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REVIEW

Advances in disease and pest resistance in faba bean

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Abstract

Faba bean (*Vicia faba*) is a grain legume crop widely cultivated in temperate areas for food and feed. Its productivity can be constrained by numerous diseases and pests that can be managed by a number of strategies, complemented with the deployment of resistant cultivars in an integrated manner. Few sources of resistance are available to some of them, although their phenotypic expression is usually insufficiently described, and their genetic basis is largely unknown. A few DNA markers have been developed for resistance to rust, ascochyta blight, and broomrape, but not yet for other diseases or pests. Still, germplasm screenings are allowing the identification of resistances that are being accumulated by classical breeding, succeeding in the development of cultivars with moderate levels of resistance. The adoption of novel phenotyping approaches and the unprecedented development of genomic resources along with speed breeding tools are speeding up resistance characterization and effective use in faba bean breeding.

State of the art on faba bean breeding for disease and pest resistance

Faba bean (*Vicia faba*) is an annual grain legume crop (pulse) mainly grown as a valuable source of seed protein for food and feed, providing an alternative to soybean (*Glycine max*) in the temperate regions (Khazaei et al. 2021). Faba bean has a high protein content and contributes to sustainability of cropping systems by fixing atmospheric nitrogen in symbiosis with *Rhizobium leguminosarum*, reducing the dependence on extensive use of synthetic nitrogen fertilizers (Karkanis et al. 2018; Mínguez and Rubiales 2020). In spite of decades of decline, faba bean cultivation is speedily recovering and extending to new areas (FAOSTAT 2021), which calls for the adjustment of cropping practices and the breeding of more adapted and productive cultivars able to address both producers' and consumer's needs.

Faba bean can be constrained by a number of diseases and pests to which some management strategies are in place that should be integrated in a concerted manner (e.g. Stoddard et al. 2010). The deployment of genetic resistance is a core component of any integrated control strategy. However, resistance breeding is shown to be slow in faba bean compared to cereal crops, or even compared to other legumes crops for which deployment of modern genomic tools has improved the efficiency of breeding programs over the past decade (Kumar et al. 2011; Varshney et al. 2019). The reasons for the slower progress in faba bean are the reduced investment in the crop, leading to an insufficient understanding of both genetic basis of most resistances identified and the etiology and genetic diversity of the pests and diseases. A battery of sources of resistance has been identified, but in most instances these have been poorly described, and their genetic basis is largely unknown. Furthermore, for most of the pests and pathogens there is little information on pathogenic variation, or not consensus on existence of races, and when these have been suggested, they have not been systematically monitored anywhere. This is paired with poorly developed genomic resources, complicating faba bean resistance breeding. This is largely due to its sizeable genome (approx. 13 Gbp) and significantly lower genomics research activity compared to other major legume crops. But significant progress is underway due to turbo-charged research in this crop (Khazaei et al. 2021). Its gigantic genome size paired with six large chromosomes made faba bean a model for cytogenetics, with asynaptic mutants identified (Sjödin 1970), that served on to develop series of trisomics that later allowed assignment of genetic markers to physical

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chromosomes (Vaz Patto et al. 1999). However, at the same time, the large genome size, together with an abundance of transposable elements (Carrillo-Perdomo et al. 2020), has delayed the faba bean genome and map-based cloning (Cooper et al. 2017). Meanwhile, transcriptome analysis is being used for enrichment of genomic resources (Mokhtar et al. 2020). This has retarded the successful application of marker-assisted selection (MAS) in faba bean breeding programs compared to other legume crops (Torres et al. 2006, 2010; Khazaei et al. 2021). Mapping studies have been using the technologies available at the time, from earlier studies with RAPD (random amplified polymorphic DNA) till SNP (single nucleotide polymorphism) markers allowing the development of high density genetic maps derived mainly from biparental populations (e.g. Satovic et al. 2013; Webb et al. 2016; Carrillo-Perdomo et al. 2020). Genomic resources are continuously expanding, till the most recent report of a high-throughput faba_bean_130K targeted next-generation sequencing (TNGS) genotyping platform (Wang et al. 2021). These genomic resources will facilitate MAS and gene discovery in faba bean. The purpose of this paper is to review and critically discuss the state of the art and future strategies on genetics and breeding of faba bean for disease and pest resistance.

Faba bean genetics resources

Access to well-characterized germplasm collections that adequately represent the available natural genetic diversity is a critical resource in any pre-breeding program. Several *ex situ* faba germplasm collections are held in genebanks globally, with a total of over 38,000 accessions including landraces, breeding lines, and improved varieties (Crop Trust 2017). Genesys displays information for about 16,000 faba bean accessions (GENESYS 2021). ICARDA (International Center for Agricultural Research in the Dry Areas) hosts the largest collection of faba bean (21%), followed by the ICGR-CAAS (Institute of Crop Germplasm Resources of the Chinese Academy of Agricultural Sciences), and the ATFCC (Australian Temperate Field Crops Collection). Still, characterization and preliminary evaluation for pre-breeding activities remains a challenge, mainly due to partial out-crossing behaviour in this species (4–84%, see Bond and Poulsen 1983). As long as all attempts to produce fertile progenies with related *Vicia* species have failed so far, the genetic diversity available for faba bean breeding is still restricted to *V. faba* germplasm, where considerable genetic diversity is available (Duc et al. 2010), including variable levels of resistance to major diseases and pests that are presented in this paper. Novel tools such as FIGS (Focused Identification of Germplasm Strategy) may also speed up the discovery of resistance genotypes or genes in germplasm collections. However, FIGS might be less effective when looking for resistance to insects (Stenberg and Ortiz 2021). The FIGS approach has been already shown to be an effective tool to enhance the discovery of new genes for abiotic stress adaptation in faba bean (Khazaei et al. 2013). The development of high-throughput genotyping platforms, a reference genome, and following pan-genomes will facilitate characterization of the genetic diversity and structure of this species (Khazaei et al. 2021). It will also aid exploitation of the diversity as a key resource for breeding for biotic stress resistance.

Current knowledge on resistance to fungi and oomycete

Faba bean rust, incited by the biotrophic fungus *Uromyces viciae-fabae* (syn. *U. fabae*), is serious disease worldwide (Emeran et al. 2011; Ijaz et al. 2018). It is an authoicos macrocyclic rust, not requiring an alternate host to complete its lifecycle, although sexual reproduction is not commonly seen in temperate regions. In fact, *U. viciae-fabae* is a species complex in which *formae speciales* might be distinguished, with faba bean, vetch (*V. sativa*), and lentil (*Lens culinaris*) host-specialized isolates (Emeran et al. 2005; Rubiales et al. 2013; Ijaz et al. 2020).

