *Ph. ramosa* (L.) Pomel on *Brassica napus* L. in France (Gauthier et al., 2012).

Further studies are needed to investigate local coevolution between hosts and *Orobanchaceae* species highlighted by different studies in the Mediterranean (e.g., Satovic et al., 2009; Molinero-Ruiz et al. 2015), on a greater number of hosts and with more populations. Such investigations could lead towards the selection of specific resistant cultivars for different agricultural regions.

The host and its vigour influenced the time of emergence, the vigour, and the morphology of the parasite. The observed host-driven variability includes variation in the size, shape, and colour of the parasites and affects almost all the individuals of the population growing on a given host. The data recorded on *O. crenata* can lead to general considerations that are valid within the whole genus and could change the taxonomic interpretation of the known variability in some groups. For example, it is plausible that some morphologically similar taxa, with limited genetic characterisation, such as *O. cernua* and *O. cumana*, are nothing more than stabilised forms, due to interaction with the host. The same may be the case for the group of *O. minor* in the Mediterranean. Similar considerations could be made for taxa associated with particular environments, such as *O. litorea* Guss. on *Asteraceae* on sandy dunes, for which a part of their

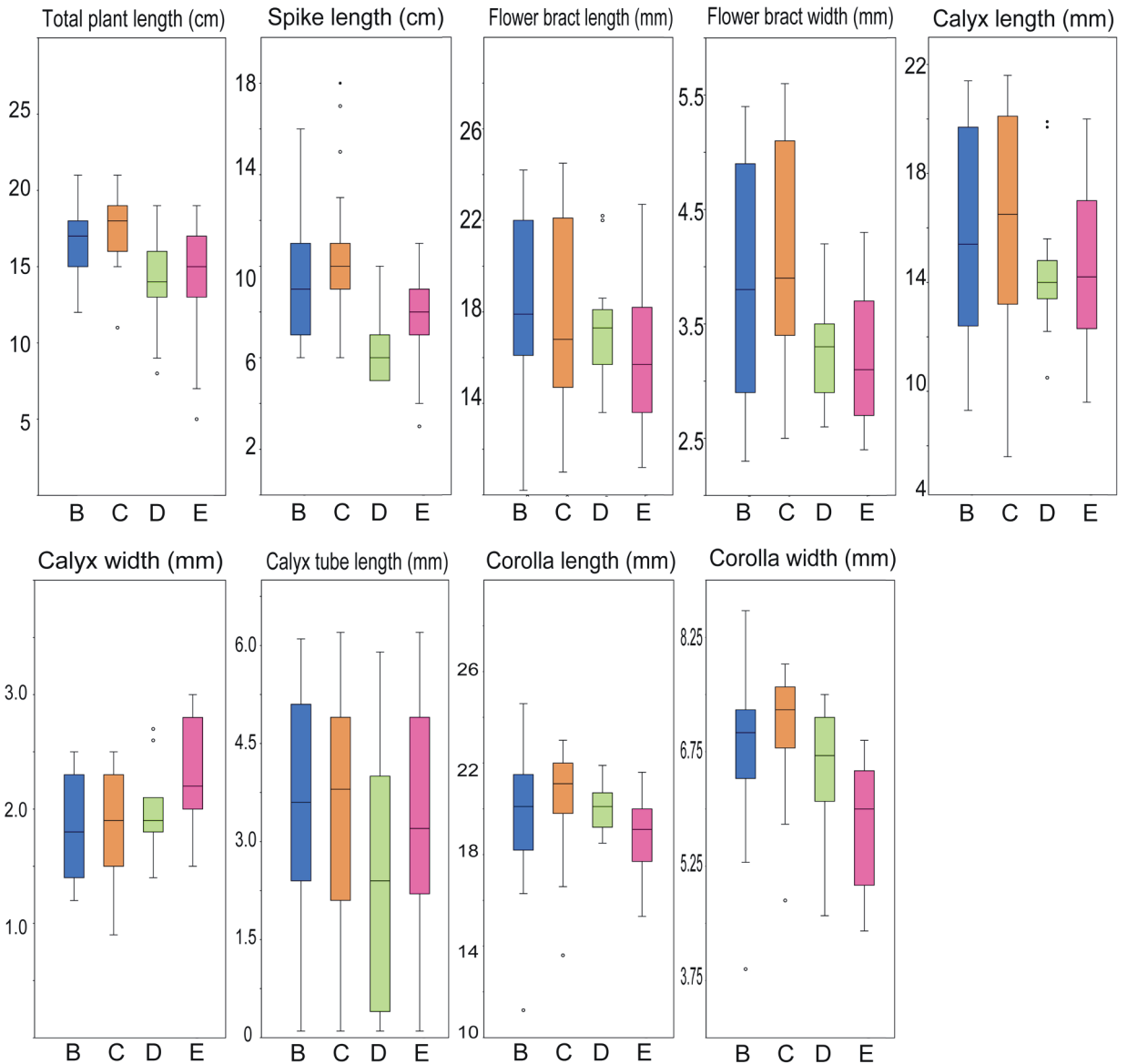


Figure 6. Box-and-whisker plots of the 12 continuous numeric characters. For each sample, the 25%–75% quartiles are drawn using a box. The median is shown with a horizontal line inside the box. The minimal and maximal values are shown with short horizontal lines, the whiskers. These are drawn from the top of the box up to the largest data point less than 1.5 times the box height from the box, and similarly below the box. Individual outlying data points are displayed as circles. Plots: #2 Total plant length (cm); #3 Spike length (cm); #6 Flower bract length (mm); #7 Flower bract width (mm); #8 Calyx length (mm); #9 Calyx width (mm); #10 Calyx tube length (mm); #11 Corolla length (mm); #12 Corolla width (mm). Groups: B) cultivated on *Vicia faba* var. *major* ‘Castelnuovo’; C) cultivated on *V. faba* var. *major* ‘Aguadulce’; D) cultivated on *Vicia sativa* subsp. *nigra*; E) cultivated on *Pisum sativum* ‘Senatore’.

morphological variability could be an adaptation to the growth environment. It is conceivable that in the long run this morphological variation can lead to speciation, but this phenomenon should be assessed case by case.

Cultivation trials, supported by genetic analysis, to test the host’s and the growth environment influences on the parasite should be done. Furthermore, the characteristics of parasites that developed on the various hosts should be cross-tested to check their stability.

