



Review

Unraveling agronomic and genetic aspects of runner bean (*Phaseolus coccineus* L.)



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ARTICLE INFO

Article history:

Received 25 November 2016

Received in revised form 20 February 2017

Accepted 27 February 2017

Keywords:

Runner bean
Small-scale agriculture
Sustainable agriculture
Breeding

ABSTRACT

The (scarlet) runner bean (*Phaseolus coccineus* L.; $2n=2x=22$) is an allogamous legume species from Mesoamerica that is cultivated as an annual crop for dry seeds and immature green pods in several parts of the world. It is grown especially in small-scale agriculture. From an agronomic perspective, it is predominantly indeterminate and climbing type of growth is associated with high labor and materials required to grow the crop with support structures. Intercropping (i.e., maize–runner bean) and seed inoculation using bio-compounds (i.e., rhizobacteria) have resulted in more efficient resource utilization, reduced risk to the environment and diminished production costs, which are valuable practices linked to sustainable agriculture. Cold tolerance and hive management due to allogamy are also distinctive features of runner bean production that have been studied. From a genomic standpoint, runner bean has been very little studied, despite the abundant development of molecular markers and genome sequencing of other legumes in the last decade, and more specifically common bean (*P. vulgaris*). The high genetic variability of runner bean is precious for breeding purposes, particularly as a source of disease resistance and cold tolerance. However, the lack of characterization of the *P. coccineus* germplasm restricts its utilization as donor species for inter-specific hybridization, and consequently limits its use in other *Phaseolus* breeding programs (i.e., common bean). Developing more broadly adapted, determinate cultivars that facilitate mechanical harvesting, assessing the potential presence of heterosis for hybrid seed production, and characterizing the germplasm of *P. coccineus* more extensively are great challenges and opportunities in the future that would increase its cultivation on a broader scale worldwide.

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1. Introduction

The (scarlet) runner bean (*P. coccineus* L.) is probably the third-most important *Phaseolus* species worldwide, after *P. vulgaris* (common bean) and *P. lunatus* (lima bean) (Santalla et al., 2004). *P. coccineus* is a perennial species of the tropical humid uplands of Mesoamerica that can live up to 10 years, although outside this region, it is usually cultivated as an annual for dry seeds and immature green pods production because its aerial parts cannot tolerate frost (Duke, 1981; Rodiño et al., 2007). It is also grown occasionally as an ornamental because of its showy scarlet or white flowers located on long racemes extruding from the foliage, especially in climbing plants (*P. Gepts*, personal observation).

Runner bean has economic relevance only in specific parts of the world, being grown in Central America, South America, Africa and Europe (Giurcă, 2009). It is of minor importance in the United States (Mullins et al., 1999). *P. coccineus* was introduced as a crop into Europe by the Spaniards after the discovery of the Americas, probably along with *P. vulgaris* (Westphal, 1974). In the United Kingdom, the unripe pods are usually sliced longitudinally or obliquely, then boiled, and the dry beans are not consumed (Santalla et al., 2004). The importance of runner bean in the United Kingdom is due to its better adaptation to cool conditions than the common bean (Rodiño et al., 2007), which is reflected in the number of registered varieties of *P. coccineus* as compared to those of common bean (Department for Environment, Food and Rural Affairs and the Plant Variety Rights Office, 2002). In the Netherlands, young pods or dry seeds are consumed, but the crop is only grown in private gardens (Zeven et al., 1993). South Italy and Spain prefer climbing cultivars of runner beans producing white seeds (e.g., ‘Corona’; Campion and Servetti, 1991), which are grown commercially and exported on a fairly small scale. The runner bean is also grown in Argentina where it is locally known as *pallar* (a vernacular name used for traditional native *P. lunatus* in Peru) (Voyses, 1983), but Parodi (1966) did not mention it among the crops of aboriginal Argentina, letting to assume that *P. coccineus* is an historic introduction in this country. In addition, there is a small-scale production of *P. coccineus* in home gardens in Southern Chile, which relies on trellis support. As the runner bean is unable to reach total maturity in Southern Chile, the crop is harvested at the end of summer, when the plants show distinct vegetative and reproductive phases, and produce pods displaying different development stages at that time (Tay et al., 2008).

