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CONSENSUS DOCUMENT ON THE BIOLOGY OF COMMON BEAN (Phaseolus vulgaris L.)

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Consensus Document on the Biology of COMMON BEAN (*Phaseolus vulgaris* L.)

Environment Directorate

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FOREWORD

Consensus Documents contain information for use during the regulatory assessment of a particular product. In the area of plant biosafety, these are being published detailing the biology of certain plant species, selected traits that may be introduced into plant species, and biosafety issues arising from certain general types of modifications made to plants.

This document addresses the biology of COMMON BEAN *(Phaseolus vulgaris L.)*.

Brazil and ILSI-CERA served as the co-leads in the preparation of this document, and the draft has been revised based on the input from other member countries and stakeholders.

This document is published under the responsibility of the Joint Meeting of the Chemicals Committee and the Working Party on Chemicals, Pesticides and Biotechnology.

TABLE OF CONTENTS

Figures

Tables

I.   SPECIES OR TAXONOMIC GROUP

1.1   Classification and nomenclature

1.   The scientific name of common bean is *Phaseolus vulgaris* L. (ITIS, 2014). Common bean is a member of the legume family, and its taxonomic hierarchy is

Order   Fabales

Family   Fabaceae

Genus   *Phaseolus* L.

Species   *Phaseolus vulgaris* L.

2.   Common synonyms are French bean, haricot bean, salad bean, snap bean, string bean, frijoles (Spanish), feijão and feijoeiro (Portuguese for the seed and the plant, respectively), and mharagwe (Swahili) (Purseglove, 1968; Wortmann, 2006; Gepts and Debouck, 1991).

3.   The genus *Phaseolus* is large, including approximately 80 cultivated and wild species, but *P. vulgaris* is the most widely cultivated species (Purseglove, 1968; Freytag and Debouck, 2002; Bailey, 1975; Porch et al., 2013). The most closely related species to *P. vulgaris* are *P. albescens*, *P. coccineus*, *P costaricensis*, *P. dumosus*, *P. parvifolius*, and *P. persistentus* (Table 1.) (Chacón et al., 2007; Broughton et al., 2003; Bellucci et al., 2014; Delgado-Salinas et al, 2006). In addition to *P. vulgaris*, four other *Phaseolus* species are cultivated: *P. dumosus* (year bean), *P. coccineus* (scarlet runner), *P. acutifolius* (tepary bean), and *P. lunatus* (lima bean) (Bellucci et al., 2014; Lioi and Piergiovanni, 2013).

Table 1. **Species closely related to *Phaseolus vulgaris***

Species	Geographic Location
P. acutifolius	Mexico, southwestern United States
P. albescens	Western Mexico
P. coccineus	Mexico, Guatemala, Honduras
P. costaricensis	Eastern Costa Rica, western Panama
P. dumosus	Western Guatemala, Mexico
P. parvifolius	Southwestern United States, Guatemala, Pacific coast of Mexico and Central America
P. persistentus	Guatemala

Sources: Porch et al. (2013); Bellucci et al. (2014)

4.   *P. vulgaris* belongs to the Fabaceae family, which comprises species displaying a wide variety of forms: trees, shrubs, and herbs, including many with a climbing growth habit. Most species bear five-petaled flowers with a distinctive papilionaceous or butterfly-like shape. The flowers have a single large

upright petal, flanked by two horizontal "wing" petals, and subtended by two petals at the bottom of the flower, partially or completely joined to form a boat-like "keel." Flowers typically have ten stamens, nine of which may form a tube surrounding the ovary and one that is separate from the others and positioned above the ovary, although there are variant stamen configurations in some species. The fruit of Fabaceae species is the legume–a single-carpelled pod of various shapes and sizes, bearing from one to many seeds. In many species the pod splits, either along one or both edges, known as the placental and central sutures, to release the seeds (Wortmann, 2006).

5.   *P. vulgaris* shares many of the features characterising the family, but two features distinguish the entire *Phaseolus* genus from the rest of the family: the keel of the flower terminates in a coil, having from 1 to 2 turns (Bailey, 1975; Purseglove, 1968; Gentry, 1969), and uncinate hairs are present on both vegetative and reproductive structures of the plant (Freytag and Debouck, 2002).

6.   The wild ancestor of *P. vulgaris* has been referred to as the same species (Gentry, 1969), as a variety of domesticated common bean, *P. vulgaris* var. *mexicanus* (Delgado-Salinas et al., 1988), as a separate species, *P. arborigineus* (Brücher 1988), and as a subspecies, *P. vulgaris* subsp. *arborigineus* (Gentry, 1969).

1.2   Description

7.   Common bean is the most commonly consumed legume worldwide, and it is the most important legume produced for direct human consumption, with a commercial value exceeding that of all other legume crops combined (Broughton et al., 2003; Porch et al., 2013; Graham and Vance, 2003). Although low in methionine and cysteine, the dried seeds, or "pulses" of *P. vulgaris* are an important source of dietary protein for millions of people throughout the tropics, supplementing those amino acids lacking in diets based on maize, rice, or other cereals (Broughton et al., 2003; Wortmann, 2006). Beans are an especially valuable source of the amino acids lysine and tryptophan, the minerals iron, copper, and zinc, and beneficial phytochemicals, antioxidants, and flavonoids (FAO, 1999).

8.   Dry beans are typically processed before consumption, usually by cooking in water, but some beans are consumed after roasting or after milling into flour (Tohme et al., 1995; Siddiq and Uebersax, 2012; FAO, 1999). Immature seed pods, called snap beans, are consumed as vegetables in some regions, and straw from the plants is used as forage (Purseglove, 1968; Broughton et al., 2003). The leaves of some specially selected varieties are consumed as a vegetable, usually when better quality food is not available (Wortmann, 2006).