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Supplementary Information 1. Synoptic table of the characters observed and measured. Measures used for statistical analysis are numbered. Characters scored for floral morphology analysis are presented in Figure 1. The spike density is indicated as the number of flowers each 2 cm; the hairiness at the base of the stamens is indicated as the number of hairs per mm.

Host	Origin	#1. Shoots per pot or clump	#2. Shoot length (cm)	#3. Spike length (cm)	Spike density	#4. No. Flowers each 2 cm	Stem colour	#5. Stem colour intensity	#6. Flower bract length (mm)	#7. Flower bract width (mm)	#8. Calyx length (mm)	#9. Calyx width (mm)	#10. Calyx tube length (mm)	#11. Corolla length (mm)	#12. Corolla width (mm)	#13. No. Corolla veins	Stigma colour	#14. Stigma colour intensity	#15. Hairiness at the base of stamens
<i>Vicia faba</i> var. <i>major</i>	wild	4	46	29	dense	3	purple	98	22.8	4.8	17.8	4.8	6.3	23.4	8.7	7	pinkish	121	8
<i>Vicia faba</i> var. <i>major</i>	wild	7	57	40	dense	3	purple	113	191	5.1	16.8	4.6	5.8	19.5	6.4	7	pinkish	126	10
<i>Vicia faba</i> var. <i>major</i>	wild	7	60	41	rare	1	purple	122	20.3	3.9	13.7	4.2	1.4	17.3	6	8	pinkish	120	12
<i>Vicia faba</i> var. <i>major</i>	wild	8	62	34	dense	4	purple	133	18.9	5	16.5	4.3	0.1	19.4	6.4	6	pinkish	113	8
<i>Vicia faba</i> var. <i>major</i>	wild	9	32	18	dense	3	brown	66	21.8	4.7	15.2	4.1	2.8	22.4	7.7	7	purple	91	9
<i>Vicia faba</i> var. <i>major</i>	wild	5	39	24	dense	4	brown	64	20.6	4	21.8	4.9	2.2	21	7.3	7	purple	90	10
<i>Vicia faba</i> var. <i>major</i>	wild	6	58	37	dense	4	purple	121	20.2	4.1	12.7	3.8	0.1	22.8	8.7	2	purple	94	12
<i>Vicia faba</i> var. <i>major</i>	wild	7	43	31	dense	4	purple	101	23	5.2	17	4.6	0.8	23.8	7.9	5	purple	80	8
<i>Vicia faba</i> var. <i>major</i>	wild	8	40	28	dense	4	purple	96	22.8	4.7	17.1	4.6	1.2	21.3	7.4	6	purple	87	15
<i>Vicia faba</i> var. <i>major</i>	wild	9	36	26	dense	3	purple	107	18.3	4.3	14.6	3.9	0.1	18.9	6.6	6	purple	85	16
<i>Vicia faba</i> var. <i>major</i>	wild	7	43	23	dense	4	purple	114	20.6	5	15.5	4.2	1.8	23.2	7.1	5	purple	86	12
<i>Vicia faba</i> var. <i>major</i>	wild	3	56	40	dense	3	purple	96	21.4	5.2	16.7	4.3	6.6	22.2	6.8	8	whitish	180	9
<i>Vicia faba</i> var. <i>major</i>	wild	8	63	48	dense	4	purple	117	20	4.3	21.5	4.9	2.6	20.7	5.7	9	whitish	190	10
<i>Vicia faba</i> var. <i>major</i>	wild	9	57	36	dense	4	purple	122	20.1	4.9	14.3	3.8	3	19.4	6.7	9	whitish	174	9
<i>Vicia faba</i> var. <i>major</i>	wild	4	66	40	dense	3	purple	101	19.5	4.8	13.5	3.7	3.6	20.2	5.3	8	whitish	181	10
<i>Vicia faba</i> var. <i>major</i>	wild	8	56	26	dense	3	purple	97	21.5	4.6	18.2	4.2	5.8	20.5	6.4	7	whitish	169	11
<i>Vicia faba</i> var. <i>major</i>	wild	9	54	30	dense	3	purple	92	20.6	3.9	11.6	3.7	2.5	19.5	5.7	7	whitish	174	2