The runner bean is a source of variability for several traits for the genetic improvement of common bean (Gepts, 1981; Delgado-Salinas, 1988; Singh, 2001). This species possesses several useful agronomic and disease resistance traits such as lodging resistance due to thick stem bases, cold tolerance, long epicotyls and racemes, presence of a tuberous root system allowing a perennial cycle (Santalla et al., 2004), a potentially high number of pods per inflorescence (Vanderborght, 1983), and resistance to *Sclerotinia sclerotiorum* (Gilmore et al., 2002), *Ascochyta* blight (Schmit and Baudoin, 1992), and the resistance to root rot caused by *Pythium* or *Fusarium* (Dickson and Boettger, 1977), among others. The genetic improvement of common bean through interspecific hybridization requires, as a preliminary step, the characterization of the whole germplasm collections of the donor species in order to identify the best populations. Researchers have successfully introgressed from runner bean to common bean moderate levels of resistance for *Fusarium* root rot (Wallace, 1985), white mold (Miklas et al., 1998),

and *Xanthomonas* bacterial blight (Zapata et al., 1985; Miklas et al., 1994a, 1994b). Wilkinson (1983) suggested that *P. coccineus* could be a potential source of high yield for common bean, although the release of commercial cultivars has been very limited so far (Hucl and Scoles, 1985; Singh, 1992; Santalla et al., 2004).

The objectives of this review are to examine the current agronomic, genomic and breeding status and advances of runner bean, focusing on the main challenges and opportunities that would allow the cultivation of *P. coccineus* on a broader scale.

2. Botanical-anatomical aspects and uses of *Phaseolus coccineus*

The *Phaseolus* genus comprises over 70 species, all of them from the Americas, and five domesticated taxa, *P. vulgaris* L., *P. lunatus* L., *P. acutifolius* A. Gray., *P. coccineus* L. and *P. dumosus* Macfad., which have distinct geographical distributions, life histories and reproductive systems (Maréchal et al., 1978; Gepts, 1996; Delgado-Salinas et al., 2006). The first scientist to make crosses with runner bean (then called *Phaseolus multiflorus*) was Gregor Mendel. In Mendel's work using pea crosses, he also performed crosses with *Phaseolus vulgaris* and runner bean (Mendel, 1866). Mendel could not confirm a 3:1 ratio in flower color segregation in the interspecific cross *P. vulgaris* (or *P. nanus*) × *P. multiflorus* (synonym for *P. coccineus*), a feature that has been observed later multiple times in interspecific crosses of *Phaseolus* (Guo et al., 1994) and other species.

P. coccineus is closely related to *Phaseolus dumosus* Macfad (synonym: *P. polyanthus* Greenman; year-bean, sometimes also called runner bean) and *Phaseolus costaricensis* (Freitag and Debouck, 2002). Hybrids between *P. coccineus* and these two species have been obtained, and natural hybridization can also occur. *P. coccineus*, *P. dumosus* and *P. costaricensis* can be crossed with common bean, with the latter as female parent, without embryo rescue, although progenies are only partially viable and fertile depending on the parental combinations (Gepts, 1981; Shii et al., 1982; Singh et al., 2009). Where runner bean and common bean grow together, natural hybridization can occur (Wall, 1970; Acosta-Gallegos et al., 2007), possibly due to a close genetic relationship between *P. vulgaris* and *P. coccineus* (Smartt, 1970). Evans (1980) successfully obtained crosses between *P. vulgaris* and wild *P. coccineus* in both sexual directions. Moreover, Bassiri and Adams (1978) suggested that not only wild *P. vulgaris* contributed to the diversity and evolution of common bean in Central America but also wild *P. coccineus*. A similar suggestion was made by Liot and Hammer (1989). However, there is loss of viability and fertility in these crosses and the lack of transmission of some traits from *P. coccineus* to *P. vulgaris* has also been reported (Lamprecht, 1948a; Guo et al., 1994; Pathania et al., 2014). In addition, the formation of abnormal embryos in reciprocal crosses of these two species was the primary crossing barrier between them when *P. coccineus* was the female parent (Shii et al., 1982). In other reciprocal crosses using *P. coccineus* as the female parent, segregants naturally reverted to the cytoplasm donor parent (*P. vulgaris*) after a few generations (Baudoin et al., 1995). Ferwerda and Basset (2000) described the inheritance of two F₁ abnormalities in *P. vulgaris* × *P. coccineus* crosses: the “blocked cotyledon lethal” (BCL) and the crinkled leaf dwarf (CLD), both of which depend on the parental genotypic combination. The BCL trait is a seedling-lethal condition, whereas the CLD phenotype is sub-lethal, but not

entirely sterile, which allows genetic analysis through selfing and backcrossing. Crossing results showed that interspecific hybrids were generally sterile at temperatures above 26 °C. At lower temperatures, the degree of interspecific F₁ sterility depended on the parental combination (as observed by Gepts (1981) already). The BCL, CLD, and DL (a crossing barrier between Andean and Mesoamerican domesticates in common bean) appeared to be independent.