9.   In developing countries in Latin America and Africa, most beans are produced by small holder farmers (Broughton et al., 2003), and a significant portion of the crop is consumed on-farm, so it is difficult to accurately estimate global production. The widespread practice of producing beans through intercropping also leads to an overestimation of the total area planted and an underestimation of global yields (Akibode and Maredia, 2011). The FAO reported that total dry bean production in 2013 was over 23 million tonnes (FAO, 2014), although this number includes other bean species as well, and possibly other minor food legumes.

10.   Due to extensive plant breeding efforts, *P. vulgaris* comprises numerous cultivars with a wide range of morphological and agronomic characteristics, including differences in seed size and colour as well as growth habit (Purseglove, 1968; Singh et al., 1991). One of the most commonly selected traits is determinate growth, which is associated with reduced branching, shorter and fewer internodes, reduced twining, insensitivity to day length, and most important, an increased allocation of biomass to reproductive growth (Kwak et al., 2012; Singh and Schwartz, 2010). Specific agronomic circumstances also favour the use of varieties with a determinate growth habit: they are better adapted to shorter growing seasons,

because they mature earlier; they produce pods over a shorter, more consistent period of time, which simplifies the harvest of green beans; and determinate varieties are more amenable to mechanised cultivation and harvest (Kwak et al., 2012). Determinate and indeterminate growth habits are shown in Figure 1.

Figure 1. **Differences in growth habit in common bean: determinate (left); indeterminate (right)**

Source: courtesy of D.G. Debouck, CIAT

Note: The arrows mark trifoliolate leaves, replaced by primary bracts in the determinate variety. The main stem is thus replaced by a terminal inflorescence in the determinate variety, while the main stem continues to produce axillary racemes in the indeterminate variety.

11.   There are also twining or climbing cultivars of *P. vulgaris* with indeterminate growth habit as well as many cultivars with a partially erect and partially trailing intermediate growth habit (Purseglove, 1968; Singh et al., 1991), although they are less frequently grown than the determinate cultivars. Prostrate to semi-climbing indeterminate varieties are favoured in cool, highland areas, with short daylength (Singh and Schwartz 2010). Typically, the length of the main stem of the plant is positively correlated with the number of nodes per stem and the number of seed pods produced (García et al., 1997).

12.   Other traits selected as a result of the domestication of *P. vulgaris* are increased pod size and fleshiness, reduced pod dehiscence, larger seeds, and increased permeability of the seeds to water (Gentry, 1969; García et al., 1997; Singh st al, 1991).

13.   Cultivated *P. vulgaris* has a taproot-based root system with lateral roots typically located within the top 15 cm of soil. The roots are colonised by *Rhizobium* bacteria, resulting in irregular root nodules (Purseglove, 1968).

14.   The stems are typically hairy, with the length and density of the hairs dependent on the cultivar. However, short, hooked hairs (uncinate hairs) are always present on the younger portions of the stems

(Debouck and Hidalgo, 1986; Singh et al., 1991; Lackey, 1981; Freytag and Debouck, 2002). The hairs have a role in both disease and insect resistance. There is evidence that the hairs interrupt the production of fungal spores, thereby reducing secondary inoculum (e.g., bean rust, *Uromyces appendiculatus*) and can physically wound insects (such as leafhoppers, *Empoasca fabae*), resulting in reduced predation (Mmbaga and Steadman, 1992; Pillemer and Tingey, 1978). When the climate is sufficiently warm to allow a semi-perennial growth habit, the stems of wild *P. vulgaris* can grow to a diameter of 1.5 cm and may develop a corky outer layer (Gentry, 1969).

15.   The leaves are trifoliolate and alternate on the stems. The leaflets are entire and somewhat hairy, 8–15 cm x 5–10 cm, with small stipules (Purseglove, 1968; Wortmann, 2006). Leaflet shape differs among the cultivars, but leaflets generally have broad bases and pointed tips (Singh et al., 1991).

16.   Flowers are borne on axillary or terminal racemes, in colours of white, pink or violet, depending on the cultivar. The bisexual flowers are keeled, and the keel terminates in a coil, with 1–2 turns (Purseglove, 1968; Bailey, 1975; Wortmann, 2006).

17.   The seed pods are narrow, 8–20 cm x 1–2 cm, with up to 12 seeds per pod, but most varieties have 4–6 seeds. Seeds are produced in a wide variety of colours, depending on the cultivar (Purseglove, 1968; Wortmann, 2006), and the seeds vary considerably in size, with a range of 150–900 g per 1 000 seeds (Brink and Belay, 2006; Wortmann, 2006).

18.   Wild *P. vulgaris* differs from the cultivated types in several characteristics. The plants are typically indeterminate climbers with shorter main stems than the cultivated varieties. Main stem branches are more numerous, but with fewer nodes (Brücher, 1988; García et al., 1997; Delgado-Salinas et al., 1988; Gentry, 1969). A twining growth habit helps the plant to better compete for sunlight with forest vegetation than a shrubby determinate habit (Kwak et al., 2012; Gentry, 1969). Flowers, seed pods, and seeds of the wild species are more numerous; pods and seeds are smaller; and the pods have a dehiscence slit near the pedicel and are explosively dehiscent (Brücher, 1988; García et al., 1997; Delgado-Salinas et al., 1988). The wild species has a much longer flowering period than cultivated varieties, and flowers can be produced up to the first killing frost (Brücher, 1988).

19.   Physiological differences have also been identified between the cultivated and wild species. For example, nitrogen use efficiency and carbon dioxide exchange rates were found to be higher in wild populations when compared to cultivated landraces (Porch et al., 2013).

1.3   Geographic distribution, ecosystems, cultivation and management practices, centres of origin and diversity

1.3.1   Geographic distribution

20.   Wild common bean populations were first documented in Guatemala in 1947 (McBryde, 1947), and they occur from northern Mexico to northern Argentina. However, the distribution is not continuous through that region, due to climatic variations unfavourable to the species, that is, regions with excessive rainfall or elevations below 700 metres or above 3 000 metres (Chacón et al., 2007; Chacón et al., 2005; Broughton et al., 2003). Habitat destruction throughout the species' range has accelerated the interest in identifying and preserving ancestral varieties (Debouck et al., 1993).