Insights into the faba bean rust genome have been initiated (Link et al. 2014), which can help in the search for secreted proteins and effectors. However, basic knowledge of pathogenic variation is still insufficient. Races have been suggested within the faba bean infecting isolates (Conner and Bernier 1982; Rojas-Molina et al. 2006; Ijaz et al. 2018), but their distribution has not been systematically monitored anywhere. Rust can be controlled with fungicides (Emeran et al. 2011). Alternative methods such as intercropping, cultivar mixtures, biological control or activation of systemic induced resistance (Gaunt 1983; Sillero et al. 2012; Shtaya et al. 2021) can contribute to reduce rust infection but are not yet available at the commercial level. So far, only incomplete levels of resistance against *U. viciae-fabae* are available, mostly described as "slow rusting" (Table 1 and associated references). More detailed observations allowed to discern two types of incomplete resistance. The most common was non-hypersensitive resistance (Sillero et al. 2000; Herath et al. 2001) reducing hyphal growth and hampering haustoria formation (Rubiales and Sillero 2003; Rojas-Molina et al. 2007) resulting in reduced epidemic progress despite a compatible interaction (high infection type, this is pustules well formed with no associated macroscopically visible necrosis). Attempts to identify alleles/QTLs (quantitative trait loci) for resistance and the development of DNA markers for non-hypersensitive resistance have been initiated, but no results are reported so far. A second type of incomplete resistance was the "late acting" hypersensitive rust resistance (Sillero

Table 1 Sources of resistance to rust (*Uromyces viciae-fabae*) in faba bean, and details on screening conditions and types of resistance identified

Accessions	Screening conditions	Phenotype description of resistances identified	Genetic basis	References*
2N34, 2N52, V-300, V-313, V-1271, V-1272, V-1273, V-1335, BPL 261, ILB 938, Primus, VF-16, VF-36, VF-40, VF-47, VF-50, VF-59	Field and controlled conditions with artificial inoculation	Incomplete: reduced DS explained by increased latent period, and reduced number and size of colonies; with reduced IT or without moderate late acting hypersensitivity	Not studied	Sillero et al. (2000)
ILB 3025, ILB 3107	Detached leaves inoculated	Incomplete: reduced severity and pustule size	Additive gene action	Stoddard and Herath (2001)
Incomplete non-hypersensitive resistance (BPL 261, BPL 484, VF-40, L82009, VF-16)/ incomplete hypersensitive resistance (V-300, V-1271, V-1273, 2N-34)	Seedlings and adult plants inoculated under controlled conditions-histology	Incomplete: reduced haustoria formation resulting in smaller colonies. Late acting hypersensitive reaction identified in some accessions resulting in a reduced colony growth. Differences more marked in adult plants than in seedlings	Not studied	Sillero and Rubiales (2002)
BPL 261, V-1273	Seedlings inoculated under controlled conditions- histology	Incomplete: increased latency period and reduced haustoria in both either late acting hypersensitivity or no-hypersensitivity	Not studied	Rubiales and Sillero (2003)
A biparental population derived from 2N52	Seedlings inoculated under controlled conditions	Incomplete: reduced IT	Monogenic	Avila et al. (2003)
ILB 3107, ILB 3025, Icarus (BPL 710), BPL 7, BPL 8, BPL 260	Detached leaf assay	Incomplete	Not studied	Herath et al. (2001)
Giza 40, Giza 429, Giza 461, Giza 643, Giza 714, Giza 716, Giza 843, Sakha 1, Sakha 2, Mostohor 103, Nubaria 1, BPL 710, Reina Blanca	Field screening under natural infection	Incomplete: reduced severity	Monogenic resistance suggested in accession BPL 710	Noorka and El-Bramawy (2011)
095-3, 090-1, BPL 710, LPF 120, 095-1, 132-3, 158-1, 135-1, 174-1, BG 1261, 152-1, 097-2, ILB 4709, BG 932, ILB 5284, 132-1, BPL 1763	Field screening in multiple environments	Incomplete: reduced DS	Not studied	Villegas-Fernández et al. (2011)
BPL 1488, BPL 2355, BPL 3492, BPL 3523, BPL 2794, BPL 3433, BPL 3442, BPL 3561, BPL 3740, BPL 4944, BPL 4944, BPL 4539, L83129	Field screening in multiple environments with natural infection	Incomplete: attention paid to multiple resistance to also ascochyta blight and chocolate spot	Not studied	Maalouf et al. (2016)
Joya, Marimba, Omeya	Field screening in multiple environments	Reduced disease severity	Not studied	RAEA (2016)
BPL 261, V-300, V-303, V-311, V-313, V-720, V-1196, V-1271, V-1022, V-1272, V-1320, V-452, V-481, V-1196	Field testing in multiple environments	Incomplete	Not studied	Sillero et al. (2017)
Doza#12035, Ac1655 (V-300), Ac1231#14905, Ac1866#15013, Ac1269 (BPL 748), AC1272 (BPL 1179), PBA Nasma, PBA Warda, PBA Nanu	Greenhouse screening with artificial inoculation	Incomplete: moderate IT	Monogenic	Adhikari et al. (2016)

Table 1 (continued)

Accessions	Screening conditions	Phenotype description of resistances identified	Genetic basis	References*
Biparental populations involving Doza and V-300	Greenhouse screening with artificial inoculation	Moderate: reduced IT	Monogenic	Ijaz et al. (2021)
Doza, Nura, Kareema, Marne, Nanu, Nasma, Warda	Field screening	Incomplete: reduced severity	Not studied	Pulse Australia (2021)

*This table details only reports since 2000. For older citations see Bond et al. (1994) and Sillero et al. (2010). IT, infection type. DS, disease severity

et al. 2000; Adhikari et al. 2016) with some haustoria failing to form due to hypersensitive cell death, but others forming successfully, allowing some colony development, although with reduced disease severity, with an intermediate infection type (moderate pustules surrounded by some macroscopically visible necrosis). Such hypersensitive resistance is controlled by single genes (Sillero et al. 2000), some of which are mapped, like *Uvf-1* (Avila et al. 2003), *Uvf-2*, and *Uvf-3* (Ijaz et al. 2021). Reported KASP (kompetitive allele specific PCR) markers should allow pyramiding of these genes to increase the level of resistance and its durability.

Ascochyta blight is a foliar disease incited by *Didymella fabae* (anamorph *Ascochyta fabae*). Infection can be started by conidiospores carried and distributed by infected seeds and crop debris or by wind-dispersed ascospores. Then, rain and wind disperse the conidiospores. The use of fungicides reduces ascochyta blight damage, but the integration of management practices is crucial to successful control (Ahmed et al. 2016). Physiological specialization has been suggested, although there is no consensus in the definition of races (Ali and Bernier 1985; Rashid et al. 1991a; Kohpina et al. 1999; Avila et al. 2004). Still, the existence of at least two virulence groups has been suggested in Australia, being more aggressive on resistant cultivars, reinforcing the need to monitor pathogen variability (Kimber et al. 2016). Some levels of incomplete resistance have been reported (Table 2) using a range of screening methods under different environmental conditions, which complicates proper comparisons of results (Tivoli et al. 2006). Earlier reports pointed towards major gene inheritance (Rashid et al. 1991b; Kopina et al. 2000). However, later linkage mapping studies suggested a number of QTLs with minor effects. More recently, an association mapping study on a winter faba bean germplasm identified 12 DNA markers associated with ascochyta blight resistance, each one explaining around 6 to 22% of the phenotypic variance (Faridi et al. 2021). Availability of such markers would facilitate pyramidation of multiple QTLs to enhance the level of resistance. Such QTL studies were performed with biparental populations. DeepSuperSAGE transcriptome profiling identified 10 tags associated with responses to the jasmonic acid pathway, pectin esterase activity or gene silencing in the resistant 29H (Madrid et al. 2013). A subsequent transcriptome of faba bean responses to ascochyta blight infection in the resistant 29H and Vf136 allowed the identification of 39,060 SNPs and 3,669 InDels for genotyping applications (Ocaña et al. 2015). Transcripts differentially expressed in the resistant genotype included leucine-rich proteins and plant growth regulators. Differential expression between the resistant and susceptible genotypes included transcripts encoding NBS-LRR proteins, enzymes involved in jasmonate and etilene pathways, heat shock proteins, MLO, MYB-related