Runner bean has a tuberized taproot, rich in starch, with nodosities and vegetative buds in the zone of neck. The 2–7 m stem is high, vigorous and slightly twisted, which fits properly to guidance with poles (León, 2000). Leaves are trifoliate, with oval folioles, acuminate to their peak and round at the base. The inflorescence is a multi-flowered raceme of racemes longer than the leaves, 25–35 cm long, with red, white, pink, bicolored flowers, and allogamous (Escalante et al., 1994). The flowers are visited by bumblebees, carpenter bees and hummingbirds (Búrquez and Sarukhan, 1980). The fruit is linear oblong to oblong, and up to 40 cm long flattened pods. Seeds are large, of 20–25 mm long, 13–14 mm wide and 8 mm thick on average. They have different colors: white, black, beige, purple and mixed. The 1000-grain weight is between 1000 and 1400 g. Cotyledon emergence is hypogeal (Giurcă, 2009). The main chemical components of the mature grains from this species are approximately 20% protein, 63% carbohydrates, 1.5% fats, 5% fibers and 3.5% ashes (Kay, 1979).

With regard to the uses of *P. coccineus*, the immature and mature seeds are consumed in Central America, elsewhere mainly the mature seed (i.e., in Ethiopia), excluding certain parts of Europe. Preparation is predominantly by boiling. In temperate regions the immature pods are most commonly eaten, sliced and cooked, as a vegetable (Smartt, 1989). In Central America the young shoots, leaves and inflorescences are sometimes used (boiled or boiled and fried) as a vegetable while the tuberous roots are consumed boiled or chewed as candy (Tindall, 1983). A root decoction is taken against malaria or applied to swollen eyes. In Central America, runner bean is grazed by livestock and dried into hay. It is also grown as an ornamental (Tindall, 1983; Smartt, 1989, 1990).

3. Germplasm collections

There are some 4685 accessions approximately of *P. coccineus* reported in the world (Genesys, 2016). The Germplasm Bank and Genetic Resources Program of the International Center for Tropical Agriculture (CIAT) in Cali, Colombia, preserves the largest and more diverse collection of beans in the world, with more than 36,000 accessions of *Phaseolus* spp. to date, corresponding to 44 taxa from 110 countries, and contains around 958 accessions of *P. coccineus* (CIAT, 2015). The European Cooperative Program for Plant Genetic Resources maintained by the Austrian Agency for Health and Food Safety in Linz, Austria maintains 2674 accessions (www.genbank.at/en/ecpgr-phaseolus.html). The Agricultural Institute of Slovenia (AISLJ) conserves 995 accessions of runner bean (Normah et al., 2012). In parallel, the Mexican collection of *P. coccineus* possesses 798 accessions and it is preserved by one national germplasm bank of INIFAP (Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias) located in Chapingo, Mexico (Vargas et al., 2014). Other institutions that preserve *P. coccineus* are the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK) in Germany (439 accessions), the United States Department of Agriculture (USDA) (374 accessions), as well as others germplasm banks in Europe and South America (Normah et al., 2012). Most of these materials remain largely uncharacterized, with some exceptions, particularly involving the European materials (Santalla et al., 2004; Rodiño et al., 2007; Rodríguez et al., 2013).

4. Agronomic features of *Phaseolus coccineus*

4.1. Management

To obtain high-quality pods, runner bean is grown on trellises, poles, fence lines, plants (e.g., maize) or other support structures (Brink and Belay, 2006). However, labor and material requirements are high and may impede cultivation (Campion, 1995; Brink and Belay, 2006). Runner bean climbing (indeterminate) types can yield without support if leading shoots are pinched out to induce bushy growth. Lapinskas and Evans (1977) provided information about Hammond's Dwarf, a determinate mutant found in 1958 in England. In keeping with this, determinacy can also be obtained by the development of dwarf cultivars as in Italy, which has facilitated mechanical harvesting (Campion and Servetti, 1991). In Chile, three runner bean ecotypes were evaluated with and without trellis support; the seed production without support was up to 3.4 t/ha, yielding slightly less than common bean and runner bean with trellis support (Tay et al., 2011). These authors concluded that the more economic seeding rate was 153 kg/ha, and recommended spacing of 20 cm intra-row and 60 cm inter-row at sowing (equivalent to 83,300 plants/ha), which is lower than the 100,000 plants/ha sown in Mexico to maximize yields (Vargas and Irizar, 2005).

