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Breeding faba bean (*Vicia faba* L.) for resistance to *Orobanche crenata* Forsk

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SUMMARY - Reports on selection for resistance of *Vicia faba* to *Orobanche crenata* and on its inheritance are discussed. The most important genetic component, always quite marked, is additivity. Dominance is not always expressed; when it is, it is partial, environmental dependent and horizontal *sensu* Van der Plank. There is at least one clear case of genetic complementation. Breeding strategy for resistance is described and the results discussed.

*RESUME - "Amélioration de la fève (*Vicia faba *L.) pour la résistance à* Orobanche crenata *Forsk." Des rapports sur la sélection pour la résistance de* Vicia faba *à* Orobanche crenata *et son hérédité sont examinés. La composante génétique la plus importante, toujours très remarquable, est l'additivité. La dominance n'est pas toujours exprimée; quand elle l'est, il s'agit d'une dominance partielle, dépendente de l'environnement et horizontale* sensu *Van der Plank. Il existe au moins un cas évident de complémentation génétique. Nous décrivons ici notre stratégie d'amélioration pour la résistance et discutons des résultats.*

Introduction

Orobanche crenata is a parasitic weed challenging the cultivation of faba bean in Mediterranean countries. Its presence as a parasite was already recognized by Greek authors. Most likely, as faba beans were not widely cultivated nor sown in dense plots, the parasite was not as widespread then as later on. Its importance as a parasite was stressed by some authors in the eighteenth century. Thus, Valcarcel, from Spain, described broomrapes in 1790 in such detail that the suggestion of an extremely important pest of the crop is easily perceived by the reader. In recent times, its presence has been detected in Southern Morocco and in the Upper Nile in Egypt.

Studies on resistance to *O. crenata* in *Vicia faba*

Table 1 provides information on the main papers concerning selection for resistance. Attempts to control *Orobanche* attack by biological, chemical or agricultural methods have been reviewed in other publications (Cubero and Moreno, 1979; Cubero, 1983; Cubero, 1986). The different control methods (agricultural, chemical, biological) have generally yielded unsatisfactory results. The only exception seems to be the application of glyphosate to control *O. crenata* on *V. faba* (although this is not so with lentils, for example). The great expectation of using the fly *Phytomyza orobanchiae* as biological control is still a hope.

Despite the failure of controlling broomrape attacks through cultural practices, genetic resistance by means of selection between and within landraces has scarcely been tested in the past (Elia, 1964; Bryssine, pers. com.; Cubero, 1973). Elia (1964) studied 15 Italian landraces and found that those belonging to the *major* group and showing dark coated seeds as well as *equina* and *minor* landraces were less susceptible to broomrape than *major* types with light coated seeds. This difference in susceptibility was, however, of no commercial use as even the least susceptible landraces suffered heavy attacks. Cubero (1973) studied 70 landraces and 50 inbred lines belonging to the four botanical groups traditionally recognized in the host species. There was a significant correlation between the average seed size of a landrace or inbred line and the average number of broomrapes per host plant recorded: the smaller the seed size, the greater the level

Table 1. Studies on resistance to *Orobanche crenata*.

Method/material	Results	References
Segregating generations Diallel 4x4	Expression of resistance depends on environmental conditions.	Cubero, 1973
Segregating generations, parasite populations	Resistance. Host-parasite interaction almost nil.	Cubero and Moreno, 1979
Diallel 6x6, F_2 Very diff. genotypes	Strong additive effects. No dominance. Scaling effect.	Cubero and Martínez, 1980
Diallel 8x8, F_1	Strong additive effects. Weak partial dominance. Suscept.< resist.	Suso, 1980
Landraces (Egypt)	Method of selection to avoid escapes.	Abdalla, 1982
Landraces, segregating generations.	Origin and description of F402.	Nassib *et al.*, 1982
Segregating generations Different genotypes	Additivity. No dominance. Influence of the level of infestation.	Hernández *et al.*, 1984, 1987.
Landraces, cultivars *in vitro* and *in vivo* tests	Apparent resistance related to vigor. Diff. behaviour *in vitro* (BPL 2210).	Aalders and Pieters, 1986
Segregating generations. Parasite populations.	See Table 2. Expression of resistance depends on environmental conditions. Host-parasite interaction almost nil.	Hernández, 1987
Landraces	Method of selection: single plant better than between plots selection.	Radwan *et al.*, 1988a
Landraces	Identification of 'Locale di Castellano' as resistant cultivar.	Perrino *et al.*, 1988