<i>Vicia faba</i> var. <i>major</i>	wild	12	42	25	dense	3	purple	111	18.7	4.1	14.1	3.8	3.5	18.4	6.4	8	yellowish	147	15
<i>Vicia faba</i> var. <i>major</i>	wild	8	78	53	dense	3	purple	117	21.6	4.7	13.9	4.3	2.5	21.9	6.9	9	yellowish	148	16
<i>Vicia faba</i> var. <i>major</i>	wild	7	65	37	dense	4	purple	104	21	5.4	20	4.6	3.8	21.4	6.8	8	yellowish	145	18
<i>Vicia faba</i> var. <i>major</i>	wild	9	56	36	dense	4	purple	102	21.3	4.5	16	4.2	2.8	19	7.1	7	yellowish	162	12
<i>Vicia faba</i> var. <i>major</i>	wild	5	34	21	dense	3	purple	93	22.6	4.5	15.7	4.3	5	22.7	7.2	8	yellowish	154	10
<i>Vicia faba</i> var. <i>major</i>	wild	6	38	25	dense	3	purple	89	19.5	4.4	14.1	3.8	5.4	19.5	6.8	8	yellowish	146	9
<i>Vicia faba</i> var. <i>major</i>	wild	7	42	22	dense	4	purple	112	18	3.7	12.9	3.9	4	20.7	7.8	8	yellowish	147	12
<i>Vicia faba</i> var. <i>major</i>	wild	8	32	19	dense	3	purple	114	20.6	4.3	16.4	3.9	2.9	19.1	5.6	7	yellowish	140	11
<i>Vicia faba</i> var. <i>major</i>	wild	9	47	28	dense	3	purple	104	21.2	4.8	14.7	4.1	3.8	20	7	7	yellowish	133	10
<i>Vicia faba</i> var. <i>major</i>	wild	9	52	31	dense	4	purple	111	23.2	5.3	19.5	4.5	4.3	22.4	7.2	8	yellowish	166	9
<i>Vicia faba</i> var. <i>major</i>	wild	6	45	28	dense	4	purple	107	19.4	4.6	17.2	4.4	4.3	18.4	5.4	9	yellowish	147	8
<i>Vicia faba</i> var. <i>major</i>	wild	7	48	29	dense	4	purple	113	22.6	4.6	15.2	4.1	4.5	19.8	7.9	9	yellowish	148	9
<i>Vicia faba</i> var. <i>major</i>	wild	9	27	19	dense	5	purple	104	23	4.8	18.7	4.5	4.2	23.2	8.7	3	yellowish	150	3
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	7	20	11	dense	4	purple	100	10.2	2.3	9.3	1.2	2.6	11.2	3.9	3	pinkish	113	13
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	7	21	16	dense	4	purple	113	15.7	2.9	12.1	1.4	5.1	17.6	6.2	4	pinkish	123	14
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	17	8	dense	4	purple	107	18.2	4	15.5	1.8	2.4	20.1	7	5	pinkish	123	4
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	2	16	7	rare	2	brown	68	16.5	3.8	14.4	1.8	5.3	20.4	7.1	5	purple	91	18
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	6	18	10	dense	4	purple	122	23.2	5.1	21.4	2.5	3.2	21.8	7.6	4	purple	88	12
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	3	19	12	dense	3	purple	113	22.6	5	19.9	2.3	4.9	22	6.7	5	purple	86	10
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	19	10	dense	4	purple	106	19.9	4.6	16.5	1.9	5.4	21.2	7.4	5	purple	89	9
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	16	8	dense	4	purple	115	22.4	4.9	19.9	2.3	3.6	21.5	7.5	6	purple	87	10
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	4	17	15	dense	4	purple	103	21.4	4.9	19.7	2.3	5.5	22.5	7.2	5	purple	91	8
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	12	7	dense	4	purple	104	23.6	5.2	21.3	2.5	4.6	22.3	7.8	4	purple	86	9