Table 2 Sources of resistance to ascochyta blight (*Didymella fabae*) in faba bean, and details on screening conditions and types of resistance identified

Accessions	Screening conditions	Phenotype description of resistances identified	Genetic basis	References*
29H, L831818, V-46, V-47, V-165, V-175, V-494, V-1120, V-1222	Field screening with artificial inoculation, comparing different screening assessments	Incomplete: reduction in symptoms in leaves and pods	Not studied	Sillero et al. (2001)
ILB 752	Greenhouse screening with artificial inoculation	Incomplete: responses not supporting existence of pathotypes	A major dominant gene	Kohpina et al. (2000)
ILB 6414, ILB 6561	Inoculated, no more details provided	Moderate resistance both to ascochyta and to chocolate spot	Not studied	Bayaa et al. (2004)
29H, A 8817, 19TB	Pots in growth chamber with artificial inoculation	Reduction in lesions on leaves and stems	Complex, including genes with major and minor effects	Kharrat et al. (2006)
Petra, 29H, L8	Field screening with artificial inoculation, complemented with detached leaves assays	Incomplete	Multigenic	Ondrej and Hunady (2007)
L-831818, V-26, V-958, V-255, V-1020, V-1085, V-1117	Field screening in multiple environments with artificial inoculation in some, and natural infection in others	Incomplete	Not studied	Rubiales et al. (2012)
B8833, B8838, L83117, S95003, Acc0735-1, L82003, L82004, L83129, BPL 9, BPL 78, BPL 271, BPL 334, BPL 419, BPL 627, BPL 1772, BPL 709, BPL 880, BPL 1715, BPL 2924, BPL 3542, BPL 3574, BPL 3740, BPL 4650, BPL 4599, BPL 4944, BPL 4951, BPL 4975, BPL 4981, BPL 4516, BPL 4539, BPL 4822, BPL 4824, BPL 4855, BPL 4870, BPL 4886, BPL 4909, BPL 5166, BPL 1488, BPL 2355, BPL 3492, BPL 3523	Field screening in multiple environments with artificial inoculation with a mixture of isolates	Incomplete (Attention paid to multiple resistance also to rust and chocolate spore)	Not studied	Maalouf et al. (2016)
Farah, Nura, Rana, Samira, Amberley, Kareema, Bendoc, Ascot, Aquadulce	Field screening	Reduced infection	Not studied	Pulse Australia (2021)
Several biparental populations involving the resistant Vf6, 29H, Ascot and Nura	Greenhouse screening with artificial inoculation	Incomplete: reduce number and size of lesions	Quantitative (2 to 12 QTLs)	Román et al. (2003); Avila et al. (2004); Kaur et al. (2014); Atienza et al. (2016); Sudheesh et al. (2019)
S_150, S_162, S_0009, S_123	Greenhouse screening with artificial inoculation	Incomplete: reduce number and size of lesions	Associated DNA markers were identified	Faridi et al. (2021)

*This table details only reports since 2000. For older citationssee Bond et al. (1994), Tivoli et al. (2006), Sillero et al. (2010)

Table 3 Sources of resistance to chocolate spot (*Botrytis fabae*) in faba bean, and details on screening conditions and types of resistance identified

Accessions	Screening conditions	Phenotype description of resistances identified	Genetic basis	References*
LPF39, LPF237, LPF44, LPF05, LPF113	Field and greenhouse screening with artificial inoculation	Incomplete: reduced AUDPC	Not studied	Rhaïem et al. (2002)
ILB 6414, ILB 6561	Inoculated, but details of plant stage not provided	Moderate resistance both to ascochyta and chocolate spot	Not studied	Bayaa et al. (2004)
FRYM167, FRYA58	Field screening under artificial inoculation complemented with detached leave assays	Incomplete: reduced AUDPC	Not studied	Bouhassan et al. (2004)
BPL 1763, Sel97Lat97-132-1, Sel97Lat97-135-1, ILB 4726, Sel-97Lat97-158-1, BPL 710, LPF120, ILB 4709, ILB 5284	Multilocation field testing, artificial inoculation	Incomplete	Not studied	Villegas-Fernández et al. (2009)
Reina Blanca, Giza 40, Giza 429, Giza 461, Giza 643, Giza 674, Giza 714, Giza 716, Giza 843, Sakha 1, Sakha 2, Mostohor 103, Triple white, Nubaria 1, BPL 710	Field screening under natural infection	Incomplete	Monogenic resistance suggested in accession BPL 710	Noorka and El-Bramawy (2011)
Sel97Lat97-135-1, Sel97Lat97-174-1, Sel97Lat97-132-1, BPL 1763, BPL 710, ILB 4726, ILB 5284, LPF120	Field and controlled screening with artificial inoculation	Incomplete reduced lesion size, DS and AUDPC	Not studied	Villegas-Fernández et al. (2012)
Degaga	Inoculation on seedlings and adult plants under controlled conditions	Incomplete	Not studied	Terefe et al. (2015)
ILB 4726, ILB 938, BPL 710, Gebel-cho, Moti, Dosha	Multilocation field screening with artificial inoculation	Incomplete	Additive gene effects that were more important than non-additive effects	Beyene et al. (2016)
CS20DK, Degaga, Nc-58, Bulga-70, Tesfa, Kasa	Field screening in multiple environments under natural infection	Incomplete: reduced DS and AUDPC	Not studied	Haile et al. (2016)
Acc0735-1, L82003, L82004, L83129, BPL 9, BPL 78, BPL 271, BPL 334, BPL 419, BPL 627, BPL 1772, BPL 709, BPL 880, BPL 1715, BPL 2924, BPL 3542, BPL 3574, BPL 3740, BPL 4650, BPL 4599, BPL 4944, BPL 4951, BPL 4975, BPL 4981, BPL 4516, BPL 4539, BPL 4822, BPL 4824, BPL 4855, BPL 4870, BPL 4886, BPL 4909, BPL 5166	Field screening in multiple environments with artificial inoculation with a mixture of isolates	Incomplete	Not studied	Maalouf et al. (2016)
ILB 4726, G4, G19, G15, G17, G8, G16, G9	Field screening in multiple environments with artificial inoculation	Incomplete: reduced DS	Not studied	Tekalign et al. (2017)
ILB 938, ILB 4726, BPL 710	Field and greenhouse screening under natural and artificial inoculation	Incomplete: reduced disease severity	Additive gene effects	Beyene et al. (2018)

Table 3 (continued)

Accessions	Screening conditions	Phenotype description of resistances identified	Genetic basis	References*
Nubaria 1, Giza 843, Sakha 4	Field screening	Reduction in disease severity	Both dominance and epistasis	Abdalla et al. (2021)
Amberley	Field screening	Reduced infection	Not studied	Pulse Australia (2021)

*This table details only reports since 2000. For older citations see Bond et al. (1994), Tivoli et al. (2006) and Sillero et al. (2010). *AUDPC* area under disease progress curve. *DS* disease severity

transcription factor, several pathogenesis-related proteins, and regulators of the plant immune response such as calmodulin and aldehyde dehydrogenase 7a.

