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Faba Bean

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1. INTRODUCTION

1.1 History, Origin, and Distribution

Vicia faba (faba bean) was not among the very first domesticated crops. It was probably introduced into agriculture only in the late Neolithic period (Körber-Grohne, 1987). Cubero (1974) concluded that the center of origin was in the Near East, Iraq, and Iran, and secondary centers evolved later on in Afghanistan and Ethiopia. Before 1000 BC, the culture of faba beans was already very established in Europe, including Britain. Large-seeded types are of recent origin and they were probably developed only 1000–1200 years ago in East Iraq, and from there spread to Asia, across North Africa to Europe, and eventually to America. In China, the crop seems to have arrived only after 1200 AD. The faba bean reached Mexico and South America by the Spaniards. From then on, it experienced there an independent evolution (Körber-Grohne, 1987; Bond, 1995). Several gene bank accessions with promising agronomic features originated from Ecuador. These are mostly large-seeded types. The more recent history has to mention the comprehensive reports of Muratova (1931), Sirks (1931) and Hanelt *et al.* (1972) on genetics, systematics, taxonomy, history, and geographical topics (Bond, 1995).

1.2 Botanical Description

The intraspecific diversity is mainly described by use of seed size. Persoon (1807) described the small-seeded group as *V. faba minor* (roundish seeds of up to 0.6 or 0.7 g weight per seed), the medium-large-seeded group as *V. faba equina* (single seed weight less than about 1 g) and *V. faba major* with its impressive, large, and flat seeds weighing more than 1 g per seed. The name "field beans" indicates to the small and medium sized types, whereas "broad beans" denotes *V. faba major*. Today, often "faba bean" is used to address the species in its total diversity. A wild ancestor of faba bean is not known, and the related vetch *Vicia narbonensis* is considered as the nearest relative to *V. faba* (Zohary and Hopf, 1973). Based on restriction fragment length polymorphism (RFLP) and polymerase chain reaction (PCR) data, more recently Van den Ven *et al.* (1993) placed *Vicia peregrina* and *Vicia michauxii* into the direct taxonomic neighborhood of *V. faba*. These related vetches have seven chromosomes. *V. faba* belongs with *Vicia villosa* and *Vicia sativa* to the genus *Vicia*. With *Lens culinaris* and *Pisum sativum*, it belongs to the tribe *Vicieae* and only at the family level of *Fabaceae* it is united with the *Phaseolus* bean, the soybean and with the lupines (Sitte *et al.*, 2002).

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The faba bean crop is annual, sown either in autumn or in spring. It bears a strong, hollow, tetragonal erect stem, with zero or up to five (or even more) basal branches arising from basal leaf axis. There are only noneffective rudiments of tendrils at the leaf tip. Different from pea, stipules are very small, with a distinct black stipule spot on the stipule's down side. The bean has got a robust tap root with profusely branched secondary roots. Nevertheless, the rooting system is not as voluminous as that of cereals like oats or wheat. The roots bear the typical nodules formed by *Rhizobium leguminosarum*, as expected for it being a leguminous species. The first, juvenile leaves bear two leaflets. After four or more nodes the maximum number of leaflets (typically six) is reached. The first, lowermost inflorescence is located in the axis of a leave with at least four leaflets, inserted on the stem as low as at the fourth node or several nodes later (higher). Two to more than eight flowers per inflorescence occur. The wild type flower color is white with a soupcon of pink traces and a very distinct, satin black spot on both wing petals (Figure 1). Brown, violet, red, and further grades of flower colors exist. Totally white flowers are a pleiotropic effect of an allele for zero tannin in the seed testa, accompanied by grayish testa color instead of buff testa and by absence of the wild type stipule spot. One to two pods with three or four seeds are to be expected per inflorescence; one plant may yield far more than 12 pods, distributed across more than six nodes. In germplasm used for human consumption, often very few, very large pods per plant are realized, with more than 20 cm pod length, more than six seeds per pod and more than 1 g weight per seed. The contrary is realized in some *V. faba minor* ssp. *paucijuga* types from the Hindukush region, showing small, 2 seeded pods with less than 0.3 g weight per seed, growing on small, gracile, tillering plants with very slender leaflets. These types are suspected to represent the most primitive version of *V. faba* (Cubero, 1974).