of resistance. Elia's results, as well as those by Cicarone and Piglionica (1979) fit well into this pattern.

Moreover, though differences between genotypes have been detected, selection performed on this material has failed to produce an authentically resistant variety. Several causes, acting separately or together, can explain these failures. First, even the highest degree of resistance found in those early attempts was not enough to produce an authentically resistant commercial variety. Second, when data are available, it can be easily seen that there is as much variation between them as within lines; genetic variance was much smaller than environmental variance, hence heritability was also very low. Consequently, response to selection was almost nil. Attempts to improve screening by studying the statistical distribution of the parasite and by performing both intra– and inter–family selection did not produce better results either: after two cycles of progeny test, the level of resistance measured by the average number of broomrapes per host plant and by its distribution was almost the same as that of the point of departure, although the proportion of zero–broomrape plants increased from 12% to 22% (Cubero, 1983). We now feel that two cycles of progeny tests are not enough to achieve a significant response to selection given the low heritability value, the low resistance level in the host and the complexity of the parasite. However, Radwan *et al.* (1988a), have reported positive results through the use of a combined selection between and within populations, even without any kind of progeny tests. Such a result is only possible under minimum values of the environmental effects in order to obtain maximum heritability values.

A *paucijuga* line, VF 172, was reported by Cubero (1973) as showing a certain degree of resistance. The suspicion that the low number of broomrapes recorded on host plants was a consequence of a poor root system was eliminated by studying the behaviour of its hybrids with susceptible lines. The comparison of these hybrids and of their segregating generations with the equivalent generations derived from susceptible x susceptible crosses showed a differential behaviour concerning resistance between material which was morphologically alike (Cubero, 1973; Cubero and Moreno, 1979). As VF 172 was, agronomically speaking, extremely poor and because its degree of resistance was still not commercially useful, there were no resistant cultivars derived from crosses involving VF 172 as a parent.

The origin of the resistant line, F402, was described by Nassib *et al.* (1982). F402 showed a high level of field resistance as well as agronomically favorable characteristics. It was also possible to perform crosses to study the genetics of resistance by using a wider variation range. F402 proved to be resistant under both greenhouse and field conditions, under very severe conditions of both natural and artificial infestation. This notwithstanding, Aalders and Pieters (1986, 1987) did not observe different reactions with *in vitro* germination between this and susceptible lines. Subsequently, F402 gave origin to the cultivar 'Giza 402'. The line VF1071 was selected out of 'Giza 402' in Andalusia. According to some reports, VF1071 kept its resistance to *Orobanche* even when 'Giza 402' had lost it. VF1071 is the resistant parental line now being used in our current breeding by crossing program.

Apart from these lines, which have been tested not only by themselves but both through their hybrids with susceptible lines and through their segregating generations, there are others reported in the literature. Aalders and Pieters (1986) mentioned the different behaviour of a line (ICARDA's BPL 2210) under *in vitro Orobanche* germination tests. Perrino *et al.* (1988) described 'Locale di Castellano', a landrace from Southern Italy, as highly tolerant under field conditions in comparison to other 50 landraces of very different origins. These lines still need to have their hybrids and segregating generations tested.