4.2. Intercropping

Intercropping has been practiced traditionally in many parts of the world (Karadag, 2004; Armstrong et al., 2008). One of its advantages may be to increase forage protein and quality through the complementary effects of two or more crops grown simultaneously on the same area of land (Anil et al., 2000). Intercropping provides efficient resource utilization, reduces risk to the environment and production costs, and assures greater financial stability, making the system more suitable particularly for labor-intensive, small-holder farmers (Anil et al., 1998). Contreras-Govea et al. (2009) showed that the addition of three different climbing beans (including *P. coccineus*) to maize increased crude protein but also had an effect on fiber concentration and fermentation profile. However, the nutritive value of maize-bean silage was similar to maize silage, indicating that maize-bean silage mixtures could be used in dairy cow rations. Another study examined nine forage legume species (including runner bean) grown in mixture with maize plants in Wisconsin, in the United States (Riday and Albrecht, 2008). Plants were evaluated by these authors for growth throughout the growing season, harvest forage, dry matter content, total dry matter yield and forage mixture components. Of the forage legumes tested, runner bean, common bean, lablab, sunn hemp and velvet bean were the most successfully intercropped with maize, and grain yields were inversely proportional to the amount of legume present. In Turkey, all of the runner bean-maize mixtures tested provided good silage and high crude protein concentrations. Even though forage yields decreased, the land equivalent ratio (LER) index linearly increased as the percentage of runner bean increased in the mixture up to a 50:50 seeding ratio, which indicates a greater utilization of land (Bildirici et al., 2009). In India, an intercropping maize with runner bean at 2:2 row ratio achieved the maximum maize-equivalent yield (63.69 q/ha), production efficiency (217.5%), LER (1.35), and several economic return and energy-use efficiency indicators over maize and runner bean grown separately, and appeared to be most productive and economically and energetically viable system, followed by maize + cowpea at 1:1 row ratio (Padhi, 2001). According to this author, this runner bean-maize system increased the total production in terms of maize-equivalent yield by 114.5% over normally sown sole maize.

4.3. Seed health

The importance of seed as vehicle for fungal diseases affecting germination and plant growth has been widely studied, in the same way fungal microbiota from common bean has been studied by different groups (Tello et al., 1990; Ruiz et al., 1996; Andrés-Ares et al., 2006). *Alternaria*, *Fusarium*, *Botrytis* and *Rhizoctonia* are some of the important reported genera that damage the crop (Boland and Hunter, 1988; Tseng et al., 1995; Andrés-Ares et al., 2006), among others. Furthermore, the ability of certain fungal genera such as *Alternaria* (Tietjen et al., 1983) or *Aspergillus* (Hagler et al., 1987) of frequent occurrence in *Phaseolus* seeds, to produce mycotoxins and secondary metabolites is relevant because runner bean seeds are aimed at consumption or processing. Consequently, obtaining seeds of the best possible biological properties is an important task in the cultivation technology of the species (Labuda, 2010), particularly in sustainable agricultural managements, including organic systems. Scarce references to *P.* seed fungal microbiota had been reported until recently (Palmero et al., 2011), although there are references to works where *P. coccineus* is included in breeding programs within common beans as a source of resistance to anthracnose (*Colletotrichum lindemuthianum*) (Schmit and Baudoin, 1992) or against the bean yellow mosaic virus (BYMV) (González, 2000; Osorno et al., 2007).

4.4. Seed inoculation

Given the negative environmental impacts of chemical fertilizers and their increasing costs, the use of plant-growth-promoting rhizobacteria (PGPR) is advantageous in sustainable agricultural systems (Chen et al., 2006). Use of bio-fertilizers containing beneficial microorganisms instead of synthetic chemical products is known to improve plant growth through supply of plant nutrients and may help to sustain environmental health and soil productivity (O'Connell, 1992). Stefan et al. (2013) showed that runner bean seed inoculation with two rhizobacterial strains (i.e., S4 and S7 strains) resulted in an increase of photosynthetic activities, water-use efficiency and chlorophyll content, leading to a significant grain yield increase of 28% relative to non-inoculated seeds when both strains were applied, suggesting a synergistic effect of them. Another study revealed the impact of pre-sowing seed dressing with a bio-preparation of chitosan and a chemical preparation of carboxin + tiuram on the healthiness of *P. coccineus* (Patkowska, 2009). Both products significantly increased the populations of *Bacillus* spp. and *Pseudomonas* spp. in the rhizosphere of runner bean relative to the control while the fungi detrimental populations decreased (i.e., *Alternaria alternata*, *Botrytis cinerea*, *Fusarium* spp., *Pythium irregulare*, *Rhizoctonia solani*, *Sclerotinia sclerotiorum*, among others).

4.5. Insect pollination

Runner bean, in contrast to common bean, undergoes outcrossing in the reproductive stage; thus, the presence of pollinating insects positively affects early pod setting and yields, using both green pod cultivars and those used for dry seeds (Labuda, 2010). *P. coccineus* is mainly pollinated by honeybees (*Apis mellifera* L.) and bumblebees (*Bombus* spp.) (Campion, 1995; Labuda, 2010). Quagliotti and Marletto (1987) concluded that honeybee is the main species of economic importance in the pollination of runner bean, suggesting a proper hive management for the economic success of the crop when it is grown commercially. However, bumblebees or carpenter bees may be more effective cross-pollinators, because of their heavier body weight resting on the left wing petal

causes stronger extrusion of the style and stigma outside the keel petal during flower visits.