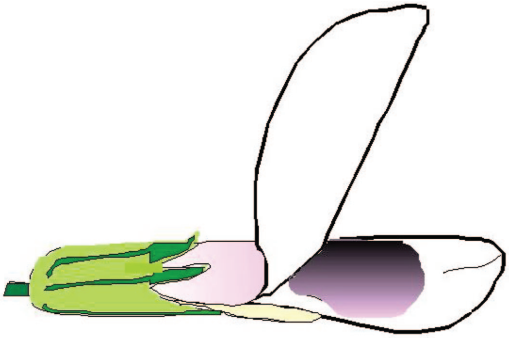

Figure 1 *Vicia faba* flower with white flag petal and black spot on wing petal

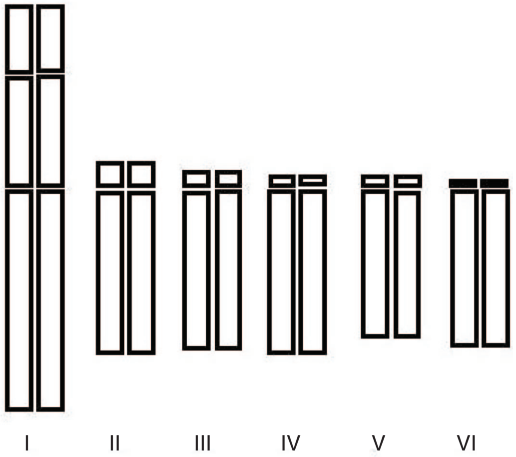

Figure 2 Karyogram of *Vicia faba* [Reproduced from Fuchs *et al.* (1998). © Springer]

V. faba is one of the cytogenetically best characterized plants. Its six chromosome pairs contain as much as 1C approximately 13 pg (picogram) of DNA, which corresponds approximately to 13000 Mbp (mega base pair). The first, very large chromosome (about 18 μm length) is metacentric, with one satellite. There are five similar (approx. 7–9 μm length) acrocentric chromosomes (Figure 2). The metacentric chromosome I of *V. faba* probably originated from a remote fusion of two telocentric chromosomes. Many cytogenetic phenomena were observed for the first time by studying *V. faba*, for instance, nucleolus formation at the secondary constrictions during telophase, or the existence of an upper tolerance limit for chromosome arm length (Schubert and Oud, 1997; Fuchs *et al.*, 1998).

1.3 Economic Importance

At the worldwide scale, faba bean occupies about 2.6 millions ha, which in 2005 represented 4%

of the total area dedicated to pulses. From the worldwide area occupied by faba bean, 41% was concentrated in Asia, 33% in Africa, only 12% in Europe, and 7% in Oceania as well as in America. China is the largest grower of faba bean in the world with 39% of the worldwide area. In Africa, faba bean is mostly concentrated in Ethiopia (15% of the world wide faba bean area). The worldwide production in 2005 was about 5.8 million tons of which China produced 43% and is, therefore, the largest producer in the world (http://faostat.fao.org/site/336/DesktopDefault.aspx?PageID=336).