21.   Wild common bean occurs from northern Mexico (Acosta-Diaz et al. 2015) to northwestern Argentina and distinct differences in both morphological characteristics and molecular markers have been identified in the northernmost and southernmost populations (Singh et al., 1991; Freyre et al., 1996). The

climate where common bean originated is sub-tropical to temperate, with defined wet and dry seasons, and bean prefers regions with moderate rainfall, rather than dry regions or areas with excessive rain (Beebe et al., 2014). Bean plants cannot tolerate frost, or elevations above 3 000 metres, but they can grow as annuals in temperate climates and as annuals or short-lived perennials in tropical climates (Purseglove, 1968; Gentry, 1969). Excessive temperatures cause flowers to abscise, and low temperatures delay pod production and can result in empty pods (Liebenberg, 2009). Common bean prefers well drained, sandy clay or sandy loam soils, with balanced fertility and moderate acidity pH 5.8–6.5 (Liebenberg, 2009).

1.3.2   *Ecosystems where common bean occurs natively and has naturalised*

22.   Having evolved in areas where taller vegetation limits the sunlight that reaches the forest floor, wild bean grows as a vigorous vine that enables it to effectively compete for sunlight (Beebe et al., 2014), a characteristic that enables wild bean to exploit disturbed sites, using other pioneer species as climbing support (Brücher, 1988; Delgado-Salinas et al., 1988).

23.   Cultivated varieties of bean do not tend to persist as feral populations in regions outside the species' native range. Genetic analyses of individual bean plants selected from feral populations and cultivated varieties indicate that the cultivated varieties have been derived from feral populations, rather than the other way around (Porch et al., 2013; Beebe et al., 1997; Toro Ch. and Ocampo, 2004).

1.3.3   *Cultivation and management practices*

24.   *P. vulgaris* is planted in pure stands of single landraces, as mixed plantings of several landraces, and intercropped with maize, sweet potatos, cotton, coffee and other crops. It is common for farmers to freely exchange their landraces (Zizumbo-Villarreal et al., 2005; Wortmann, 2006). Typically beans planted for vegetable use are planted in monoculture (Singh and Schwartz, 2010; Wortmann, 2006). Because bean varieties consumed as a vegetable produce pods in as little as two months, rotations with other crops is a common practice (Purseglove, 1968; Broughton et al., 2003).

25.   Whether a farmer plants one or two bean crops per year is determined largely by rainfall patterns. In tropical regions having a bimodal pattern, two plantings per year are possible, but in more temperate climates with a single rainy season, only one crop is planted (Beebe et al., 2014).

26.   Seed is either sown in rows or broadcast, with seeding rates of 150 000 to 400 000 seeds per hectare. When intercropped, beans are sown at a lower rate (Wortmann, 2006). Examples of intercropping with coffee and maize are shown in Figures 2 and 3. Bush-type varieties are typically planted at higher densities (30–90 cm x 15–30 cm) than pole-type varieties (hills 30–120 cm apart, 3–6 plants per hill). Even within the type, planting densities vary widely, depending on local practice and degree of mechanisation (Purseglove, 1968; Liebenberg, 2009; Wortmann, 2006); however, increasing the planting density generally increases yields (Russo and Perkins-Veazie, 1992).

Figure 2. **Common beans intercropped with coffee**   Figure 3. **Common beans intercropped with maize**

Source: Embrapa   *Source:* Embrapa

27.   In developed countries, where mechanised cultivation is practiced, row planting is common, using inter-row distances of 75–90 cm, depending on the variety (Liebenberg, 2009). Greater degrees of mechanisation require varieties with more uniform growth habit and maturation time (FAO, 1999). More widely spaced rows facilitate cultivation, while planting more closely spaced rows results in larger plants, more numerous pods, and higher yields, depending on the environmental conditions (Goulden, 1975). However, close spacing can increase disease incidence (Sandoval-Avila et al., 1994).

28.   Beans are typically planted on level land, but sowing on hills or ridges may be practiced in areas with heavy soils or where the water table is high (Wortmann, 2006). Soil preparation in developed countries includes cultivation and the application of any needed fertiliser (Purseglove, 1968). Due to the variable effectiveness of nitrogen fixation by common bean, nitrogen content of the soil is typically supplemented in commercial production (Liebenberg, 2009). Phosphorus and potassium deficiencies severe enough to cause yield losses are not common in developed countries (Liebenberg, 2009).

29.   Seed germination needs a minimum soil temperature of 12°C, with an optimum of 22–30°C. Depending on the variety, flowering begins 4–6 weeks after sowing (Wortmann, 2006). High night temperatures during anthesis can cause flowers to abort and reduce seed set (Russo and Perkins-Veazie, 1992). Determinate bean varieties face greater competition from weeds, because weeds may overgrow the crop, so weed control, especially in the early establishment of the crop, is important (Liebenberg, 2009; Wortmann, 2006).

30.   Harvest times depend on the use of the crop. For snap beans consumed as a vegetable, harvest begins 2–4 weeks after flowering (7–8 weeks after sowing). For dry beans, harvest occurs when the pods have turned yellow, and the seeds have matured (Purseglove, 1968; Wortmann, 2006). Seed filling takes from 3–7 weeks. Although seed maturity occurs when the moisture content is approximately 50%, harvesting does not typically occur until the seeds dry down to 15–16%. Significant losses can occur post-harvest if plants are left to dry excessively before moving them to the threshing area, because seed pods may open spontaneously and drop seeds on the ground (FAO, 1999). Additionally, allowing seeds to lose additional moisture prior to harvest increases the risk of split seeds, which is a problem in commercial production (Liebenberg, 2009).