4.6. Harvesting

Green pods of runner bean are harvested when pod length reaches its maximum length, before the phase of rapid seed development. Picking is usually at 4–5 day intervals. For dry seed production, plants are pulled or cut when most pods are dry and then allowed to dry for a few days, followed by threshing. Alternatively, pods may be handpicked in several rounds because of asynchronous flowering and ripening (Brink and Belay, 2006).

5. Domestication and genetic diversity

The runner bean is a diploid ($2n=2x=22$), perennial species native to Mexico, Guatemala and Honduras (Delgado-Salinas, 1988). Three botanical varieties have been described for *P. coccineus*: var. *albiflorus* (DC.) Bailey (white-flowered and white seeded type), var. *coccineus* (red-flowered type) and var. *bicolor* (Velloso) Van Eselt. (white and red flowered type) (Delgado-Salinas, 1988).

The knowledge about the domestication process of *P. coccineus* is still incomplete. The first records of wild *P. coccineus* used for human consumption have been dated as over 7000 years old in Ocampo, Mexico (Smartt, 1990), whereas the domesticated form have been dated more recently, around 2000 years B.P. in Tehuacán and Puebla, Mexico (Vargas et al., 2012). Debouck and Smartt (1995) reported that the specific areas where the domestication occurred need to be elucidated yet. However, recent bio-geographic research using cpSSR and nuSSR suggests the occurrence of multiple domestication events in Mesoamerica (Angioi et al., 2009; Spataro et al., 2011; Rodriguez et al., 2013).

The modern history of this species is related to the discovery of America. It is believed that it was introduced into Spain by the Spanish conquerors and it quickly spread throughout Europe because of its adaptation to lower temperatures (Spataro et al., 2011; Rodriguez et al., 2013). Rodriguez et al. (2013) concluded that the European accessions suffered a moderate bottleneck after the Spanish introduction into Europe; they became clearly differentiated from the Mesoamerican wild forms and landraces due to the domestication and dissemination processes.

There is scarce information about the genetic structure of the wild and the cultivated accessions of runner bean. Spataro et al. (2011) determined that Mesoamerican wild and landraces accessions maintain high but similar levels of genetic variability ($A=7.0$; $H_o=0.14-0.16$; $H_e=0.5-0.54$; Table 1). In parallel, European accessions show lower genetic variability ($A=4.4-6.0$; $H_o=0.12-0.31$; $H_e=0.36-0.43$; Spataro et al., 2011; Mercati et al., 2015) than the Mesoamerican materials. In this context, the domestication process has not eroded the genetic variation. This is concordant with previous studies using isozymes, where the genetic variation was similar between wild and cultivated materials, which could be due to high gene flow between the two forms (Escalante et al., 1994). Recent research using a global accessions sample of *P. coccineus* suggests that the current structure of the genetic variation was probably generated by the effects of human selection, rapid adaptation to the new growing conditions, and/or demographic phenomena, such as bottlenecks and founder effects (Sicard et al., 2005; Spataro et al., 2011; Rodriguez et al., 2013).

At the interspecific level (Table 1), the observed heterozygosity of *P. coccineus* ($H_o=0.12-0.31$) is superior to those reported for *P. vulgaris* ($H_o=0.008-0.10$) and *P. lunatus* ($H_o=0.01$). The breeding system plays a fundamental role in the organization of the genetic diversity of these species. According to Escalante et al. (1994) and González et al. (2014), *P. coccineus* displays a mixed mating system

Table 1
Microsatellite (SSR) genetic diversity of the three most important cultivated *Phaseolus* species, in which N = number of accession per species, L = loci number, A = allele number, H_o = observed heterozygosity, H_e = expected heterozygosity, F = Fixation index or homozygosity, s = selfing rate and t = outcrossing rate.

	N	L	A	H_o	H_e	F	s	t
<i>P. coccineus</i>								
Europe	148 ^g	12	4.4	0.12	0.36	0.68	0.81	0.19
Mesoameric LR	52	12	7.0	0.14	0.54	0.74	0.85	0.15
Mesoameric WF	28	12	7.0	0.16	0.50	0.69	0.82	0.18
Italy								
Lazio (Fagiolone)	200 ^h	14	6	0.31	0.43	0.28	0.44	0.56
Central and Southern	140	14	5.7	0.29	0.39	0.26	0.41	0.59
<i>P. vulgaris</i>								
	246 ^a	26	5.4	0.02	0.47	0.95	0.97	0.03
	85 ^b	10	6.9	0.008	0.62	0.99	0.99	0.01
	104 ^c	36	13	0.09	0.66	0.86	0.92	0.08
	114 ^d	24	8.3	0.03	0.64	0.95	0.97	0.03
	146 ^f	10	7.8	0.10	0.50	0.80	0.89	0.11
<i>P. lunatus</i>	359 ^e	9	1.65	0.01	0.14	0.91	0.95	0.05

^a Becerra et al., 2010.