Faba bean is a very minor crop in Germany (16 000 ha in 2005), in Poland (12 000 ha), and Austria (4000 ha). France did grow a total of 105 000 ha, amounting to one third of the French pea acreage. In the United Kingdom, faba beans were grown in 188 000 ha, this is double the area grown to pea plus lupins. Spain had in 2005 about 53 000 ha of faba bean. Mediterranean types are sown in late autumn. In parts of the United Kingdom and France, where winter is relatively mild, autumn sowing of faba beans is to some extent practiced as well using "true" winter beans that can survive winters north of Pyrenees Mountains and Alps. In the United Kingdom, more or less, half of the faba beans are such winter types. All types of faba bean can survive very mild frosts as young plants (until about −6 °C). Beans from the Hindukush do even show some frost tolerance in later stages. Autumn sowing is as well realized in North Africa, in southeast China (along the Yangtze Valley), and parts of Japan.

Cultivated faba bean is used as human food and as animal feed, mainly for pigs, horses, poultry, and pigeons in developing countries and almost strictly as animal feed in developed countries. For the human consumption, it can be used as a vegetable, either green or dried. Feeding value of faba bean is high; with about 30% of protein it is considered in some areas to be superior to field peas or other legumes. It is one of the most important winter crops for human consumption in the Middle East. Faba bean has been considered as a meat extender or substitute and as a skim milk substitute. Roasted seeds are eaten like peanuts in India. The proportion of the dried faba bean used as human food in the developing countries is not defined but data are available for green faba bean and allow assessing the contribution of faba bean in the human nutrition. Its use as green vegetable amounts to 20% of the total production of faba bean. It is a common food in the Middle East, Mediterranean region, Latin America, China, and Ethiopia. The production of green faba bean in the Mediterranean region accounts for 40% of the worldwide green bean production. The Middle East and Latin America contribute equally with about 19% to the worldwide green bean production. Other uses of faba bean have been identified. Indeed, haulm from faba bean harvest fetches a premium in Egypt and Sudan and is considered as a cash crop. The haulm can also be used for brick making and as a fuel in parts of Sudan and Ethiopia (http://faostat.fao.org).

1.4 Traditional Breeding

The breeding objectives for this crop totally depend on the economic and agro-ecological conditions and on the geographical region and use. For combine harvest of dry, mature seeds, all pods and even stem and leaves of the crop have to become mature simultaneously, whereas for manual harvest of vegetable green bean pods, a long-lasting harvesting period is sought. For combine harvesting, nonshattering and nonlodging habits are essential, whereas they are of lesser importance for the production of green pods. For the production of feed, mostly small grains are bred, whereas for human consumption, equina and major types are preferred in most areas (except Ethiopia, where small types are used for food). Moreover, color, taste, and cooking features are important for vegetable type germplasm. If grown for animal feed, primarily mature grain yield and yield stability are sought, and to sustain high performance, resistance against drought (and winter frost in case of winter bean breeding) and against fungi, pathogens, and pests is needed. An additional objective is mature grain quality, depending on the actual animal species to be fed.

Normal faba beans show indeterminate growth; flowers and very young pods grow in competition with the vegetative apex of the stems. Several alternative growth types have been studied as a strategy to strengthen the pods as sinks for assimilates. The so-called *ti*-type (terminal inflorescence, or "topless") and the so-called stable type (*st*, somewhat stunted habit, and very stiff stem) were introduced. Dwarfism is known as well. These phenotypes are all caused by a single recessive allele (ICARDA, 1986). Several corresponding cultivars have been bred in Germany, like "Tina" (*ti*), "Tinova" (*ti*) or like "Boss" (*st*) and "Mythos" (*st*). Still, these are not widely used, and no such type is present on the 2005 German list of varieties. On the other hand, very recently, Nadal *et al.* (2005) in Spain proposed the use of the *ti*-type as a solution in broomrape-infested (see below) conditions (production of young pods for fresh consumption). There has been a remarkable input into a type named "independent vascular supply" (*ivs*). Gates *et al.* (1983) proposed to circumvent the physiological interaction and competition between pods and flowers within the same inflorescence by independent vascular traces to each flower, so that direct interaction between flowers and young pods cannot occur, and distinguished this type from the "usual" branched vascular pattern. The conclusion was that selection for *ivs* would be most reliable to improve pod set. By microscopic studies, Ruckenbauer and Mollenkopf (1983) found that a classification into independent and branched vascular bundles is not adequate. In material that was claimed to express the *ivs* features, these authors found no hints on any structural deviation of the vascular traces from "normal" beans.