Chocolate spot, incited *Botrytis fabae* (teleomorph: *Botryotinia fabae*), can be particularly severe in humid environments (Tivoli et al. 2006). *B. cinerea* infections have also been reported, but not so virulently. Management is possible with fungicides and agronomic practices such as intercropping (Fernández-Aparicio et al. 2011). Another species (*B. fabiopsis*) has also been reported infecting faba bean in China (Zhang et al. 2010). The three species can be distinguished by a PCR (polymerase chain reaction)-based assay using the species-specific primer sets (Fan et al. 2015). The *B. fabae* specialization of faba bean has been ascribed to its production of the phytotoxins botrytone and regiolone (Cimmino et al. 2011). Regiolone is an enantiomer of isosclerone produced by *B. cinerea* (Evidente et al. 2011). Variation in virulence has been suggested among *B. fabae* isolates (Hutson and Mansfield 1980), but no races have been described so far. Some sources of incomplete resistance have been described in germplasm (Table 3 and associated references) and introduced into breeding programs resulting in the release of several cultivars with moderate levels of resistance (Temesgen et al. 2015). Although several advanced recombinant inbred line populations and association mapping panels have been developed (i.e. CSIC-Spain, University of Helsinki-Finland and Aarhus University-Denmark) to study genetics of chocolate spot resistance, the fact is that no QTLs or genes have been reported so far. Some biochemical markers such as wyerone acid, phytoalexin synthesis, and peroxidase activity have been proposed as markers for resistance (Nawar and Kuti 2003). As is typical in the response to infection by necrotrophic pathogens, the levels of H_2O_2 and lipid peroxidation have been reported to increase both in susceptible and resistant genotypes; the increase, however, is higher in susceptible genotypes. In the resistant genotypes, there is earlier and higher expression of pathogenesis-related protein gene transcripts and a more efficient antioxidative system in the removal of the excess of ROS (reactive oxygen species) generated during the infectious process, limiting the cellular damage (El-Komy 2014; Villegas-Fernández et al. 2014). Resistance has recently been associated with a more efficient photosystem II repair cycle in the resistant accession (Castillejo et al. 2021).

Cercospora leaf spot, incited by *Cercospora zonata*, was reported as emerging disease in Australia in the late 2000s (Kimber et al. 2007). It develops early in the season affecting leaves, stems, and pods, causing premature defoliation (Egan et al. 2006). The disease can be managed by repeated fungicide treatments (Kimber et al. 2007). Resistance germplasm has been identified and postulated to be monogenic (Kimber and Paull 2011). However, cultivars available so far are susceptible (Pulse Australia 2021).

Table 4 Sources of resistance to other pathogens (either fungi or oomycetes) in faba bean, and details on screening conditions and types of resistance identified

Disease (causal agent)	Accessions	Screening conditions	Phenotype description of resistances identified	Genetic basis	References*
Cercospora leaf spot (*Cercospora zonata*)	S95007/1, 1103/3, 1107/2, 1108/2, 1332/2, 1269×483/6, AF03002	Field screening with natural infection complemented with inoculations under controlled conditions	Incomplete: reduced severity (reduced number and size of lesions)	Monogenic, dominant	Kimber and Paull (2011)
Stemphylium blight (*S. botryosum*)	S2001-096-BC, Line F6latt/285/08, FLIP03-35FB, Icarus	Field screening with natural infection	Incomplete	Not studied	Sheikh et al. (2015)
Alternaria blight (*Alternaria* sp.)	S2011-134, S2011-116, FLIP15-139, FLIP15-156, FLIP15-159, FLIP15-164-S2, FLIP15-169	Field screening with natural infection	Incomplete: reduced severity (2–3 in a 0–8 scale)	Not studied	Tiwari et al. (2021)
	Zereshki	Greenhouse screening	Incomplete: reduced AUDPC	Not studied	Tajik Ghanbari et al. (2020)
Downy mildew (*Peronospora viciae*)	Maris Bead, Compass	Field screening	Incomplete	Not studied	Thomas and Kenyon (2004)
	Laura	Field screening	Reduced AUDPC	Not studied	Bimšteine and Bankina (2017)
New gall disease (*Physoderma viciae*)	Degaga, Nc58	Field screening with natural infection	Incomplete	Not studied	Yitayih and Azmeraw (2017); Alehegn et al. (2018); Kassa et al. (2020)
Stem root (*Sclerotinia trifoliorum*)	A-246, E-101, A-90, A-58, A-161, ILB 1814, A-156, Alto	Pot screening under controlled conditions with artificial inoculation	Reduced disease severity	Monogenic	Lithourgidis et al. (2005)
Black root rot (*Fusarium solani*)	Wayu	Field screening	Reduced incidence	Not studied	Habtegebriel and Boydom (2016)
	Giza 2, Sakha 4, Nobaria 1, Nobaria 2, Nobaria 3	Pot screening in greenhouse, artificial inoculation	Moderate reduced infection	Not studied	Ali et al. (2019)
Fusarium wilt (*F. oxysporum*)	Assiut 215, Roomy 3, Marut 2, Giza 2	Pot screening with artificial inoculation	Moderate reduction in symptoms	Not studied	Mahmoud and Ab El-Fatah (2020)
Aphanomyces root rot (*A. euteiches*)	Most faba bean accessions were resistant, however, a few could be susceptible (e.g. Icarus, Baraca, Di-340)	Pot screening under controlled conditions with artificial inoculation	Resistance is common to the pea and lentil isolates.	Not studied	van Leur et al. (2008); Moussart et al. (2008)

*This table details only reports since 2000. For older citations see Tivoli et al. (2006) and Sillero et al. (2010)

Table 5 Sources of resistance to parasitic weeds in faba bean, and details on screening conditions and types of resistance identified