31.   Physiological and biochemical ripening continues even after harvest, and some of these processes can impair the quality of the harvest. The beans develop a brown discolouration and off-flavours as well as textural defects that appear after cooking—a condition called "bin burn." The potential for bin burn and

cooking defects is both genetically and environmentally determined, but allowing the beans to dry to 11-12% moisture content and storing seed under cool conditions generally helps preserve seed quality (FAO, 1999).

32.   Plants may be hand harvested and threshed in the case of small holder farms, or in the case of commercial production, the harvest and threshing processes may be mechanised (Liebenberg, 2009). In some regions, seeds are sorted by variety, while in other areas, seeds of various varieties with similar cooking requirements are commingled and consumed as a mixture (Wortmann, 2006; FAO, 1999).

33.   Inputs also vary depending on the region. Beans are produced successfully without irrigation in regions receiving from 25 cm to over 40 cm of rainfall during the growing season (Wortmann, 2006). Commercial production in developed countries and in arid subtropical regions may use irrigation to supplement natural rainfall (Purseglove, 1968). In developing countries, beans may be grown with no mineral fertilisers or manure, while in developed countries mineral fertilisers are used routinely.

34.   In developing countries, significant yield losses from disease, insect pests, low soil fertility, and abiotic stresses are common (Broughton et al., 2003). Low soil phosphorus is a major constraint to common bean production, especially when grown by resource-poor farmers in tropical and subtropical regions, where acidic soils tend to be phosphorus deficient (Beebe et al., 2014; Beebe et al., 2006; Graham and Vance, 2003; Porch et al., 2013). In addition, many farmers in developing countries treat beans as a low-input crop, choosing to allocate scarce resources to other crops, such as cereals (Akibode and Maredia, 2011). Because of these limitations, bean yields in developed countries are typically several times that of yields in developing countries (Porch et al., 2013).

35.   Improvements in heat and drought tolerance have the potential to significantly increase bean yields in a majority of regions where beans are grown (Porch et al., 2013). However, breeding efforts to create bean varieties able to cope with abiotic and biotic stresses are hampered by a lack of available genes for stress resistance. Identifying new varieties is made even more difficult by the need for breeders to meet consumer requirements for what are often very specific bean size, taste, colour, and quality characteristics (Singh and Schwartz, 2010). The tepary bean, *P. acutifolius*, is thought to be a promising source of genes for increasing tolerance to abiotic stresses, such as high temperature, drought, and high salinity (Porch et al., 2013).

1.3.4   *Centres of origin and diversity*

36.   Although 200 years ago it was believed that common bean originated in Asia, a large body of evidence indicates that *P. vulgaris* originated in the New World (Kaplan and Lynch, 1999; Gepts and Debouck, 1991). Archaeological records indicate that the species originated and was first domesticated as early as 5 000 B.C. (Purseglove, 1968; Bitocchi et al., 2013; Bitocchi et al., 2012), although there is evidence for a more recent origin in Mesoamerica (Kaplan and Lynch, 1999). Multi-locus sequence data have indicated that the domestication of common bean was initiated 8 000 years ago (Mamidi et al., 2011).

37.   Polymorphisms among cultivated varieties and molecular markers, such as isozymes and variants of the seed protein phaseolin, indicate that there may have been at least two independent centres of domestication in Central and South America (Purseglove, 1968; Singh et al., 1991; Bitocchi et al., 2013; Bitocchi et al., 2012; Chacón et al., 2005; Bellucci et al., 2014; Kaplan and Lynch, 1999; Freyre et al., 1996), resulting in the Middle American and the Andean gene pools (Acosta-Gallegos et al., 2007; Brücher, 1988; Kwak and Gepts, 2009; Angioi et al., 2010). Some evidence indicates that these two gene pools had already diverged before domestication efforts began (Brücher, 1988; Delgado-Salinas et al., 1988). The South American types tend to have seeds and leaves of larger size than the Central American varieties (Wortmann, 2006).

38.   Cultivated common bean were developed from wild common bean, and domestication has introduced several agronomically useful traits: indeterminate and bush types, increased leaf, pod, and seed size, and suppression of pod dehiscence and seed dormancy. Vast diversity of seed size, shape, and colour has also resulted from domestication (Singh et al., 1991; Broughton et al., 2003). Crop earliness has been enhanced by selecting for photoperiod insensitivity (White and Laing, 1989). Domestication of common bean has also resulted in a significant reduction in genetic diversity, compared to the species in the wild (Bitocchi et al., 2013; Chacón et al., 2005).

39.   Spanish and Portuguese explorers eventually brought *P. vulgaris* (Figure 4) to Europe in the 16th century (Purseglove 1968), and Portuguese traders are believed to have then brought beans to Africa, where they spread from the highland areas of Central Africa to the rest of the continent (Wortmann, 2006).

Figure 4. **Wild species of common bean (*P. vulgaris*)**

Source: courtesy of Dr. Ismael Hernández', INIFAP-México

II.   REPRODUCTIVE BIOLOGY

2.1   Generation time and duration

40.   Common bean can grow as annuals in temperate climates and as annuals or short-lived perennials in tropical climates (Purseglove, 1968; Gentry, 1969). The number of days to seed maturity varies widely, from 50 to more than 250 days, and it is dependent on the cultivar, its photoperiod response, and the environmental conditions (Singh et al., 1991; Sandoval-Avila et al., 1994; White and Laing, 1989).

2.2   Reproduction

2.2.1   *Floral biology*

41.   Flowers of wild *P. vulgaris* are generally purple, pink, or white (Gentry, 1969) (Figure 5). The floral structure of *P. vulgaris* contributes to the high rate of self-pollination: anther dehiscence and stigma receptivity occur at the same time, before the flower is fully open, and the anthers and stigma are positioned near one another at the time of anther dehiscence and stigma receptivity (Webster et al., 1977).