Faba bean, in spite of its high importance in several semiarid regions like the Mediterranean Basin, is rather susceptible to drought. Its main mechanism to deal with this stress is a very early and sensitive stomata closure. Adapted material escapes terminal drought by earliness, whereas no powerful strategy is known to deal with unpredictable, intermittent drought. Several physiological traits may be used to assist in breeding for drought tolerance. Germplasm from gene banks like ICARDA was used to specifically enlarge diversity. Frost resistance is mostly analyzed as a component of winter survival. Very few genotypes with outstanding frost resistance are known (Stoddard *et al.*, 2006). Similar to drought, physiological traits might help in breeding, such as fatty acid composition of leaves (Arbaoui and Link, 2006). No molecular tools are as yet available in faba bean breeding for these two traits.

The most important fungal foliar diseases are *Botrytis fabae*, *Ascochyta fabae*, and *Uromyces viciae-fabae*; besides, root rot caused by *Rhizoctonia solani*, *Fusarium* species, and other fungi can occur. *Botrytis* is seen in a wide range of growing conditions, it is often a very serious threat, and still no convincing source of resistance is known. Severe outbreaks are most common in the Nile delta, near rivers in China, rainy coastal areas of the Mediterranean Basin, and the more oceanic climate of western France and western United Kingdom (Tivoli *et al.*, 2006). Differences in susceptibility follow a quantitative genetic pattern. Several less susceptible bean genotypes are known (e.g., some ICARDA lines originating from South America). For *Ascochyta* and *Uromyces*, specific resistances are known and even molecular markers were developed. The line 29H, amongst others, was repeatedly used to improve *Ascochyta* resistance. Bean rust (*Uromyces*) resistance is available in many cultivars. Qualitative resistance is common and widely used by breeders (Sillero *et al.*, 2006). *Phoma* and mildew cause further less well-studied foliar diseases in *V. faba*. Few, if any, convincing sources of resistance against root rot are known. Material with a zero content of tannin (see below) in the seed testa (monogenic recessive feature) seems to be more susceptible at germinating and emergence than tannin-containing germplasm.

Viruses are not a frequent problem for the faba bean producer; still, viral diseases may occur as serious epidemic. The bean yellow mosaic virus, bean leaf roll virus, broad bean true mosaic virus, and the broad bean stain virus must be named. Since no direct pesticide protection exists, the genetic strategy must hold. The two latter viruses are to some extent seed transmitted and not aphid transmitted. Yet, the beetle *Sitona lineatus* (see below) spread these two viruses early in the season (Rohloff, 1980). There has been promising breeding research prior to 1989 in GDR, but these programs were then abandoned (Lötsch, 1989). In 1992 and again in 1999, a new, aphid-transmitted virus (faba bean necrotic yellow virus) occurred at a devastating level in the Nile Valley. Meanwhile resistant genotypes have been identified (e.g., "ILB132" Khaled *et al.*, 2000).

The most important pest is *Aphis fabae*, the black aphid. It occurs very often at significant levels, therefore, insecticides are used. In addition to the direct damage, it is spreading viruses. No useful resistance is known. Even earlier in the season than this aphid, the weevil *S. lineatus* feeds on the first, very young leaves. More important is the damage of its larvae, which feed on the root nodules and thus cause direct damage and probably increase root rot (Salt, 1983). *Bruchus rufimanus*, a seed-infesting weevil, is present in most faba bean fields and stocks. The female deposits the eggs in the field onto the very young pods. Infested seeds are not accepted for human consumption, thus the beetle is a serious threat for this aspect of production. Additional *Bruchus* and *Callosobruchus* species live in bean seeds (mainly in the Middle East); several of them complete their cycle in the store, the female laying the eggs onto the testa of mature dry seeds. The dry seed coat is a barrier, and not all the larvae can enter and overcome it; there is no connection to the seed coat's tannin content. The present breeding of new cultivars with reduced vicine and convicine content (see below) of the seed can favor the colonization of faba bean by additional weevils such as *Callosobruchus maculatus* that does not infest normal-vicine faba beans (Desroches *et al.*, 1995).