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<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	6	16	9	dense	3	purple	112	242	5.4	21	2.3	4.8	21.3	7.1	5	purple	87	8
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	18	9	dense	4	purple	104	239	5.3	21	2.4	2.7	24.6	8.6	4	purple	94	11
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	3	17	8	dense	3	purple	98	22	5	19.7	2.3	5.5	21.8	7.6	5	purple	89	13
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	4	18	9	dense	4	purple	102	181	4.2	15.4	1.8	2.3	20.4	7.1	3	purple	94	9
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	7	18	11	dense	3	purple	107	15.6	3.6	16	1.9	2.1	18.1	6.3	4	purple	101	12
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	15	7	dense	4	purple	113	16	2.8	11.9	1.4	0.1	18.8	6.6	5	purple	95	11
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	6	18	12	dense	4	purple	118	188	3.9	16.8	2	4.5	20.2	7.1	6	purple	89	10
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	19	11	dense	3	purple	122	19.7	4.5	16.3	1.9	6.1	21	7.3	5	purple	82	3
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	3	15	6	dense	3	purple	111	15.2	3	12.8	1.5	2.2	16.3	5.3	4	whitish	176	8
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	14	6	dense	3	purple	106	16.1	3.7	13.1	1.5	1.5	18.2	7.2	5	whitish	178	9
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	17	7	dense	3	purple	103	16.5	3.8	12.2	1.4	3.6	18.2	6.4	4	yellowish	144	10
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	18	9	dense	4	purple	88	15.4	3.5	15.3	1.8	2.8	18.6	6.5	3	yellowish	142	11
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	14	6	dense	3	purple	97	17.9	2.9	10.2	1.3	5.4	19.6	6.9	6	yellowish	153	12
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	8	17	8	rare	2	purple	121	16.2	2.8	12.4	1.4	2.8	16.4	5.7	5	yellowish	151	12
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	18	11	dense	3	purple	116	16.8	2.9	10	1.2	3.2	20.1	6.5	4	yellowish	156	9
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	14	7	dense	3	purple	104	17.7	2.7	12.9	1.5	4.3	18.7	6.4	5	yellowish	142	9
<i>Vicia faba</i> var. <i>major</i> 'Castelnuovo'	cultivated	5	15	7	dense	4	purple	118	16.3	3.5	14.4	1.7	2.2	18.1	6	5	yellowish	157	9
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	8	11	6	dense	3	brown	106	11.6	2.7	7.6	0.9	0.1	17.1	6	4	pinkish	122	10
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	5	16	8	rare	2	purple	101	22.1	5.1	19.8	2.1	6.2	21.9	7.7	6	pinkish	116	8
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	8	18	10	dense	4	purple	95	14.7	3.4	16	1.8	2.8	21.1	7.4	6	pinkish	116	10
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	8	19	9	dense	3	purple	107	25.6	5.3	21.4	2.5	4.9	22.3	6.8	6	purple	87	11
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	7	18	9	dense	3	purple	113	24.2	5.6	21.6	2.4	4.6	23	7	5	purple	89	11