Screening has almost always been performed under field conditions and with both natural and artificial infestations. Kukula and Masri (1985) and Pieterse (1986) have described greenhouse techniques, still not widely used by faba bean breeders, despite their simplicity, as demonstrated in lentils (Sauerborn *et al.*, 1987).

Measuring resistance

A comment on how to measure resistance seems necessary. Several indices have been used by different authors: total weight of broomrapes per host plant, height of the tallest (or the average) parasitic shoot, dry mater of parasitic plants per host plant, number of broomrapes per unit sown surface, etc. Hanunik and Besri (this volume) have used the broomrape rate of reproduction as a measure of effectiveness of host resistance. Even though such an index may be perfect for a plant pathologist, its applicability by breeders is not so clear as even with a reduced rate of reproduction, a broomrape plant can yield an incredible amount of seeds. This index could be useful in combination with other better ones than as a single measure of resistance.

The number of broomrape shoots per host plant seems to be the most reliable. Studies on *Vicia sativa/O. crenata* (Gil *et al.*, 1982, 1984, 1987) also confirm this election. The best index would be the total number of seeds germinated by the stimulant substance excreted by the roots of the host, but this number is impossible to evaluate in field experiments or even under *in vitro* conditions. Thus, the best approach to this number is the total number of *Orobanche* plants attached to the roots of the host. Although it is difficult to record under field conditions, the extremely high correlation between this number and the total number of *Orobanche* shoots emerged after plant maturity make it otherwise easy to record (Cubero, 1983). A logarithmic transformation is required for statistical analysis (Cubero, 1983). Nevertheless, for direct genetic studies, as those designed to determine the partition of the total genetic variance in its main components, the number of emerged broomrapes per host plant can be confidently used (Hernández, 1987).

A word of caution: to select a plant with zero broomrapes can be meaningless if the statistical distribution of the number of parasitic shoots on individual host plants is not considered. Thus, plants to be selected must not only show zero broomrapes but must also belong to a family with a high proportion of zero–broomrape plants. Most F_2 or F_3 families always give a certain proportion of zero–broomrape plants, even those coming from crosses between very susceptible lines. It is necessary to be as sure as possible that the selected plants are not escapes; a zero–broomrape host plant can always be an escape, but the probability of this event will be smaller if its family is characterized by a high proportion of such plants. Of course, the comparison with the statistical distribution shown by adequate testers (susceptible lines) is compulsory. For practical purposes, the analysis of the distribution of individual lines, which could be an impossible task if a great number of lines is handled, can be substituted by a double index: the proportion of plants with zero broomrapes and the mean number of broomrapes/plant.

Studies on the genetics of resistance

Until quite recently most of the published works dealt only with moderately resistant genotypes, especially the *paucijuga* line VF172. Cubero (1973), by means of a diallel cross including VF172, found partial dominance for resistance; however, this dominance was dependent on environmental conditions, as the expression of resistance disappeared under hot and dry spring weather. Cubero and Martínez (1980) studied a 7*7 diallel cross (also including VF172) finding a scale effect as well as no dominance for resistance. Suso (1980), who only included Spanish lines in her 8*8 diallel cross, also found similar results: very marked additive and environmental effects, and almost nil dominance effects.

Very recently, an extensive set of crosses was performed including the resistant line VF1071 in the scheme. This time, F_1, F_2 and F_3 as well as backcrosses (BC) and selfed BC were studied for two years in a naturally infested plot. Even though the results are similar to those mentioned above, especially regarding the importance of additivity and environmental dependence of resistance in the sense previously explained, it is not possible to rule out the existence of a type of resistance which is dominant over susceptibility. Moreover, at least a case of clear genic complementation was also evident: a cross between two very highly susceptible lines gave a significant proportion of resistance in both F_2 and F_3 (Hernandez, 1987). These results suggest the existence of genetic heterogeneity in *V. faba* for resistance to *O. crenata* much more important than previously thought. Results described by Aalders and Pieters (1986) support this conclusion at the *in vitro* level. From the breeder's point of view the importance of this finding lies in the possibility of identifying useful genes from many genetically unrelated sources, in order to build up new genotypes with a higher level of resistance than the line VF1071.