Accessions	Screening conditions	Phenotype description of resistances identified	Genetic basis	References*
Giza 402, Giza 429, Giza 674, Giza 843, Misr 1, Cairo 1, Cairo 2, Cairo 241	Field screening	Reduced infection	Not studied	Abdalla and Darwish (2002)
ILB 4347, ILB 4357, ILB 4360	Multilocation field screening	Reduced incidence	Not studies	Khalil et al. (2004)
Baraca	Rhizotrons under controlled conditions, complemented with histology	Reduced penetration by callose deposition and lignification of endodermal cells	Not studied	Pérez-de-Luque et al. (2007)
Bader, Badi, Baraca, XBJ90.03-16-1-1-1	Field screening in plots heavily infested by *O. foetida*	Reduced infection	Not studied	Abbes et al. (2007)
ILB 4338, ILB 4347, ILB 4357, ILB 4358, Giza4/2000, Sel.F5/3034/2003/3, Sel. F5/3034/2003/14, Sel. F5/3053/2003/3, Sel. F5/3087/2003/14, Sel.F5/3382/2003/4	Field selection in multiple environments, with different broomrape species at each site	Incomplete: reduced number of emerged broomrapes per plant	Not studied	Maalouf et al. (2011)
Quijote, Navio	Field and mini-rhizotron screening inoculated under controlled conditions (*O. crenata*, *O. foetida* and *P. aegyptiaca*)	Incomplete resistance based on low induction of germination, explained by low exudation of strigolactones, resulting on reduced infection	Not studied	Fernández-Aparicio et al. (2012, 2014)
Baraca, V-1268, V-319, V-1302, V-1196, V-252, V-1301, V-268, V-231, V-245, V-1272, V-1271, V-1375	Multilocation field testing at sites highly infested with either *O. crenata* or *O. foetida*	Incomplete	Not studied	Rubiales et al. (2014)
Alameda, Baraca, Chipen, Joya	Multilocation field testing	Reduced emergence	Not studied	RAEA (2016)
Baraca, ILB 4350, ILB 4347, ILB 4351	Rhizotrons under controlled conditions inoculated with *O. crenata*, *O. foetida* and *P. aegyptiaca*	Incomplete: reduced establishment not based on reduced induction of germination or negative tropism	Not studied	Rubiales et al. (2016)
Chourouk, Najeh	Field, pot and mini-rhizotron screenings with *O. crenata* and *O. foetida*	Reduced infection	Not studied	Amri et al. (2019)
Hashbenge, Misr 3, F402, ILB 4338, ILB 4357, ILB 4358, Giza 843, Najah, Amcor, Hend	Field screening	Reduced emergence	Not studied	Maalouf et al. (2019)
Several biparental populations derived from Vf136 and Assiut 125	Field screening	Reduced emergence	Quantitaive (2 to 7 QTLs)	Román et al. (2002); Díaz-Ruiz et al. (2009a, b, 2010); Gutiérrez et al. (2013); Abd El-Fatah and Nassef (2020)

*This table details only reports since 2000. For older citations see Bond et al. (1994), Rubiales et al. (2006), Pérez-de-Luque et al. (2010) and Sillero et al. (2010)

Table 6 Sources of resistance to virus in faba bean, and details on screening conditions and types of resistance identified

Virus	Accessions	Screening conditions	Phenotype description of resistances identified	Genetic basis	References*
BLRV	BPL 5271 to BPL 5285	Field screening with artificial inoculation	Incomplete: reduced symptoms, reduced virus concentration in plant tissues	Not studied	Makkouk et al. (2002)
	BPL 5276, BPL 5277, BPL 5278, BPL 5279, BPL 5272, BPL 5274, BPL 5280	Greenhouse screening	Reduced replication and systemic movement of the virus	Not studied	Kumari and Makkouk (2003)
	ATC 65255, ATC 65259, ATC 65271	No details provided	Incomplete (<4 in a 0–9 scale)	Not studied	Redden et al. (2008)
	15 accessions (not listed)	Repeated inoculation and continued re-selection	Incomplete: reduced symptoms, reduced virus concentration in plant tissues	Not studied	Kumari et al. (2018)
	Nanu, Nasma, Ayla	No details provided	No details provided	Not studied	Pulse Australia (2021)
FBNYV	27 accessions (not listed)	Repeated inoculation and continued re-selection	Incomplete: reduced symptoms, reduced virus concentration in plant tissues	Not studied	Kumari et al. (2018)
BYMV	Fiord, Barkool, Icarus, Ascot	Field and greenhouse experiments with three isolates	Reduced infection	Not studied	McKirdy et al. (2000)
	BPL 758, BPL 1311, BPL 1314, Giza 3, BPL 1351, BPL 1363, BPL 1366, BPL 1371	Field and controlled conditions	Reduced infection	Not studied	Makkouk et al. (2002); Kumari and Makkouk (2003); Redden et al. (2008); Kumari et al. (2018)
	BPL 710	Greenhouse screening	No symptoms	Monogenic	El-Bramawy and El-Beshehy (2012)
PSbMV	Rana, Marne	No details provided	No details provided	Not studied	Pulse Australia (2021)

*This table details only reports since 2000. For older citations see Bond et al. (1994), Sillero et al. (2010) and Makkouk et al. (2014)

Stemphylium blight of faba bean is mainly caused by *Stemphylium botryosum* (Aghajani 2009) although also *S. solani*, *S. botryosum,* and *S. vesicarium* have been mentioned. Some resistance has been reported, with insufficient information available on genetic basis or underlying mechanisms operative (Sheikh et al. 2015).

Alternaria blight has been reported as being of importance in areas of India and Egypt (Tiwari et al. 2021), occurring generally occurs late in the season. There are reports of occurrence of *A. alternata* and of *A. tenuissima* (Gupta et al. 1992; Honda et al. 2001) with no clear study on their distribution and relative prevalence. Some sources of resistance have been reported based on field screenings under natural infection in India (Tiwari et al. 2021) or in greenhouse in Iran (Tajik Ghanbari et al. 2020). Downy mildew of faba bean is caused by *Peronospora viciae* f.sp. *fabae*. It is widespread, but problematic only in cooler areas particularly when infection starts early. There is no information on variation of pathogen populations. Some sources of incomplete resistance have been reported, but there is no information on their genetic control (Thomas and Kenyon 2004).

New gall disease is emerging as a major disease in Ethiopia, causing typical galling of leaves and stems, and browning of the affected tissues over time (Hailu et al. 2014). The disease was first ascribed to *Olpidium viciae* based on similarity of symptoms with "faba bean blister disease" earlier reported in China (Zhesheng et al. 1984). However, recent studies show that the gall disease emerging in Ethiopia is not caused by the soilborne *Olpidium* but by the rain-splashed *Physoderma* (You et al. 2021), which has major implications in epidemiology and management. Moderate levels of resistance have been identified (Table 4), but no genetic studies are so far available.

Table 7 Sources of resistance to nematodes in faba bean, and details on screening conditions and types of resistance identified

Nematode	Accessions	Screening conditions	Phenotype description of resistances identified	Genetic basis	References*
Stem nematode (*Ditylenchus dipsaci*)	F308, F356, F1356A, F1734, F1752, T41, T42, T52, T110, M83, LPF126, LPF157, 29H, S82033-3	Field testing in multiple sites with artificial inoculation with mixtures of nematode populations of the Giant race (today is *D. giga*)	Incomplete: reduced damage and nematode reproduction and	Not studied	Abbad-Andaloussi (2001)
Root lesion nematodes (*Pratylenchus* spp.)	FRYT98-6, FRYT98-60	Greenhouse screening under artificial inoculation	Resistant to *P. neglectus*	Not studied	Di Vito et al. (2002)
	FRYA98-48, FRYT98-44		Moderately resistant to *P. penetrans* and *P. pinguicaudatus*		
	FRYT98-35, FRYT98-47, FRYT98-56		Moderately resistant to *P. thornei*		
Reniform nematode (*Rotylenchulus reniformis*)	G3, L47, L49, L52, L57, L71, L92, L99, L375	Greenhouse screening under artificial inoculation	Reduced number of females/plant	Not studied	Ismail and Amin (2013)
Stunt nematode (*Tylenchorhynchus latus*)	L241	Field screening in naturally infested soil	Reduced nematode population	Not studied	Ismail et al. (2013)

*This table details only reports since 2000. For older citations see Bond et al. (1994), Sharma et al. (1994) and Sillero et al. (2010)

Stem, foot, and root rots

Many different species may cause foot and root rot complex of faba bean, mainly of the genus *Fusarium* but also *Rhizoctonia*, *Pythium*, *Phoma* or *Aphanomyces*. Different resistance screening methods have been proposed, but the wide range of species involved complicates the screening and comparison of results (Infantino et al. 2006). Little information is available on the availability of sources of resistance and none on their genetic basis (Table 4). Some sources of moderate resistance have been described to *F. solani* (Habtegebriel and Boydom 2016) and to *F. oxysporum* (Mahmoud and Ab El-Fatah 2020), yet no information on their genetic basis. Monogenic resistance has been identified for stem root (*Sclerotinia trifoliorum*) (Lithourgidis et al. 2005).