Figure 5. **Flower of *Phaseolus vulgaris*, showing coiled keel**

Source: courtesy of D.G. Debouck, CIAT

42.   Bracts on the rachis of the inflorescences are persistent (Lackey, 1981), and the size and shape of the bracteoles are distinguishing characteristics of bean cultivars (Singh et al., 1991).

2.2.2   Pollination and pollen dispersal

43.   The pollen grains of common bean have a diameter of approximately 30 micrometres. They are spherical to triangular and tricolporate in shape, with a reticulate exine (Ferguson, 1984). Little is known about the longevity of bean pollen (Andersson and de Vicente, 2010).

44.   Common bean is regarded primarily as a self-pollinating species, due to floral morphology (Purseglove, 1968; Singh et al., 1991). However bumble bees, carpenter bees, and honeybees have been identified as potential pollen carriers between cultivated bean plants. These species, as well as other insects such as thrips, are responsible for the low frequencies of outcrossing observed between bean varieties grown in close proximity (Ferreira et al., 2006; Free, 1966; Proctor et al., 1996; Faria, 2010). Published reports indicate that the outcrossing frequency approaches zero when bean plants are separated by 3 to 10 metres (Ferreira et al., 2006; Faria et al., 2010), but outcrossing rates are dependent on both the bean genotype and the environmental conditions (Wells et al., 1988; Ibarra-Perez et al., 1997). Intervarietal cross-pollination would also depend on synchrony of flowering (Ferreira et al., 2000). Examples of standard isolation distances established for the production of certified bean seed are three metres (Canada) (Canadian Seed Growers' Association, 2013), five metres (Common Market of Eastern and Southern Africa and India) (Indian Ministry of Agriculture, 2013; COMESA, 2014), and zero metres or a distance adequate to prevent mechanical mixture (USA) (AOSCA, 2009).

2.2.3   Seed production, and natural dispersal of fruits or seeds

45.   The number of days for seed maturity varies widely, from 50 to more than 250 days, and is dependent both on the cultivar and the environmental conditions (Singh, 1991).

46.   Seed dispersal is minimal when beans are grown as snap beans for vegetable use, because the pods are harvested before the seeds are mature. Modern bean varieties are selected for non-dehiscence of mature pods, so few seeds are dispersed via this route, and any dispersal would occur over only short distances (Gentry, 1969; Acosta-Gallegos, 2007; García et al., 1997). Birds are known to consume immature seeds while still in the developing pods, but there is little evidence that animals disperse mature seeds, probably due to their toxicity (Debouck et al., 1993).

2.2.4   Seed viability, dormancy, and natural seed banks

47.   True seed dormancy in common bean is rarely encountered (Acosta-Gallegos, 2007; Westphal, 1974); however, seeds of wild bean and some cultivars have a hard seed coat that is only partially permeable to water, thereby inhibiting germination (Brücher, 1988; Freyre et al., 1996). As a result, seeds can remain ungerminated in the soil for two years (Purseglove, 1968). Breeding efforts have had success in increasing the permeability of the seed coat as a means of ensuring more uniform germination (García et al., 1997; Singh et al., 1991; Bellucci et al., 2014).

2.2.5   Asexual propagation (apomixis, vegetative reproduction)

48.   Bean is propagated primarily using seeds, although it is possible to propagate bean vegetatively, using stem cuttings (Wortmann, 2006; Brink and Belay, 2006).

III.   GENETICS

49.   Both cultivated and wild forms of the species are diploid (2n = 22), and the two forms hybridise readily (Delgado-Salinas et al., 1988; Singh et al., 1991).

50.   Crosses between the Middle American and Andean gene pools are easily accomplished, although differences in flowering time can make crossing difficult (Porch et al., 2013). It has been noted that divergences between the two gene pools may make recovery of progeny more difficult than with crosses within the two pools, and occasionally crosses result in dwarfism or lethality (Acosta-Gallegos et al., 2007; Singh and Schwartz, 2010). This hybrid weakness is thought to be due to semi-dominant alleles of two "Dosage-dependent Lethal" (DI) genes. Depending on the heterozygosity of these two genes, hybrids between the two gene pools may exhibit complete lethality, lethality at high temperatures, or only sublethal symptoms (Table 2) (Koinange and Gepts, 1992).

Table 2. **Hybrid weakness in wild *P. vulgaris***

	Homozygous Dl2 locus	*Heterozygous Dl2 locus*
Homozygous Dl1 locus	Lethal	Sublethal
Heterozygous Dl1 locus	Sublethal	Abnormal phenotype at high temperature

IV.   HYBRIDISATION AND INTROGRESSION

51.   Natural crosses between common bean and other *Phaseolus* species are inhibited by a variety of incompatibility mechanisms, such as incomplete chromosome pairing, sterility of F1 hybrids, and embryo abortion (Broughton et al., 2003). Other barriers, such as photoperiod sensitivity and flowering time have also been noted as limiting opportunities for interspecific crossing without human intervention (Porch et al., 2013). However, wild-collected plants representing hybrids of *P. vulgaris* x *P. coccineus*, have been reported (Escalante et al., 1994).

52.   Experimental crosses have been attempted between *P. vulgaris* and several closely related species, such as *P. coccineus*, *P. dumosus*, *P. costaricensis*, *P. acutifolius*, *P. parvifolius*, *P. filiformis* and *P. angustissimus*, to take advantage of disease and insect resistance and abiotic stress tolerance traits that these species possess (Acosta-Gallegos et al., 2007; Escalante et al., 1994; Schwartz and Singh, 2013; Beebe et al., 2014). However due to partial incompatibility, viable offspring from such crosses may require embryo rescue, and hybrids frequently exhibit dwarfism and partial or complete sterility (Broughton et al., 2003; Brücher, 1988; Acosta-Gallegos et al., 2007; Singh and Schwartz, 2010). Using *P. vulgaris* as the female parent may reduce the need for embryo rescue (Porch et al., 2013).