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	3	19	8	dense	4	purple	118	23.6	5.3	21.2	2.5	4.4	22	7.3	5	purple	93	12
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	10	18	11	dense	4	purple	102	21.6	5	21.3	2.5	3.4	21.9	7.6	5	purple	92	13
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	8	17	9	dense	3	purple	104	24.5	5.3	21	2.4	3.8	22.1	7.5	4	purple	91	10
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	9	18	11	dense	3	purple	97	21.6	5	17.4	2	5	21.1	7.4	4	purple	96	10
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	8	19	18	dense	3	purple	112	22.3	5.1	17.5	2	5.2	22.3	7.6	4	purple	87	9
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	9	16	8	dense	3	purple	113	19	4.4	16.3	1.9	6.1	19.8	6.9	5	purple	86	9
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	8	16	9	dense	3	purple	117	22.1	5.1	19.8	2.3	6.2	21.9	7.7	4	purple	81	10
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	6	19	10	dense	3	purple	111	21.6	5	17.5	2	6	21	7.3	5	purple	88	11
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	9	18	9	dense	3	purple	112	23.6	5.4	21.4	2.5	4.9	22.3	7.8	3	purple	93	11
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	4	17	11	dense	3	purple	107	23.9	4.8	21.5	2.5	4.9	22	7	5	purple	94	12
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	11	15	9	dense	4	purple	92	21.4	4.9	20.1	2.3	5.9	22.6	7.9	4	purple	95	10
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	8	19	10	dense	3	purple	108	11.6	2.7	15	1.7	2.7	17.8	6.2	3	purple	92	9
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	11	17	11	dense	4	purple	109	15.8	3.6	15.5	1.8	2.1	21.6	7.6	5	purple	90	9
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	9	19	11	rare	1	purple	117	14.7	3.4	10.1	1.2	0.1	18.9	6.6	5	purple	86	8
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	8	19	17	dense	3	purple	121	11	2.5	8.3	1	0.1	16.6	5.8	5	purple	87	10
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	5	20	15	dense	3	purple	127	15.6	3.7	14.5	1.7	2.3	19.8	6.9	5	purple	88	8
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	6	18	10	dense	4	purple	102	12.8	2.9	8.1	1	0.1	13.6	4.8	4	purple	91	12
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	8	19	10	dense	3	purple	108	15.1	3.5	11.4	1.3	3.4	20.6	7.6	4	purple	92	11
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	13	15	9	dense	3	purple	97	16.8	3.9	17	2.1	4.8	21.2	7.4	5	purple	89	12
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	8	15	8	dense	3	purple	98	15.8	3.6	16.4	1.9	2.1	18.5	6.5	5	purple	89	9
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	8	17	10	dense	3	purple	104	16.7	3.8	16.5	1.9	4.4	20.2	7.1	5	purple	87	8
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	9	18	9	dense	3	purple	105	11.9	2.8	9.3	1.1	0.1	20.1	7	4	purple	93	9
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	8	20	13	dense	3	purple	101	15.8	3.6	14	1.6	2.8	20.9	7.3	5	purple	92	9