In addition to aphids and beetles, nematodes have to be mentioned. Faba bean may be infested by the stem nematode (*Ditylenchus dipsaci*) and the cyst nematode (*Heterodera goettingiana*). The stem nematode is widespread, and its "giant" race, common in North Africa, is a serious pest, especially in cases where nematode-infested seeds are sown. Small-seeded beans are generally a poorer host, several resistant genotypes were identified, amongst them is the *Ascochyta* resistant line 29H. The cyst nematode is important in many temperate regions. Obviously no resistances have been found (Sharma *et al.*, 1994). Broomrape, *Orobanche crenata,* is a parasitic plant, devastating pulses and other crops in the Mediterranean Basin and Nile Valley. Hand weeding, use of glyphosate, late sowing and breeding is used to fight it. Breeders have up to now not produced a bean with reliable resistance. Screening is mostly done in fields where this parasitic weed occurs naturally, which is a difficult test situation. Evaluations in controlled environments are possible but expensive. These shortcomings make broomrape resistance a problematic trait. Partially resistant genotypes are available; the resistance trait shows a quantitative genetic variation. The rather resistant genotype F402 identified by Egyptians was repeatedly used. Several improved genotypes have been bred from this common source in Egypt ("Giza 402", "Giza 429", "Giza 674") and in Spain ("Vf1071", "Vf136", "Baraca"). Meanwhile, three quantitative trait loci (QTLs) for resistance were identified (Torres *et al.*, 2006). *Orobanche* resistance is a trait that shows all features to make it a candidate for marker-assisted selection. It is a very serious problem, resistance shows quantitative genetic variation, difficult to phenotype the trait, and there is only one unique, common source of resistance ("F402"). Up to now, the level of cooperation among breeders and scientists in the Mediterranean Basin and Nile Valley is scanty to realize the importance of this pest and to employ modern breeding techniques.

Breeding for improved quality aims mainly at increase of the seed protein content and protein quality. Protein content could easily be increased to over 30%. Still, as long as there is no economic incentive to do so, breeders will not invest significant effort in achieving this goal. Protein quality is mainly limited due to a low sulfur-containing amino acids such as methionine and cysteine. Classical methods are not promising, since the variation is low and there is a negative genetic correlation between seed protein content and sulfur-containing amino acids' content of this protein (Link *et al.*, 2005). Quality, moreover, depends on the content of antinutritional factors like condensed tannins and vicine. Zero-tannin cultivars, for example those for feeding pigs, do exist (e.g., "Gloria"). The recessive monogenetic segregation of this gene and the pure white flower, as its pleiotropic effect, make this trait easy to handle. Low vicine cultivars do as well exist (e.g., "Mélodie"). The trait is again monogenetic recessive, a morphological marker (white hilum) and even molecular markers are available. Vicine may have negative effects on human health. A rare human enzyme deficiency, favism, leads to anemia upon faba bean consumption in affected individuals. Also, vicine negatively effects monogastric animal nutrition like pigs and chicken. Further antinutritional compounds are not of importance in faba beans (Duc *et al.*, 1999).