Resistance to the pea (*Pisum sativum*) and lentil isolates of *A. euteiches* is common in faba bean. Although, a few accessions could be susceptible (Levenfors et al. 2003; Van Leur et al. 2008; Moussart et al. 2008; Karppinen et al. 2020). In fact, faba bean root exudates have been shown to have a repellent effect (negative chemotaxis) on zoospore germination and growth, reducing colonization (Laloum et al. 2021). Still, there is the risk of adaptation of the pathogen developing populations more aggressive on faba bean.

Current knowledge on resistance to parasitic weeds

Broomrapes are obligate parasitic plants that complete their life cycle by feeding on roots of their host plants, causing a true disease rather than competing for light and water and soil nutrients like standard weeds do (Rubiales and Fernández-Aparicio 2012). The most widespread species is crenate broomrape (*Orobanche crenata*) being a major constraint for faba bean cultivation in the Mediterranean Basin and the Middle East. Fetida broomrape (*O. foetida*) infections on faba bean have been reported only in the Beja province of Tunisia. Egyptian broomrape (*Phelipanche aegyptiaca*) can infect faba bean in Eastern Mediterranean. Management of broomrapes by systemic herbicides is feasible, but its applicability is limited in low input systems where faba bean is used to be grown, calling for the need to integrate control measures, with genetic resistance having a core role (Pérez-de-Luque et al. 2010; Fernández-Aparicio et al. 2016).

There is no consensus on the existence of specialization in any of those three broomrape species, neither at the level of races nor even at the level of *formae speciales* (Rubiales 2018). Broomrape resistance breeding has

Table 8 Sources of resistance to insect pests in faba bean, and details on screening conditions and types of resistance identified

Pest	Accessions	Screening conditions	Phenotype description of resistances identified	Genetic basis	References*
Seed weevil (*Bruchus rufimanus*)	Merkur, Divine	Field screening	Incomplete: levels of no-preference and/or antibiosis	Not studied	Seidenglanz and Huňady (2016)
	Bobick Rod115, Côte D'Or, 221516, Nova Gradiska, Quasar, 109.669, 223303	Field screening under natural infestation	Incomplete: reduced seed penetration and/or larvae development	Not studied	Carrillo-Perdomo et al. (2019)
Seed weevil (*Callosobruchus chinensis*)	Tongcan 5, Yuncan 82, H5067, H5631, H5032, H4956, H5629	Indoor artificial infestation and free choice test	Incomplete: reduced damage as a result of reduced eggs on their surfaces, lower eclosion rates, and fewer wormholes	Not studied	Duan et al. (2014)
Stem borer (*Lixus algirus*)	IG 11561, IG 72498, IG 72498	Field screening under natural infestation, complemented with cage screenings with artificial infestation	Incomplete: reduced egg lying and/or antibiosis	Not studied	Ait Taadaouit et al. (2021)
Leaf miner (*Liriomyza congesta*)	Giza 716, Giza 843, Sakha 1	Field screening under natural infestation	Moderate reduction in mines and larvae	Additive gene action	Awaad et al. (2005)
	Nubaria 1, BPL 710	Field screening under natural infestation	Moderate reduction in mines and larvae	Additive gene action	El-Bramawy and Osman (2012)
Black aphid (*Aphis fabae*)	V1, V9, V16, V2e, V7e	Field screening	Incomplete: reduced infestation rate	Not studied	Béji et al. (2015)
Cowpea aphid (*Aphis craccivora*)	BPL 710	Field screening under natural infestation	Moderate reduction in aphid colonization	Additive gene action	El-Bramawy and Osman (2012)
	V51	Field trials complemented with greenhouse screening with artificial infestation	Incomplete: tolerance and antibiosis	Not studied	Laamari et al. (2008)
	Gazira 2	Whole plant and detached-leaf assays with artificial infestation	Incomplete: reduced colony development	Not studied	Soffan and Aldawood (2014)

*This table details only reports since 2000. For older citations see Bond et al. (1994) and Sillero et al. (2010)

proven difficult, with few sources of incomplete resistance identified, showing complex inheritance. Faba bean breeding for resistance against *O. crenata* mainly relied on the use of resistance from the Egyptian line F402, widely deployed by ICARDA in their multilocation resistance screenings. This resulted in the development of several cultivars with moderate resistance (Table 5). Interestingly, reported resistances were found to be effective against both *O. foetida* and *O. crenata* or even against *P. aegyptiaca* (Abbes et al. 2007; Maalouf et al. 2011, 2019; Rubiales et al. 2014; Amri et al. 2019). Such a broad sense resistance is promising in terms of durability, but we cannot conclude on the durability of their resistance until these resistant cultivars are widely deployed (Rubiales 2018).

Several mechanisms of resistance against broomrape have been described in faba bean, including reduced induction of broomrape seed germination (Fernández-Aparicio et al. 2012, 2014), hampered establishment (Rubiales et al. 2016) by reinforcement of cell walls by callose deposition, complemented by lignification of endodermal cells (Pérez-de-Luque et al. 2007). Interestingly, some of these mechanisms were operative against several broomrape species. Preliminary observations suggest that the inheritance of this non-germination trait in faba bean may be simple, which would facilitate resistance breeding and its pyramiding with other resistance mechanisms (Rubiales 2018).

Genetic mapping studies suggested a polygenic control of resistance against *O. crenata* or *O. foetida* (e.g. Román et al. 2002; Gutiérrez et al. 2013; Gutiérrez and Torres 2021). Several QTLs with minor effects were identified which some of them overlap genomic regions controlling resistance to both species. Although promising, results are still far from being usable in MAS. Further saturation of QTLs is needed, not only genotyping should be improved, but also phenotyping. Field phenotyping should be complemented by mini-rhizotron screenings to enable identification of QTLs/alleles governing specific mechanisms of resistance, from seed germination, radicle elongation and attachment and penetration and tubercle development (Fernández-Aparicio et al. 2012; Rubiales et al. 2016).