53.   Data indicate that under the right environmental conditions, cultivated *P. vulgaris* plants can pollinate nearby wild *P. vulgaris* plants, resulting in fertile hybrids and the potential for domestication traits to introgress into wild populations (Zizumbo-Villarreal et al., 2005; Delgado-Salinas et al., 1988; Freyre et al., 1996). Conversely, when the wild plants act as the male parent, gene flow to cultivated varieties can also occur, although at much lower frequency than when the cultivated variety acts as the male parent (Papa and Gepts, 2003). These hybrids, when harvested by the farmer and replanted, increase the genetic diversity of regional landraces and are considered to have a positive impact on the cultivated species (Zizumbo-Villarreal et al., 2005; Beebe et al. 1997). However, data indicate that, in spite of the possibilities for hybridisation between feral and cultivated populations of bean, the two populations generally remain strongly differentiated (Papa and Gepts, 2003).

54.   Manual crosses between cultivated bean varieties and wild *P. vulgaris* are easily made, resulting in viable, fertile F1 offspring (Brücher, 1988). There is evidence that under certain conditions, low to moderate levels of natural outcrossing with the wild species can occur (Singh, 1991; Kwak et al., 2009; Ibarra-Perez, 1997), possibly mediated by insect pollinators, such as bumblebees (Brücher, 1988; Delgado-Salinas et al., 1988). The high level of homozygosity in wild populations indicates that outcrossing is generally a rare occurrence (Kwak et al., 2009).

V.   GENERAL INTERACTIONS WITH OTHER ORGANISMS (ECOLOGY)

55.   Like other legumes, *P. vulgaris* associates with *Rhizobium* bacteria in the soil, which form root nodules (Figure 6). Through nitrogenase activity, the bacteria within the nodules fix atmospheric nitrogen to form ammonia, which the bean plant uses as a nitrogen source, reducing the need for externally applied fertilisers (Ramos et al., 2003). However, the nitrogen fixing capacity of *P. vulgaris* varies by variety and is generally less than that of other agronomically important legumes, such as soybeans, which tend to have larger root nodules with higher nitrogenase activity (Isoi and Yoshida, 1991; Hardarson et al., 1993). *P. vulgaris* roots are colonised by a wide range of native *Rhizobium* species and strains, some of which have little or no nitrogenase activity (Isoi and Yoshida, 1991; Ribeiro et al., 2013; Vásquez-Arroyo et al., 1998), and this may be one of the reasons for reduced nitrogen fixation capacity.

56.   Several environmental factors present in regions where beans are commonly grown, such as drought, flooding, and either high or low temperatures, impact nitrogen fixation. *Rhizobium* populations, nodulation, ammonium assimilation, and nitrogenase activity are all reduced under these conditions (Beebe et al., 2014; Devi et al., 2012; Hungria and Kaschuk 2014; Ramos et al., 2003; Vásquez-Arroyo et al., 1998; Graham, 1981). Low soil phosphorus and manganese levels as well as low soil pH are also associated with sub-optimal nitrogen fixation capacity (Graham and Vance, 2003; Ramos et al. 2003; Wortmann 2006; Graham, 1981). *Rhizobium*-mediated nitrogen fixation can be enhanced by increasing planting density (Graham, 1981), but there is evidence that intercropping may inhibit nitrogen fixation by increasing competition for water and soil nutrients (Graham, 1981).

Figure 6. *Rhizobium* **nodules on the roots of common bean**

57.   Planting beans in soil where they have not been grown before can also result in poor nitrogen fixation, due to insufficient *Rhizobium* in the soil to initiate nodulation (Wortmann, 2006). However, small holder farmers do not typically use *Rhizobium* inoculants prior to planting beans (Graham, 1981). In addition, the use of some pesticides, such as fungicides that are toxic to *Rhizobium*, can inhibit root nodulation.

Source: Embrapa

VI. HUMAN HEALTH

58. Information on common bean and its major products, as well as food and feed safety considerations including composition in terms of key food and feed nutrients, anti-nutrients and other constituents have been summarised by the OECD in other document issued in the Series on the Safety of Novel Foods and Feeds (OECD, 2015). Therefore, it is not included here.

APPENDIX 1.   COMMON PESTS AND PATHOGENS

59.   Common bean is susceptible to many pests and diseases, although endemic pests and diseases vary with geographic location. In combination with sub-optimal growing conditions, common in the low-input scenarios used in developing countries, pests and diseases may act synergistically to cause significant, and sometimes total, yield losses (Graham and Vance, 2003; Singh and Schwartz, 2010). The value of harvested seed is reduced due to decreased germination and poor quality (Singh and Schwartz, 2010).

1.   Pests

60.   There are several serious insect pests that attack the common bean, depending on the geographic location, but predation by a wide range of arthropods – aphids, beetles, caterpillars, leafhoppers, whiteflies, mites, and thrips – is seen worldwide (Cardona, 1989; Karel and Autrique, 1989; Quintela, 2009). Post-harvest damage from rodents is less of a problem, because uncooked dry beans are toxic to mammals (FAO, 1999). Typically, chemical pesticides are used more commonly in the commercial production setting, rather than by smallholder farmers (FAO, 1999). Table 3 summarises the main arthropods identified as potential pests for common bean.