Classical breeding in faba bean looks back on very marked improvements, e.g., for non-shattering, improved yield and yield stability, highly improved lodging resistance. Still, breeding progress is hampered by the partial allogamy of the bean. The pollinators are bumble bees and honey bees (Link *et al.*, 1994a; Suso and Moreno, 1999). The degree of cross-fertilization is about 50%, with

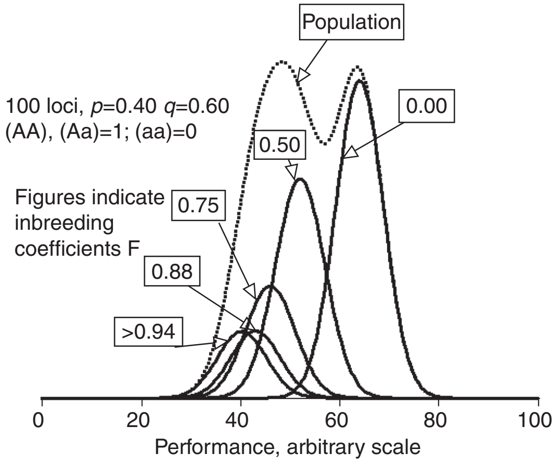

Figure 3 Theoretical distribution of individual plant's performances in case of partially allogamy like in faba bean, here with 50% outcrossing of inbred plants and 30% outcrossing of noninbred plants. The population is shown as composition of cohorts of plants with different levels of inbreeding [Reproduced from Link *et al.* (1994b)]

a large genotypic and environmental component of variation and with marked heterosis; heterozygous plants show on average less outcrossing than homozygous plants. Inbreeding depression for grain yield is marked; F_1-hybrids outyield their inbred parents mostly by more than 40%. The partial allogamy and the marked heterosis for vigor and productivity cause the genetic variation of a faba bean population to be very much inflated (Figure 3), compared to a situation of pure selfing or pure outcrossing. This reduces markedly the gain from mass selection for these traits. The reason is that the superiority of the selected plants is mainly caused by their high heterozygosity, not by a high breeding value; heterozygosity, however, is not inherited. A solution is to strictly select among entries of identical level of inbreeding, preferentially among pure lines.

The first approaches to realize the production of hybrid cultivars (based on cytoplasmic-genetic male sterility) in faba bean trace back to Bond in Cambridge in 1957 and to Berthelem in Rennes in 1967. Bond worked with the system CMS447, discovered by him in winter beans in Newcastle upon Tyne. Berthelem discovered the system CMS350 in an English bean population. The system CMS350 was found to be sensitive to environmental conditions. The system CMS447 is very peculiar, since a genetic restoration of pollen fertility becomes permanent; offspring that segregates from a heterozygously restored plant does not segregate for the pollen sterility as expected from textbook schemes on cytoplasmic male sterility (CMS) systems. Molecular genetic findings proposed that CMS447 may be the result of an infection with a defect virus, and that restoration corresponds to nontransmittance by seeds (Pfeiffer *et al.*, 1993). In Germany, Link *et al.* (1997) detected two other CMS systems (CMS199, CMS297), yet due to instability of the sterility, especially due to spontaneous reversions to pollen fertility, hybrid breeding still could not be realized in faba bean.

As classical breeding category, line breeding is applied. An important bottleneck in line breeding is the production of purely selfed seed. In the open field situation of a breeding nursery, with small plots and large numbers of genotypes, seed multiplication suffers from uncontrolled contamination with cross-pollen, unless spatial isolation and pure lines are used. In cages, pollinators can be excluded and pure self-fertilization can be enforced. Still, without pollinator visit, most genotypes admit a need of tripping (a mechanical stimulation of the stigma, caused by the pollinator, which induces successful pollination and fertilization). As a consequence of absence of pollinators, yield of purely selfed seed in cages is variable and mostly very low. Germplasm from Southern Europe and Northern Africa often shows a lower or no need of tripping. Tripping can be done manually, to substitute for the missing pollinators in the cages, thereby allowing true selfing and high seed set, but this is a very labor-intensive procedure. A very successful alternative to pure inbred line cultivars is the breeding of synthetic cultivars. Still, due to the limited degree of natural outcrossing, only about half of the potential hybrid vigor is used in a synthetic cultivar.

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