Current knowledge on resistance to viruses

A number of viruses can damage faba bean, including broad bean mottle virus (BBMV), broad bean stain virus (BBSV), bean leaf roll virus (BLRV), bean yellow mosaic virus (BYMV), faba bean necrotic yellow virus (FBNYV), pea enation mosaic virus (PEMV), and true broad bean mosaic virus (TBBMV) (Kumari and Makkouk 2007; Makkouk et al. 2012; Kumari et al. 2018). These viruses have a rather large host range, affecting several food and pasture legumes and weeds, which facilitates a 'green bridge' for transmission. Because of the lack of virus control options, genetic resistance is most needed. Resistance to some of these viruses has been reported in either field or controlled conditions screening (see Table 6 and associated citations). However, in most instances, there is no information on the genetics basis of the resistance. The only genetic analysis available so far points towards dominant monogenic resistance to the BYMV in accession BPL 710 (El-Bramawy and El-Beshehy 2012), in agreement with earlier reports suggesting two recessive complementary genes (Rohloff and Stülpnagel 1984; Schmidt et al. 1989). Resistance to BLRV has been associated with reduced replication and systemic movement of the virus (Kumari and Makkouk 2003).

Current knowledge on resistance to nematodes

Several nematodes can be damaging to faba bean, including cyst nematode (*Heterodera goettingiana*), reniform nematode (*Rotylenchulus reniformis*), root-knot nematode (*Meloidogyne* spp.), root lesion nematode (*Pratylenchus thornei*, *P. penetrans* and *P. pinguicaudatus*), stem nematode (*Ditylenchus dipsaci* and *D. giga*), and stunt nematode (*Tylenchorhynchus latus*). Resistance has been reported against some of these nematodes (Table 7), but little information is available on the nature and genetics of resistance. Some sources of resistance against different populations of the root lesion nematode (*Pratylenchus* spp.) have been reported, being effective against one species but not against others (Di Vito et al. 2002). Also, reported resistance against *D. dipsaci* was not confirmed when testing with the "giant race" (Abbad-Andaloussi 2001). *D. dipsaci* has a broad host range and is today acknowledged as a complex species, with the earlier called giant race being more damaging to faba bean, is today accepted as a different species *D. gigas*, having in fact a limited host range (Vovlas et al. 2011).

Current knowledge on resistance to insect pests

A number of weevils (Coleoptera) can constrain faba bean, affecting different organs. Storage seeds can be damaged mainly by larvae of faba bean weevil (*Bruchus rufimanus*), but also *Callosobruchus chinensis* has been reported (Keneni et al. 2011). Another damaging species is *Sitona lineatus* whose adults feed on leaves and foliage, but even more damaging can be the larvae that feed on Rhizobium nodules, limiting nitrogen fixation (Cárcamo et al. 2015). They can be controlled with insecticides (Keneni et al. 2011; Cárcamo et al. 2012). Levels of non-preference and antibiosis (larvae and pupae mortality) against *B. rufimanus* have

been reported (Seidenglanz and Huňady 2016). Resistance against *C. chinensis* has also been identified in free choice laboratory tests, being associated with quality traits (Duan et al. 2014). Like this, accessions with brown and black seed colours are less damaged than light-seed-coloured ones. Recently, new sources of resistance to seed weevils (*Bruchus* spp.) have been identified (Carrillo-Perdomo et al. 2019) based on either reduced seed penetration and/or larvae development, but no information is available on genetic basis of any reported resistance.

The faba bean stem borer (*Lixus algirus*) (Coleoptera: Curculionidae) damage is caused by the larvae which grow and feed within the stems, affecting crop growth and yield. Reduced levels of infestation have been reported in faba bean genotypes in the field and under cages, which could be based either on reduced egg-laying preference and/or antibiosis with mortality of instars, with no adult exit holes (Ait Taadaouit et al. 2021).

Faba bean can be damaged by black bean aphid (*Aphis fabae*) and the cowpea aphid (*A. craccivora*). *A. fabae* is one being predominant in cooler regions and *A. craccivora* in warmer climates. Levels of resistance have been identified in faba bean germplasm against both species (Table 8). These resistances combine antibiosis and antixenosis (Holt and Wratten 1986; Laamari et al. 2008; Soffan and Aldawood 2012). There is no report on their genetic basis or associated DNA markers so far.

Leaf miner—Some differences among faba bean accessions in level of infestation by leaf miner (*Liriomyza congesta*) have been reported in field screenings (Awaad et al. 2005; El-Bramawy and Osman 2012) with the high influence of environmental conditions suggesting additive gene action.

Breeding opportunities offered by development of genomic resources

Faba bean is a partially allogamous diploid crop (2n = 12) with a large genome that is currently being assembled (Fabagenome consortium 2021). Meanwhile, this genome is released, transcriptome data have provided efficient resources for disease resistance studies (e.g. Kaur et al. 2014; Ocaña et al. 2015). Several genetic maps have been generated so far, majority suffering from low to medium saturation (reviewed by Khazaei et al. 2021). These maps were based on restriction fragment length polymorphism (RFLPs), RAPD, expressed sequence tags (ESTs), single sequence repeats (SSRs), EST-SSRs, and SNP markers. The first saturated SNP-based map was just reported a few years ago, consisting of 750 SNP markers (Webb et al. 2016). Recently, a high saturated consensus genetic map of faba bean was constructed using three RIL populations that enclosed over 1,700 SNP markers (Carrillo-Perdomo et al. 2020). The recent genomic sequence and transcriptome data are being allowed the development of a greater collection of DNA markers. This will lead to an increase in faba bean map coverage and marker density (Khazaei et al. 2021). A 60 K high-density genotyping array was developed and soon will be available for faba bean researchers (Donald O'Sullivan, personal communication). Furthermore, a high-throughput faba_bean_130K targeted TNGS genotyping platform has been developed (Wang et al. 2021). The development of high-density genetic maps derived from multiple mapping populations along with transcriptome data has paved the road to MAS and gene discovery. This also means that genetic resolution is improving in tandem in this species. Ascochyta blight has been widely subjected to QTL studies reflecting its importance as the major fungal diseases of faba bean globally (Table 9). For example, the QTLs associated with ascochyta blight resistance have been validated in multi-environments (Gutiérrez et al. 2013; Atienza et al. 2016) and genetic resolution recently improved replacing previous pedigree-specific RAPD markers with SNP markers that allowed identification of candidate genes conferring resistance against this pathogen (Gutiérrez and Torres 2021). Some attentions were also given to DNA maker development for broomrape and rust resistance in this species (Table 9).

Chocolate spot is the major biotic threat to faba bean production globally; however, no publication on QTLs or genes governing this disease is out in the literature. The Mélodie/2 × ILB 938/2 mapping population (Khazaei et al. 2018a; Khazaei et al. 2014) has offered a few stable genomic regions governing chocolate spot resistance for the first time in this crop (Gela et al. 2021). No information on genomic regions associated with pest's resistance is available in this species.