Tables 1 and 2 summarize the papers on the genetics of *V. faba* to *O. crenata* published until now. The main conclusions obtained from these papers can be summarized as follows:

Table 2. Genetics of resistance to *O. crenata*.[a]

Cross	Year	Generations	Fitting to additive model	Additivity	Dominance
1071 x 172 R S	1984 1985	P_1 P_1 P_2 F_1 F_2 B_1 B_2 P_1 P_2 F_1 F_2 F_3 $(B_1)(B_2)$	yes yes	yes yes	no yes S>R
1071 x 119	1984	P_1 P_{2-} F_2 B_1 B_2	yes	yes	no
VS	1985	P_1 P_2 F_1 F_2 F_3 $(B_1)(B_2)$	yes	yes	yes S>R
1071 x 06 MS	1984 1985	P_1 P_2 F_1 F_2 B_1 B_2 P_1 P_2 F_1 F_2 F_3 $(B_1)(B_2)$	yes	yes	yes S>R
1071 x 26 VS	1984	P_1 P_2 F_1 F_2 BC_1 BC_2	yes	yes	S>R
172 x 06	1984	P_1 P_2 F_1 F_2 B_1 B_2	yes	yes	yes S>R
172 x 119	1984	P_1 P_{2-} F_2 B_1 B_2	yes	yes	yes R>S
172 x 26	1984	P_1 P_2 F_1 F_2 B_1 B_2	yes	yes	no
119 x 26	1984	P_1 P_{2-} B_1 B_2	yes	yes	Compl.
119 x 06	1984	P_1 P_{2-} F_2 B_1 B_2	yes	yes	yes S>R
26 x 06	1984	P_1 P_{2-} F_2 B_1 B_2	no	–	–

[a]R: resistant; S: susceptible; VS: very susceptible; MS: moderately susceptible

- Additivity is always very strong, very frequently being the only genetic component.
- When dominance effects are present, susceptibility is usually dominant over resistance; dominance, if present, is always partial; however, there are cases where resistance is dominant over susceptibility. There is at least one case where there was genetic complementation: a cross between two very highly susceptible lines gave a certain degree of resistance in F_2 and F_3.
- This genetic heterogeneity for resistance has to be a consequence of the coexistence of different resistant mechanisms. Thus, genes for resistance can be found in many different lines and can be either dominant or recessive.
- There are biotypes of the parasite showing differential aggressiveness. The parasite x host interaction is very small.
- Resistance seems to be horizontal, *sensu* Van der Plank (1968). The behaviour of resistant lines is, therefore, predictable; it is possible to use them in a wide range of environments.

Pathogenic biotypes

The interaction between host and parasite at the genotypic level can represent a problem for the breeder. The possible existence of races or biotypes has been studied by Cubero and Moreno (1979) with the use of 25 host inbred lines and 5 populations of the parasite and by Hernández (1987) by means of 10 inbred host lines and 6 parasite populations. The main result of these studies is that there is a very low level of host/parasite interaction. Host genotypes react almost uniformly to parasitic races, and *vice versa*. This suggestion is supported by the good performance in Lattakia (Syria) of resistant lines selected in Córdoba (Spain), in both cases under field conditions (Robertson and Hannounik, pers. com.). New parasitic biotypes can originate, however, as *Orobanche crenata* populations are very heterogeneous chromosomically as well as genetically. However, they can also originate through interspecific crosses in *Orobanche* (Cubero *et al.*, 1979).

Radwan *et al.* (1988b) studied 9 geographic accessions of *O. crenata* on 22 different stocks of faba bean. They also did not find any strong interaction between host and parasite. Broomrape biotypes showed differences in aggressiveness but host and parasite relationships seemed to be dependent on the environmental conditions rather than on genotype interactions. These results confirm those previously discussed, even though both of them were obtained under very different environmental conditions.