<i>Vicia faba</i> var. <i>major</i> 'Agnadulice'	cultivated	12	21	13	dense	4	purple	98	13.7	3.1	12.6	1.5	0.1	20	7	4	purple	92	10

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<i>Vicia faba</i> var. <i>majov-Aguadulce</i>	cultivated	8	15	7	dense	4	purple	112	16	3.7	13.2	1.5	2.6	18.2	6.4	5	whitish	176	9
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	4	16	5	rare	2	yellow	203	18.6	3.5	13.8	1.9	0.4	20.1	6.1	2	pinkish	122	10
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	4	9	6	rare	2	yellow	191	14.3	2.6	13.2	1.7	1.2	20.3	6.7	3	pinkish	118	11
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	5	16	5	rare	2	yellow	207	15.2	2.9	13.4	1.8	2.6	19.3	6.3	2	purple	91	12
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	7	14	6	rare	2	yellow	184	18.1	3.5	14	1.9	1.3	20.1	7.1	3	purple	93	9
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	5	14	5	rare	2	yellow	192	18.3	3.6	13.9	1.9	0.1	21.9	7.4	4	purple	89	8
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	3	13	7	rare	1	yellow	203	15.8	2.9	14	2	2.8	20.7	6.4	3	purple	87	8
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	3	16	5	rare	2	yellow	201	16.8	3.2	14.8	2.1	2.3	21.7	7.4	2	purple	86	9
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	4	13	6	rare	2	yellow	180	15.8	3	14.4	2	2.8	20.3	6.3	2	purple	91	10
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	5	12	6	rare	2	yellow	196	16.9	3.2	15.3	2.1	0.1	20.8	6.6	3	purple	90	11
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	4	19	8	dense	3	yellow	193	17.3	3.3	13.6	1.9	0.1	19.8	7.3	4	purple	94	11
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	2	16	6	rare	2	yellow	192	17.7	3.5	15.6	2.1	2.4	18.6	6.9	3	purple	96	12
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	4	10	7	rare	2	yellow	193	17.3	3.4	13.2	1.8	1.9	19.7	7.2	2	purple	91	8
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	4	16	8	rare	2	yellow	191	17.7	3.4	14.6	2	4	20.5	7.5	3	purple	90	9
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	4	14	5	rare	2	yellow	202	17.5	3.3	14.5	2	2.8	18.5	6.8	4	purple	87	9
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	2	15	10	rare	1	yellow	205	17.6	3.4	14.1	1.9	4.5	19.3	6.8	3	purple	89	9
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	6	14	6	rare	2	yellow	201	22.2	4.1	19.9	2.6	5.9	20.7	4.6	2	purple	91	8
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	4	15	10	rare	2	yellow	192	13.6	2.6	10.5	1.4	4.6	18.8	4.9	2	purple	86	9
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	3	8	5	dense	3	yellow	186	13.9	2.7	14.1	1.9	0.1	19.2	4.6	4	purple	78	10
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	4	14	5	rare	1	pink	149	15.7	3	12.2	1.8	2.9	19	7	2	whitish	77	11
<i>Vicia sativa</i> subsp. <i>nigra</i>	cultivated	5	14	5	rare	2	pink	184	22	4.2	19.7	2.7	5.7	20.6	4.7	2	whitish	106	11