^b Buso et al., 2006.

^c Blair et al., 2012.

^d Cardoso et al., 2014.

^e Ouédraogo, 2003.

^f Raggi et al., 2013.

^g Spataro et al., 2011.

^h Mercati et al., 2015.

Fixation index (F) = $1 - (H_o/H_e)$; selfing rate (s) = $2F/1 + F$; outcrossing rate (t) = $1 - s$ (Crow and Kimura, 1970)
LR = Landrace; WF = Wild Form.

between selfing and outcrossing, while *P. vulgaris* and *P. lunatus* are mainly autogamous species. Consequently, *P. coccineus* shows lower levels of homozygosity (F [fixation index] = 0.26–0.74) and selfing rate (s = 0.41–0.85) compared to *P. vulgaris* (F = 0.80–0.99; s = 0.89–0.99) and *P. lunatus* (F = 0.91; s = 0.95). In contrast, the outcrossing rates (t) were superior for *P. coccineus* (t = 0.15–0.59) than *P. vulgaris* (t = 0.01–0.11) and *P. lunatus* (t = 0.05).

In one global study, which included different plant species (selfing, mixed and outcrossing), Nybom (2004) reported that mixed breeding species (up to 15 species studied) and selfing (up to 15 species studied) species showed F values ranging between 0.26 and 0.88, respectively, s (selfing) values between 0.15 and 0.94, respectively, and t (outcrossing) values between 0.85 and 0.06, respectively. Based on this study, runner bean could be considered an intermediate case between mixed breeding system and selfing reproductive biology.

The runner bean has been considered as a predominantly allogamous species because some biological characteristics of its flowers. *P. coccineus* displays bright red flowers, different to most other *Phaseolus* species that have white, pale blue and pink flowers (Duke, 1981), which are less attractive to insect pollinators, explaining partially the outcrossing nature of *P. coccineus* relative to *P. vulgaris*. Sousa-Peña et al. (1996) showed that there is a different reflectance under ultraviolet light between the wings and the terminal coil of the keel, displaying a contrasting topography for a landing bumblebee while for the human eye the facing corolla will simply appear as uniform scarlet red. An important feature of *P. coccineus* is the presence of an active discoid nectary at the floral disk or flower receptacle (Webster et al., 1980), which is a shared trait

by all members of section Phaseoli of the genus. In addition, runner bean flowers have several anatomical features that favor outcrossing or limit selfing, including an extrorse stigma located at the tip of the style (instead of both terminally and laterally on the style as in common bean). The stigma is also located above the anthers (instead of the same height as in common bean) and is surrounded by hairs oriented downwards, limiting the landing of pollen grains shed by anthers on top of the stigma (Webster et al., 1980). In addition, the *P. coccineus* flowers secrete abundant pollen and nectar with 35–45% of sugar concentration, which is very attractive for insects such as honeybees and bumblebees favoring the pollen flow (Kotowski, 2004).

6. Genome sequencing and functional genomics

There are currently six legume species that have been entirely sequenced (with completed and annotated genomes, Table 2): *Cajanus cajan* (833 Mb genome), *Cicer arietinum* (738 Mb; Varshney et al., 2013), *Glycine max* (1112 Mb; Schmutz et al., 2014), *Lotus japonicus* (472 Mb), *Medicago truncatula* (373 Mb) and *Phaseolus vulgaris* (588 Mbp). The estimated amount of genes and transcripts in these species ranges between 28,269 and 48,680 and 25,640 and 243,067, respectively. There are ongoing or additional genome sequencing efforts in *Phaseolus vulgaris* (587 Mb genome), *Pisum sativum* (4450 Mb), *Lupinus angustifolius* (924 Mb), *Trifolium praetense* (440 Mb), and *Arachis hypogaea* (2800 Mb) (Smýkal et al., 2015). Regarding the *Phaseolus* genus, an Andean landrace of the common bean has been sequenced (G19833; Schmutz et al., 2014). A Mesoamerican breeding line has also been sequenced (BAT93;

Table 2
Genetic information of the six fully-sequenced genomes to date of different legume species plus *Phaseolus vulgaris* (www.phytozome.net; www.comparative-legume.net; McClean et al., 2004; Varshney et al., 2013; O'Rourke et al., 2014; Schmutz et al., 2014; Wu et al., 2014; Smýkal et al., 2015).