Most of genetic mapping studies in faba bean consisted of biparental populations. This limits the number of QTLs captured as their mapping precision is not very high due to the low total amount of genetic recombination shared by only two founders. Multi-parent advanced generation inter-cross (MAGIC) and genome-wide association study (GWAS) are advocated to maximize the allele frequency and genetic diversity lacking in biparental populations. For instance, the first MAGIC population based on 11 winter faba bean founders was developed and used to study frost tolerance (Sallam and Martsch 2015). Another multi-parental population based on four founders (Khazaei et al. 2018b) was mapped using a 60 K Axiom SNP genotyping array (O'Sullivan et al. 2019). Other MAGIC populations are underway involving parents with reported resistance, e.g. Maalouf et al. (2019) and NORDFAB (2021), which may help to unravel their genetics basis in a near future. Similarly, only a few GWAS panels have been reported in faba bean (e.g. Puspitasari 2017; Warsame 2021) despite the fact they investigate diverse genetic material with the potential

Table 9 Summary of reported QTL/loci in faba bean for fungal diseases and parasitic weeds

Disease/Parasitic weed	No. of QTL/loci	Chromosome	Main output	References
Rust (*U. viciae-fabae*)	1	Unknown	Identifying the first DNA markers linked to *Uvf-1* conferring hypersensitive resistance against rust	Avila et al. (2003)
	2	3, 5	KASP markers for rust resistance genes *Uvf-2* and *Uvf-3*	Ijaz et al. (2021)
Ascochyta blight (*D. fabae*)	2	2, 3	QTLs associated with ascochyta blight resistance, *Af1* and *Af2* explained ~ 50% of phenotypic variation. The QTLs were later confirmed by Díaz-Ruiz et al. (2009a)	Román et al. (2003)
	6	3	Isolate and organ-specific QTLs for ascochyta blight resistance. *Af3* to *Af8* were identified	Avila et al. (2004)
	4	1, 2, 6	Detecting genes associated with ascochyta blight resistance using SNP markers	Kaur et al. (2014)
	–	–	Transcriptome analysis under ascochyta blight Infection. 21,243 transcripts, 39,060 SNPs and 3,669 InDels were identified	Ocaña et al. (2015)
	3	2, 3, 6	Validation of *Af1* and *Af2* under different environments and suggestion an additional source of resistance, *Af3*	Atienza et al. (2016)
	2	1, 6	Two QTL identified, AB_N1 and AB_N2. They are comparable to QTL-1 and QTL-4 reported in Kaur et al. (2014), respectively	Sudheesh et al. (2019)
	12 markers	3, 6	Association mapping approach to identify DNA markers for ascochyta resistance. *Af1* was validated from Román et al. (2003)	Faridi et al. (2021)
	3	2,3,6	Fine mapping of *Af2* and *Af3* using a high-density SNPbased map. QTLs F_DSP1, F_DSP2 and DSL_Lo98 were detected in chromosome 6 that were in agreement with results of Ocaña-Moral et al. (2017).	Gutiérrez and Torres (2021)
Crenate broomrape (*O. crenata*)	3	1, 2, 6	QTLs *Oc1*, *Oc2* and *Oc3* explained more than 70% of phenotypic variation	Román et al. (2002)
	4	1, 2, 6	QTLs *Oc2*, *Oc3*, *Oc4, Oc5* in multi-site-year environments detected	Díaz-Ruiz et al. (2010)
	7	6	Two more QTLs added, *Oc7* and *Oc8*	Gutiérrez et al. (2013)
	2	–	QTLs NB/p and HPS were identified	Abd El-Fatah and Nassef (2020)
		6	Fine mapping of *Oc7* and *Oc8* using a high-density SNP-based map	Gutiérrez and Torres (2021)
Fetida broomrape (*O. foetida*)	2	1, 3	Mapping *Of1* and *Of2*	Díaz-Ruiz et al. (2009b)
	3	5	Co-localization of *Oc8* and *Of3* in chromosome 5 confirms a common resistance against *O. crenata* and *O. foetida*	Gutiérrez et al. (2013)

to identify multiple alleles underlying traits of interests. Out of these, a single report is available so far on the use of GWAS to decipher resistance to a faba bean disease resistance (Faridi et al. 2021), but this is underway for a number of resistances (e.g. DiVicia 2021).

Genomic selection may become accessible for orphan crop species such as faba bean with the availability of low-cost high-throughput genotyping platform. The status of genomic selection in faba bean has been reviewed by Adhikari et al. (2021). No empirical genomic selection studies reported for faba bean yet. Integrating genomic selection together with speed breeding and genomics have come together to accelerate faba bean improvement.

Faba bean breeding may benefit from gene editing. The power of gene editing entirely depends on having a stable transformation system. Hairy root transformation of faba bean can be achieved with high efficiency (Marcin Nadzieja, personal communication). In the absence of a faba bean reference genome, the application of CRISPR/Cas gene editing remains challenging. Böttinger et al. (2001) and Hanafy et al. (2005) were the early attempt on transgenic approaches in faba bean. Later, Hanafy et al. (2013) showed faba bean transgenic lines overexpressing potato PR10a. With the recent advances in faba bean genome sequencing activities, rapidly maturing genome-editing technologies could potentially be applied to improve traits of interest in this crop (Bhowmik et al. 2021).

Speed breeding is a must-have tool to shorten breeding cycles in plant breeding programs (Watson et al. 2018). It has the great potential to reduce the reproductive cycle or cultivar development phase in several crops including grain legumes (Wanga et al. 2021). For faba bean, Mobini et al. (2020) developed an in vivo rapid generation system by application of cytokinin and/or cold shock that could decrease the length of the breeding cycle by about three weeks. More efforts are needed to reduce breeding cycles in this species until speed breeding becomes a powerful tool for developing improved varieties with disease or pest resistance in a shorter time span. Speed breeding could be combined with biotic screening platforms to speed up selection and screening time. Speed breeding can accelerate the development of faba bean cultivars with improved disease and pest resistance and may be integrated with fast-forward breeding tools such as high-throughput phenotyping and genotyping platforms and genomic selection (Varshney et al. 2021).

Concluding remarks

Success in resistance breeding largely depends on the availability of good sources of resistance, their inheritance, and the availability of fast and reliable screening techniques. Faba bean breeders have succeeded in developing resistant cultivars, but progress has been slow as most resistances identified so far in faba bean are of incomplete expression and in most cases their genetics basis is largely unknown. This is further complicated by the insufficient knowledge on the biology of the causal agents, with host ranges at times not clearly delineated, and seldom with sufficient info on pathogenic variation, with no consensus on the existence of races nor even of *formae speciales* in some of the key pests and diseases. Attention is urgently needed to clarify these aspects, as the genotype of the pathogens is also crucial to understand plant pathogen interactions. Most importantly, understanding the biology of the pathogen is relevant to design breeding strategies and to predict risks not only of emergence of new virulences in response to deployed resistance but also on their dispersal (McDonald and Linde 2002). Diversity is key for the development of durable resistance. This involves diversity at the spatial and temporal gene deployment, and diversity in the genetic basis of resistance, by pyramiding more than one genes/QTLs (Mundt 2014). This requires information not only on the genetics of resistance in the plant, but also on deciphering existence of races in the pathogen and monitoring their distribution, which presently is clearly insufficient for most faba bean pathogens.

Faba bean resistance breeding will be facilitated by adoption of novel phenotyping and genotyping tools that although started slowly, have developed fast in the last decade. The genome sequences of both the hosts (Fabagenome consortium 2021) and some of the faba bean pests and pathogens are being drafted (Link et al. 2014; Lee et al. 2020; Voronova et al. 2020) or are available for closely related pathogen species (e.g. Lee et al. 2021), which will help in understanding both host resistance and parasite virulence and their interactions. Reducing genotyping costs is allowing genomic selection on faba bean that integrated with speed breeding methods already in place, and the adoption of low-cost affordable phenotyping tools will accelerate faba bean improvement.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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