Our breeding strategy

The main problem in breeding for resistance to *Orobanche* is to avoid the 'dilution' of favorable genes once the crosses between the resistant and the adapted (susceptible) lines have been performed. Our source of resistance so far has been the line VF1071, which has been continuously checked both under field and glasshouse conditions. VF1071 plants selected as parents were always derived from seeds obtained from selfed plants. We have not maintained the same VF1071 lines as parentals; they have been chosen every year in order to increase the resistance of the VF1071 itself.

Because of the quantitative genetic system underlying the resistance to broomrape in faba bean, Cubero (1983) suggested a recurrent selection method to accumulate genes for resistance in the host at the quickest possible rate. We follow a modified recurrent selection method which included a progeny test within each one of the recurrent cycles to breed for resistance in faba bean. Use of insect–proof cages is obviously required because of the partial allogamy of the host species, but yield tests have to be performed under open field conditions in a highly and homogeneously infested plot (the homogeneity of the plot infestation has to be periodically checked). Because of the statistical distribution of the parasite, selection between lines and/or segregating generations is preferable to the simple average value of any kind of index. Statistical designs should include many repetitions. It is essential to try to modify the statistical distribution rather than use averages.

The expected progress in selection will always be slow, as the main characteristics involved (resistance to *Orobanche,* yield per plant and seed size) are quantitative characters from a genetic point of view. In spite of this difficulty, recent results show that it is feasible to combine resistance and yield in the same genotype.

Fig. 1 shows the steps followed by us since 1981. The basic ideas in our program are:

- Different well adapted but susceptible cultivars used as parent lines at different times.
- Selection performed in an extremely high (even 'unrealistically') level of infestation; material under selection kept in insect–proof cages, although, open field tests are also performed.
- The best plants from the best lines, taking into account the within–line distribution of the parasite selected and selfed in glasshouse early in the following year to provide seeds for an usual second sowing under cage in the same year.
- In order not to dilute favorable genes, crosses between the best lines performed.