Species	Chromosome number	Genomesize (Mbp)	Protein-coding loci	Transcripts
<i>Phaseolus vulgaris</i>	22	587	27,197	31,638
<i>Glycine max</i>	40	1112	54,175	73,320
<i>Cicer arietinum</i>	16	738	28,269	46,064
<i>Medicago truncatula</i>	16	373	44,135	45,888
<i>Lotus japonicus</i>	12	472	30,799	243,067
<i>Cajanus cajan</i>	22	833	48,680	25,640

Vlasova et al., 2016). Third, a Mesoamerican variety introgressed with *P. acutifolius* to transfer bacterial blight resistance has also been sequenced (OAC Rex; Applied Bean Genomics, 2016). This valuable information will serve as reference in the future for sequencing new legume species such as runner and lima beans so that comparative genomic studies can be performed between these species.

Next-Generation Sequencing technology coupled to genetic mapping and synteny approaches are powerful methodologies to identify functional SNPs and Indels associated to agronomically important traits. A database has been developed that presents both legacy and genomics-based markers (e.g., SSRs, SNPs and indels) in *Phaseolus*, primarily common bean (PhaseolusGenes, 2016). These new tools will be useful to assist breeding programs of *Phaseolus* species. Highly saturated mapping is an important tool to discover genes and polymorphisms with the objective to understand the genetic basis of valuable agronomic and nutritional traits, and to accelerate the advances of the breeding programs through marker-assisted selection (MAS). Galeano et al. (2011) reported a consensus genetic map for legumes using SSR, SNPs and gene-based markers. In this study, more than a thousand markers were mapped in the consensus map, spanning over 2041 cM and 11 linkage groups (<http://abccmap.bioinformatics.ucdavis.edu/cgi-bin/cmap/>). Also, high levels of synteny were reported between *P. vulgaris* and *Glycine max* (i.e., 44 syntenic blocks), which will be useful for comparative genomic and genome selection studies in *Phaseolus* species (McConnell et al., 2010; McClean et al., 2010).

7. Genetic improvement

The knowledge of homozygosity levels and outcrossing rates are relevant to develop proper genetic improvement strategies for *P. coccineus*. For example, the mating behavior will define whether to develop new cultivars as pure lines or hybrids. In this regard, González et al. (2014) reached around 90% of homozygosity after five generations of selfing without apparent inbreeding depression. Moreover, they were able to produce a uniform population of progeny and acceptable agronomic performance using inbreds in their study.

Another strategy for genetic improvement of *P. coccineus* is the interspecific hybridization. Although *P. coccineus* and *P. vulgaris* have important differences on their mating systems, they are somewhat cross-fertile, especially when *P. vulgaris* is employed as maternal parent (Singh, 2001). The actual level of viability and fertility of *P. vulgaris* x *P. coccineus* depends strongly on the parental genotype combination. Thus, if a *P. coccineus* accession has been identified, which harbors a trait of interest, this accession has to be crossed with multiple and diverse *P. vulgaris* accessions to identify empirically which parental combination will be more viable and fertile and, thus, facilitate the introgression of novel traits into common bean (Gepts, 1981).

Furthermore, mapping of the genes controlling traits of interest in the *P. coccineus* genome should also be actively pursued. Such mapping may facilitate genetic improvement of *P. coccineus* per se, but also help design introgression program into *P. vulgaris*. Under these circumstances, the runner bean could also be a useful source of biotic and abiotic diversity (i.e., disease resistance and cold tolerance, respectively), valuable for *P. vulgaris* breeding programs (Singh and Schwartz, 2010).

Nevertheless, as observed by Mendel (1866) but also Lamprecht (1948a,b), Smartt (1970), and Wall (1970), the mating system (e.g., reciprocal crosses and selfing and backcross generations) will influence the easiness and extent of introgression of traits into *P. vulgaris*. Several authors have also observed that certain traits such as the scarlet flower color, the extrorse stigma, and the hypogeal

germination are linked to lack of viability and fertility factors, which prevent their introgression into common bean (Lamprecht, 1948a; Smartt, 1970; P. Gepts, personal observation). Mapping of these viability and fertility factors relative to genes for agronomic traits will also assist in introgression breeding.

The breeding strategies utilized for genetic improvement in common bean include phenotypic selection of parental lines, recurrent or congruity backcrossing, pedigree selection, single-seed descent and bulking, plus variations of these strategies (Kalloo, 1993; Anderson et al., 1996; Singh, 2001). All of these methods introduce genetic variability by hybridization followed by backcrossing or selfing, plus selection for at least six generations to recover the natural homozygosity of this species ($F=98.44\%$) (Singh, 2001). Because runner beans are able to reach high levels of homozygosity through backcrossing and selfing without suffering severe inbreeding depression (González et al., 2014), the breeding strategies used for the genetic improvement of common beans can also be applied to runner beans. However, there are no studies to our knowledge that evaluate the levels of heterosis of runner beans. In case hybrid vigor of this species is moderate to high, this could be relevant to potentially produce hybrids in breeding programs of *P. coccineus* that would benefit growers.