Table 3. **Arthropod pests of common bean**

Scientific and Common Name	Types of Damage	Control Methods	Resistant Species
Storage Pests			
Zabrotes subfasciatus Mexican bean weevil	Damage to mature seed in storage	Mixing seeds with ash, sand, or lime; refrigerated storage; coating with edible oil; fumigation	*P. vulgaris*
Acanthoscelides obtectus Bean weevil, bean beetle	Damage to mature seed in storage	Mixing seeds with ash, sand, or lime; refrigerated storage; coating with edible oil; fumigation	*P. vulgaris*
Seedling-Attacking Pests			
Delia pratura Seedcorn maggot	Larvae feed on bean seeds or seedlings	Cultural practices (shallow planting in warm, moist soil) seed	*P. vulgaris*
Elasmopalpus lignosellus Lesser cornstalk borer	Larvae enter the stem just below soil surface and tunnel upwards	Heavy irrigation and proper land preparation and weed control	No good resistance
Agrotis ipsilon, Spodoptera spp. Cutworms	Larvae cut stems of young seedlings. Older plants can be damaged by stem girdling	Proper land preparation and weed control	No good resistance
Teratopactus nodicollis	Larvae cause damage at germination, emergence, and during early vegetative growth. When larvae feed on the radicle and hypocotyl, the seedlings die before emergence.	Cultural practices (proper land preparation, weed control increasing planting rate)	No good resistance
Ophiomyia phaseoli, O. specerella Bean fly, bean stem maggot	Feed on stem at seedling stage	Seed and seedling treatments with systemic insecticides	*P. vulgaris, P. coccineus*

Leaf-Feeding Pests			
Diabrotica spp., *Cerotoma* spp. Chrysomelids	Larvae damage roots and roots nodules, adults feed on foliage and are vectors of important viral diseases	Yellow traps; neem oil as antifeedant agent	No good resistance
Liriomyza spp. Leafminers	Larvae damage leaves by making serpentine tunnels while feeding on leaf palisade tissues	The insect is usually controlled by natural enemies.	No good resistance
Omiodes indicata Webworm	Larvae weave leaves together and feed on the parenchyma	The insect is usually controlled by natural enemies.	No good resistance
Urbanus proteus Bean leafroller	Larvae fold the leaf margin and feed within the fold	Chemical control is seldom required	No good resistance
Chrysodeixis (*=Pseudoplusia*) includes Soybean looper	Larvae feed on underside of the leaves, avoiding the veins of the leaves, leaving a transparent appearance on parts of the leaf	*Bacillus thuringiensis* sprays, *Trichogramma* releases	No good resistance
Helicoverpa armigera	Larvae feed on leaves and pods	*Bacillus thuringiensis* and *Baculovirus* sprays, *Trichogramma* releases	No good resistance
Epilachna varivesta, Mexican bean beetle	Adults and larvae feed on leaves. Stems and pods can also be damaged when populations are high.		*P. vulgaris*
Ootheca spp. Foliage beetles	Feed on leaves during pre-flowering period; virus vector	Crop rotation, intercropping, resistant cultivars	No good resistance
Epinotia aporema			No good resistance
Piercing and Sucking Pests			
Empoasca spp. Leafhoppers	Desiccation and necrosis of leaves; transmission of viral diseases	Intercropping with corn; *Zoophthora* spp. epizootics	*P. vulgaris*
Aphis fabae, *A. craccivora* Aphids	Sucks plant sap from leaves and stems at seedling stage and from pods; virus vector	Crop rotation, intercropping, resistant cultivars	*P. vulgaris*
Thrips palmi, *T. tabaci*, *Frankliniella occidentalis*, *F. schultzei*, *Caliothrips brasiliensis*, *Megalurothrips sjostedti* Thrips	Damage to leaves and growing tips	Crop rotation, intercropping resistant cultivars	*P. vulgaris*
Bemisia tabaci, *Trialeurodes vaporariorum* Whitefly	Adults and nymphs suck sap from leaves; main damage as virus vector	Crop rotation, intercropping, resistant cultivars	*P. vulgaris*
Polyphagotarsonemus latus, *Tetranhychus urticae* Mites	Suck sap from the lower surfaces of leaves	Insecticide sprays for egg and nymph control	No good resistance
Pod-Attacking Pests			
Apion godmani Bean pod weevil	Damage to immature pods and seeds	Bean-corn associations	*P. vulgaris*
Maruca vitrata, *Spodoptera* spp., *Etiella zinchenella* Pod borer	Larvae feed on developing seeds, and expel frass into pod	*Bacillus thuringiensis* sprays	No good resistance
Clavigralla spp. Spiny bug	Suck sap from green pods, causing premature drying	Insecticide sprays	No good resistance
Neomegalotomus simplex	Adults and nymphs suck sap from green pods	Insecticide sprays	No good resistance
Nezara viridula; *Euschistus heros*, *Piezodorus guildini*; *Thyanta perditor*, *Edessa meditabunda*, *Chinavia* spp. Stink bugs	Suck sap from developing pods, thereby shriveling pods and seeds. Cause loss of yield and reduce germination of surviving seeds	Insecticide sprays	No good resistance

Sources: Porch et al., (2013); Purseglove, (1968); Miklas et al., (2006); Sanchez-Arroyo, (2014); Wortmann, (2006); FAO, (1999); Cardona, (1989); Karel and Autrique, (1989); Quintela, (2009)

2. Diseases

61. Main fungal diseases affecting common bean are listed in Table 4 below, bacterial in Table 5 and viral diseases in Table 6 below.