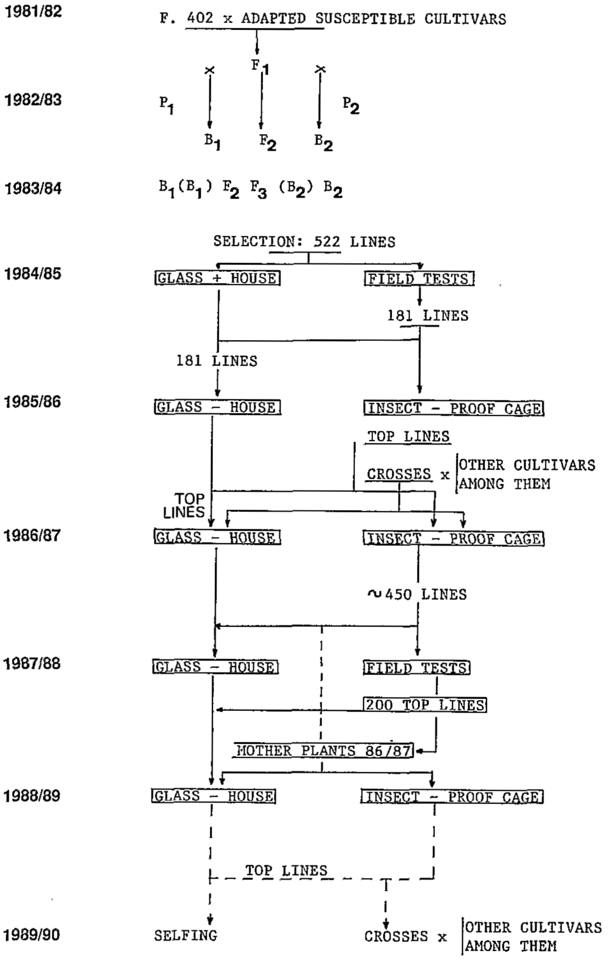
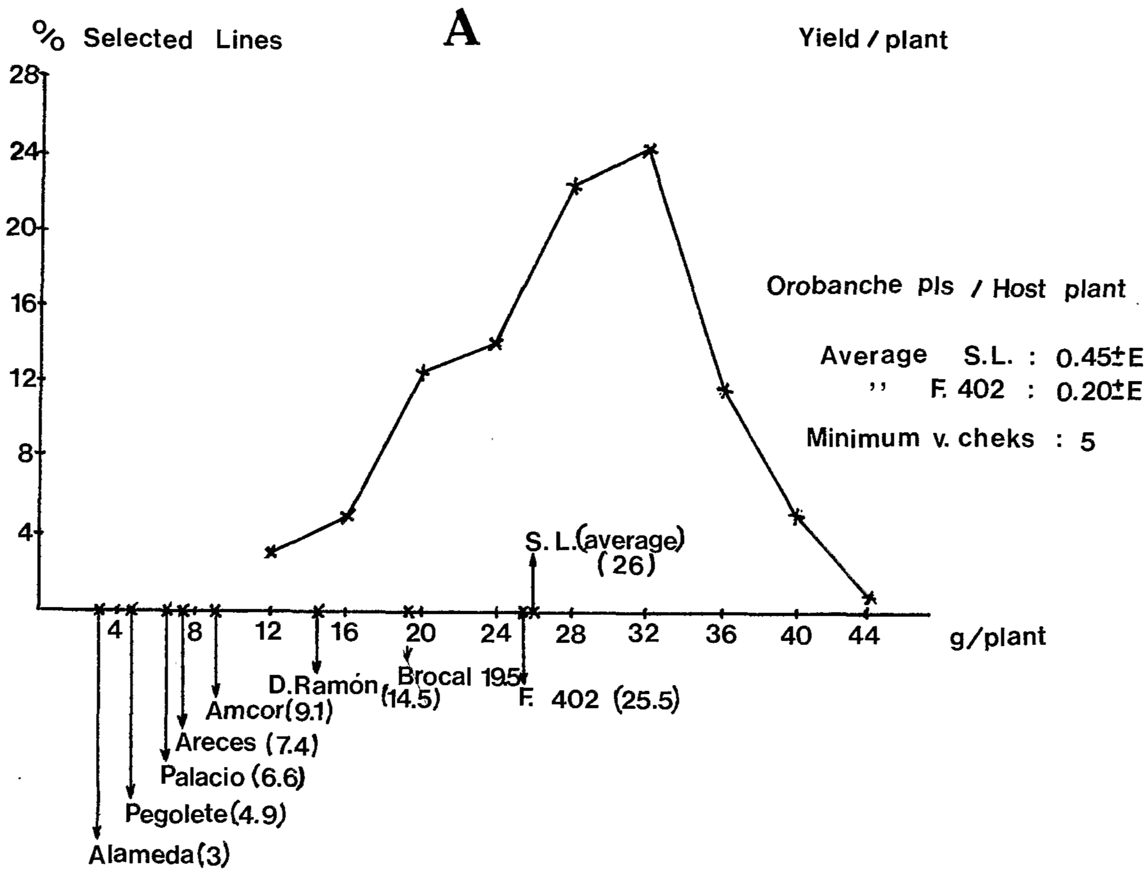


Fig. 1. Breeding scheme.