As previously noted, one important characteristic valuable in runner beans is cold tolerance. Rodiño et al. (2007) reported lower temperature requirements for seed germination and plant growth of *P. coccineus*, enabling cultivation under cooler environmental conditions as required by *P. vulgaris*, leading to agronomic differences between both species and the possibility to conduct early sowings, as in the case of England (i.e., April) (Hardwick, 1972). In addition, Rodiño et al. (2007) identified seven cultivars of *P. coccineus* that showed great ability to emerge and grow under cool conditions, which could be used in interspecific hybridization with the common bean as a source for cold tolerance.

8. Future trends and conclusions

The agronomic developments of runner bean have mainly focused on small growers due to the indeterminate type of growth of a high proportion of its germplasm. This focus, however, has resulted in an important amount of labor and materials required to grow the crop using support structures. The advances that would benefit bigger-scale growers rely on the creation of bush cultivars (determinate or indeterminate), which would facilitate mechanical harvesting leading to reduced labor, as in Italy. The determinacy trait has been identified in *P. coccineus*, which may have an agronomic significance because of the reduced plant biomass and the earliness associated with this trait relative to the indeterminate genotypes. More research needs to be carried out to determine the specific recommended populations and the convenience of utilizing support structures. Other agronomic practices such as fertilization, irrigation and crop protection need to be further studied since most of the current recommendations are derived from common bean and, consequently, not specific to runner bean. One sustainable component of growing runner bean is using bio-compounds containing beneficial microorganisms through seed inoculation. For example, the application of different rhizobacterial strains (PGPR) and other bio-compounds to runner bean seeds have resulted in increased yields and reductions of detrimental soil diseases. Other particularities of runner bean are its low temperature tolerance and the need to conduct proper hive management due to its allogamy to maximize yields.

Until recently, a very limited number of genomic resources were available in most of the legumes. Over the last decade, several tools of genomic resources have been developed. Molecular marker technologies, however, are currently experiencing a tran-

sition from largely serial technologies based on separating DNA fragments according to their size (SSR and AFLP) to highly parallel, hybridization-based methods that can simultaneously assay hundreds to tens of thousands of variations, particularly in genes. In addition, with completed and annotated genomes of model legumes and some grain legume crops, and the ongoing genome sequencing efforts in other legume crops, there is strong potential for comparative genomics and its applications, including specific gene/allele mining and deeper diversity studies of legume germplasm collections. From a genomic perspective, however, runner bean has been very little studied.

The runner bean could be considered an intermediate case between mixed breeding system and selfing reproductive biology. Self-fertilization is reported in an increasing number of plants (Goodwillie et al., 2005) and support predictions that despite the potential for reduced fitness of progeny due to severe inbreeding depression, selfing is likely to be an important mode of reproduction of *P. coccineus*.

The genetic improvement of common bean through interspecific hybridization requires, as a preliminary step, the characterization of the whole germplasm collections of the donor species (i.e., runner bean) to identify the best populations and how these materials could be potentially used in common bean-breeding programs. This article highlighted the sources of genetic variability of runner bean that would be very useful and valuable for breeding purposes, considering that the European materials have been more characterized, but are less diverse than the Mesoamerican genotypes. In this context, runner bean is an important source of disease resistance, cold tolerance, lodging resistance and a perennial cycle, among others, which could be useful traits to improve common beans and other *Phaseolus* species breeding programs. However, despite the great potential of runner bean for breeding purposes, germplasm has not been sufficiently evaluated and used to the development of interspecific breeding lines. Two main challenges for the future will be the maintenance and seed multiplication in gene banks, while maintaining accession identity, and the phenotypic and genotypic characterizations of these runner bean accessions, exploiting the high genetic variability of the species and the possibility to conduct comparative genomics among *Phaseolus* species so that the identified traits/genes can benefit the growers and the consumers through the different breeding programs worldwide. One incentive to undertake all the agronomic and genetic studies is to take advantage of the high price of runner beans as an export crop for European markets. Finally, studies about the potential presence of heterosis in runner beans would favor the production of hybrids, which would in turn benefit the growers in terms of earliness, uniformity, disease resistance and higher yields of the crop.

Acknowledgments

The authors thank the Innovation Fund for Competitiveness of the Region of O'Higgins, Chile, FIC-R-2014, code 30343832-0, involving the project "Innovation and transfer to improve the cultivation of legumes in the O'Higgins Region" (2014–2017), for funding.

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