2.1 Fungal diseases

Table 4. **Fungal diseases of common bean**

Name	Disease Symptoms	Control Methods	Resistant Species
Thanatephorus cucumeris Web blight	Brownish, irregular lesions on pods; under humid conditions, mycelia will cover pods	Application of fungicides, planting disease-free seed	*P. vulgaris*
Colletotrichum lindemuthianum Anthracnose	Dark brown to black lesions affecting stems, pods, and lower surfaces of leaves	Plant disease-free seed, application of fungicides, crop rotation	*P. vulgaris, P. coccineus, P. dumosus*
Sclerotinia sclerotiorum White mold	Destruction of the tissue, followed by superficial growth of white mycelia, under humid conditions. Seed transmitted disease	Application of chemical or biological pesticides, wide-row spacing, use of upright cultivars	*P. vulgaris, P. coccineus, P. dumosus, P. costaricensis,*
Phoma exigua var. *diversispora, P. exigua* var. *exigua* Ascochyta blight	Red-brown lesions on leaves, stems, pods. Can cause rapid plant death	Plant resistant varieties, plant clean seed, long crop rotations	*P. coccineus, P. dumosus*
Fusarium solani Fusarium root rot	Reddish-brown lesions on stems, lengthwise cracks that may extend down the main taproot, which decays	Good soil drainage, long crop rotations	No good resistance
Fusarium oxysporum Fusarium wilt	Yellowing and wilting of lower leaves, stunting	Plant resistant varieties	*P. vulgaris*
Rhizoctonia solani Rhizoctonia root rot	Damping off, oval, reddish-brown lesions on the hypocotyl, cankers on older stems	Fungicidal seed treatments, crop rotation	No good resistance
Uromyces phaseoli, U. appendiculatus Bean rust	Dry yellow to reddish spore masses on lower leaf surfaces and pods	Plant resistant varieties, fungicide applications	*P. vulgaris*
Phaeoisariopsis griseola Angular leaf spot	Grey to brown leaf lesions becoming necrotic; lesions may appear on stems and pods; pod lesions are oval and reddish-brown	Planting disease-free seed, fungicides, sanitation practices	*P. vulgaris, P. dumosus, P. coccineus*

Sources: Singh and Schwartz, (2010); Schwartz and Singh, (2013); Purseglove, (1968); Kelly et al., (2003); Porch et al., (2013); Schmit and Baudoin, (1992); Miklas et al. (2006)

2.2 Bacterial diseases

Table 5. **Bacterial diseases of common bean**

Name	Disease Symptoms	Control Methods	Resistant Species
Xanthomonas campestris pv. *phaseoli* or *Xanthomonas axonopodis* pv. *phaseoli* Common bean blight	Necrotic lesions on leaves, pods, and seeds; seed transmitted disease	Planting of disease-free seed, removal of disease reservoir plants in the field, and the application of copper-based bactericides	*P. vulgaris, P. acutifolius, P. coccineus*
Pseudomonas syringae pv. *phaseolicola* or *Pseudomonas savastonoi* pv. *phaseolicola* Halo blight	Brown necrotic spots surrounded by a light green halo, appearing on both leaves and stems. Infections can be systemic, and seeds may carry the disease.	Planting of disease-free seed, removal of disease reservoir plants in the field, and the application of copper-based bactericides	*P. vulgaris*
Pseudomonas syringae pv. *syringae* Bacterial brown spot	Brown lesions on both leaves and pods; seed transmitted disease	Planting of disease-free seed, removal of disease reservoir plants in the field, and the application of copper-based bactericides	*P. coccineus*

Sources: Liebenberg, (2009); Singh and Schwartz, (2010); Kelly et al., (2003); Porch et al., (2013)

2.3 Viral diseases

Table 6. **Viral diseases of common bean**

Name	Disease Symptoms	Control Methods	Resistant Species
Bean common mosaic virus Potyvirus	Mosaic mottling of the leaves; vectored by aphids; seed transmitted disease	Planting virus-free seed and using pesticides to control aphid populations	*P. vulgaris*
Bean golden mosaic virus Geminivirus	Yellow-green mosaic on leaves, stunted growth, and distorted pods. Significant losses, as high as 100%. Vectored by whitefly (*Bemisia tabaci*)	Insecticide applications to control the vector	*P. vulgaris* (low level), *P. coccineus*
Bean common mosaic necrosis virus Potyvirus	light green to yellow mosaic pattern on leaves, with puckering and rolling of the leaves	Plant resistant varieties; virus-free seed	*P. vulgaris*
Beet curly top virus Curtovirus	Strong down-cupping and puckering of leaves. Leaves are thickened and brittle and turn dark green. Plants are dwarfed. Vectored by leafhoppers	Plant resistant varieties, virus-free seed; insecticide sprays to control leafhopper vectors	*P. vulgaris*
Bean yellow mosaic virus Potyvirus	Bright yellow to green mosaic pattern on leaves, cupping and wrinkling of leaves. Vectored by aphids	Plant resistant varieties, virus-free seed, insecticide sprays to control aphid vectors	*P. vulgaris*

Sources: Singh et al., (2009); Singh and Schwartz, (2010); Miklas et al., (2006); Bonfim et al., (2007); Aragão et al., (2013); Faria et al., (2014)

APPENDIX 2.   BIOTECHNOLOGICAL DEVELOPMENTS

62.   Yield-limiting factors in common bean include insect predation, diseases, and abiotic stressors. Biotechnological approaches to address these factors are the subject of numerous ongoing research efforts. Although the transformation and successful regeneration of common bean remains challenging (Veltcheva et al., 2005; Bonfim et al., 2007), bean has been successfully transformed by treating a variety of explants with *Agrobacterium tumefaciens* and via biolistic methods (Bonfim et al., 2007; Aragão and Faria, 2009; Faria et al., 2014; Faria et al., 2010; Zhang et al., 1997; Kwapata et al, 2012).

63.   Common bean has been transformed using marker genes: *GUS* (ß-glucuronidase) (Zhang et al., 1997), *bar* (Faria et al., 2010), and *ahas* (Bonfim et al., 2007). The *bar* and *ahas* genes confer resistance to the herbicides phosphinothricin and imazapyr, respectively.

64.   Bean has also been transformed to be resistant to the bean golden mosaic virus (Faria et al., 2014; Aragão et al., 2013; Bonfim et al., 2007; Aragão and Faria, 2009). Resistance was mediated using RNA interference, and the target of interference was the AC1 viral gene, which encodes a protein responsible for virus replication (Bonfim et al., 2007). In 2011, a transgenic bean event was approved for commercial cultivation in Brazil, which is resistant to bean golden mosaic virus (Calvalho et al., 2015).

65.   Significant progress has been made on the sequencing of the bean genome, and approximately 80% of the genome has been sequenced and assembled (Schmutz et al., 2014).

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