- Backcrosses and selfed backcrosses have provided a very valuable set of families for selection. Because of the essentially additive genetic system responsible for resistance, backcrosses are very different at the resistance level. However, lines must be selected from both backcrosses and their selfed descendants. Otherwise, lines derived from the backcross to the resistant parent will show more resistance but less adaptation. It is essential to keep genes for resistance and genes for yield together, and to allow for recombination.
- Field trials with advanced materials performed following a design based on a high number of repetitions, each one consisting of small individual plots. The most advanced lines tested during the last season (1987/88) were distributed in 24 blocks, each one consisting of 25 plots. Each plot consisted of one advanced selected line surrounded by a check (cv. 'Alameda') and the resistant parent (VF1071).



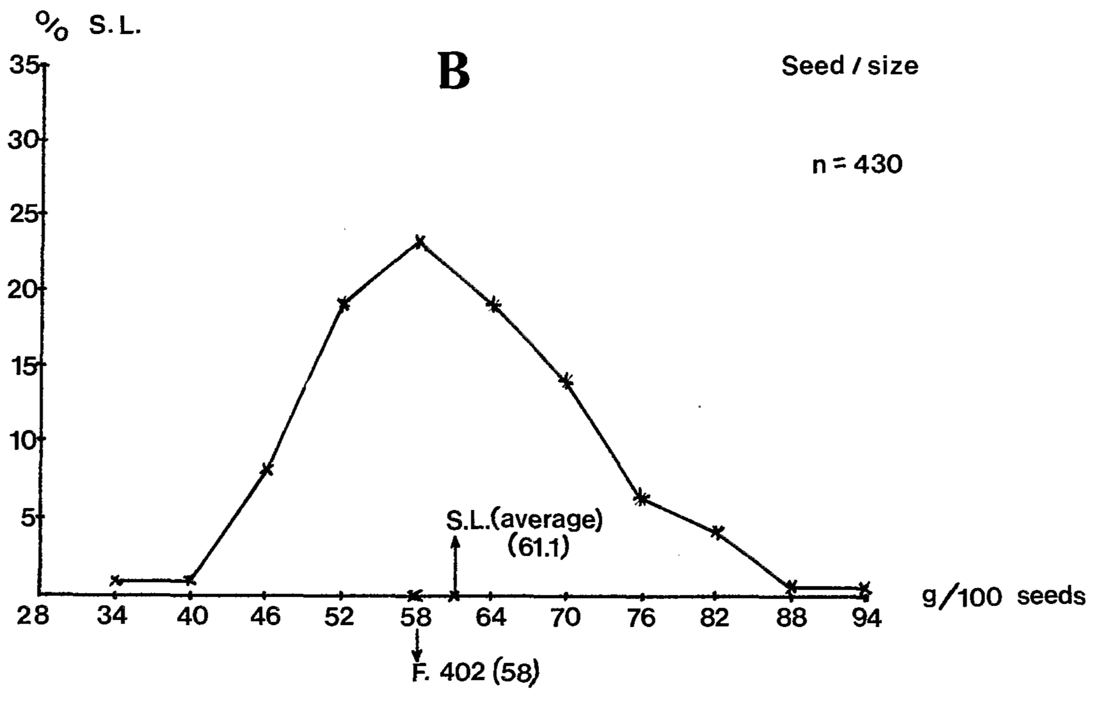


Fig. 2. Distribution of selected lines (S.L.) resistant to broomrape for: (A) yield/plant (g/plant), (B) faba bean seed size (g/100 seeds); n = 430. Averages of seven commercial susceptible checks and one resistant (VF 1071) check are shown.

Fig. 2 shows the results obtained for the selected lines for two important characteristics, namely, yield per plant and seed size. There is hope of improving both characters. Even though the advance in selection is obvious, the use of the genes from VF1071 represent a ceiling in the expected level of gains. It is necessary to include in the breeding program genes from different origin. Lines derived from other crosses as well as genes from other origins, such as 'Localle di Castellano' and BPL 2210 could also be included after a careful check.

The expected progress in selection will always be slow, as the three characteristics involved (resistance to *Orobanche,* yield per plant and seed size) are quantitative characters from a genetic point of view. But our results show that it is feasible to obtain resistant cultivars.

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