<i>Pisum sativum</i> 'Senatore'	cultivated	3	17	9	dense	3	yellow	202	22.7	4.2	19.6	2.9	3.4	19.5	6.2	3	pinkish	125	12
<i>Pisum sativum</i> 'Senatore'	cultivated	4	16	8	rare	2	pink	147	16.1	2.4	13.3	2	2.6	17.2	6	5	pinkish	119	10
<i>Pisum sativum</i> 'Senatore'	cultivated	7	9	5	rare	2	yellow	211	12.8	2.5	12.3	1.9	5.1	17	5.9	5	pinkish	123	8
<i>Pisum sativum</i> 'Senatore'	cultivated	4	15	10	rare	2	yellow	203	12.4	2.5	9.6	1.5	3.7	15.6	5.5	3	pinkish	115	8
<i>Pisum sativum</i> 'Senatore'	cultivated	3	17	10	rare	2	yellow	203	16.8	3.1	17	2.4	3.4	19.3	6.6	4	purple	91	9
<i>Pisum sativum</i> 'Senatore'	cultivated	4	18	10	rare	2	yellow	202	18.2	3.3	15.5	2.3	2.2	20.1	6	5	purple	87	9
<i>Pisum sativum</i> 'Senatore'	cultivated	4	17	8	dense	3	yellow	191	15.1	3	14.2	3	3.2	18.7	6.5	4	purple	85	7
<i>Pisum sativum</i> 'Senatore'	cultivated	5	5	3	dense	3	yellow	201	21.4	4.1	19.5	2.9	5.3	19.3	6	3	purple	96	9
<i>Pisum sativum</i> 'Senatore'	cultivated	5	12	6	dense	4	yellow	204	22.1	4.3	19.7	2.8	4.3	21	6.4	7	purple	91	8
<i>Pisum sativum</i> 'Senatore'	cultivated	4	16	9	dense	3	yellow	192	16.2	3.2	15.8	2.5	0.1	20	6.9	5	purple	82	9
<i>Pisum sativum</i> 'Senatore'	cultivated	4	14	8	rare	2	yellow	191	15	2.9	13.4	2.2	3.2	21.6	6.7	4	purple	83	8
<i>Pisum sativum</i> 'Senatore'	cultivated	2	17	9	dense	3	yellow	187	11.8	2.4	13.5	2.1	2.2	17.9	6.9	3	purple	86	10
<i>Pisum sativum</i> 'Senatore'	cultivated	2	14	7	dense	3	yellow	182	16	3.1	14.4	2.1	4.6	20.2	5	4	purple	94	9
<i>Pisum sativum</i> 'Senatore'	cultivated	6	16	8	rare	2	yellow	212	16.6	3.3	11.5	1.7	0.1	17.12	6.5	5	purple	90	8
<i>Pisum sativum</i> 'Senatore'	cultivated	4	13	7	dense	3	yellow	208	19.8	3.7	20	2.9	4.9	19.2	4.4	4	purple	91	8
<i>Pisum sativum</i> 'Senatore'	cultivated	5	16	8	rare	2	yellow	201	21.4	4.1	20	3	6.2	20.3	4.4	4	purple	95	7
<i>Pisum sativum</i> 'Senatore'	cultivated	5	15	9	rare	2	yellow	196	13.1	2.7	14.2	2.4	3	17.8	4.5	3	purple	90	8
<i>Pisum sativum</i> 'Senatore'	cultivated	3	16	7	rare	2	yellow	211	18	3.7	15.4	2.7	4.5	18	4.6	4	purple	78	9
<i>Pisum sativum</i> 'Senatore'	cultivated	4	19	11	dense	3	yellow	203	14.3	2.9	12.2	1.9	2.7	19.1	4.4	3	purple	82	9
<i>Pisum sativum</i> 'Senatore'	cultivated	6	13	7	rare	2	yellow	193	15.7	3.1	13	2.2	2.3	19.4	6.2	4	purple	86	8
<i>Pisum sativum</i> 'Senatore'	cultivated	4	17	7	dense	3	pink	157	15.4	2.9	12.5	2.1	6.2	17.7	6.2	5	whitish	181	8
<i>Pisum sativum</i> 'Senatore'	cultivated	4	9	5	rare	2	pink	151	13.8	2.8	11.9	2	5	18.3	6.4	5	whitish	186	7
<i>Pisum sativum</i> 'Senatore'	cultivated	2	14	9	rare	2	pink	199	11.2	2.4	13.2	2	0.1	19.8	6.1	2	whitish	189	8
<i>Pisum sativum</i> 'Senatore'	cultivated	3	7	4	dense	3	yellow	209	13.6	3.9	14.8	2.2	3	18.3	5.8	2	yellowish	162	9
<i>Pisum sativum</i> 'Senatore'	cultivated	4	15	8	rare	2	yellow	203	14.8	2.9	10	1.7	1.3	15.3	5	2	yellowish	157	9

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