The Domestication Syndrome in *Phaseolus* Crop Plants: A Review of Two Key Domestication Traits

María Isabel Chacón-Sánchez

Abstract Plant domestication can be seen as a long-term experiment that involves a complex interplay among demographic processes and evolutionary forces. Long-standing questions about plant domestication are the number of times a species was domesticated, the extent of the domestication bottleneck, and the genetic basis of adaptive processes. Crops such as *Phaseolus* beans offer an excellent opportunity to answer these questions, especially the ones related to the genetic basis of the adaptive domestication syndrome. In the genus *Phaseolus*, five species have been domesticated: the common bean (*P. vulgaris*), the runner bean (*P. coccineus*), the tepary bean (*P. acutifolius*), the year bean (*P. dumosus*) and the Lima bean (*P. Lunatus*). These five species were domesticated in seven independent events that resulted in phenotypic convergence for several traits of the domestication syndrome. Two of these traits, namely reduced pod shattering and increased seed weight, are of special interest due to their role in the initial adaptation of these species during domestication. The objective of the present study was to review current evidence about (1) the effects of domestication on phenotypic variation of these two domestication traits in *Phaseolus* beans to understand whether adaptation led to clear-cut differences among wild and domestic forms or to a phenotypic continuum, and (2) the genetic basis of these two traits in *Phaseolus* beans to understand whether phenotypic convergence has been driven by parallel or convergent evolution. Research on these subjects in *Phaseolus* beans has been very scarce, and areas in need of urgent development are highlighted in this review.

1 Introduction

Domestication may be considered a dynamic and continuous process that began when humans started to exploit, manage, and/or deliberately cultivate wild populations (Pickersgill 2007). With time, cultivated populations diverged from their

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P. Pontarotti (ed.), *Origin and Evolution of Biodiversity*,
https://doi.org/10.1007/978-3-319-95954-2_3

wild ancestors and became better adapted to agro-ecological environments and more dependent on humans for their own survival (Meyer and Purugganan 2013). Many of the genetic modifications underlying the adaptation process have led to a set of phenotypic changes of all kind (morphological, physiological, etc.) between domesticated species and their wild ancestors, which are collectively known as the domestication syndrome. Sometimes, these differences are not clear-cut, but rather a phenotypic continuum is observed among crop and wild progenitors, which makes it difficult to distinguish between traits that were crucial for the domestication episode (e.g., loss of seed dispersal mechanisms and reduced seed dormancy) and traits that evolved after domestication during landrace diversification (e.g., changes in seed color) (Abbo et al. 2014).

The genus *Phaseolus* contains five domesticated bean species, namely *Phaseolus vulgaris* L., *Phaseolus coccineus* L., *Phaseolus acutifolius* A. Gray, *Phaseolus dumosus* Macfady, and *Phaseolus lunatus* L. These five domesticated *Phaseolus* species offer the opportunity to investigate traits of the domestication syndrome and their genetic bases. For these five crop species, similar morphological changes have been observed for several traits of the domestication syndrome. For legume species, reduced pod shattering, increased seed germination, and increase in seed size are among the most important traits that allowed adaptation of domesticated populations (Harlan 1992); other traits are changes in growth habit and photoperiod sensitivity. In spite of the importance of these traits in legume domestication, not only from an evolutionary perspective but also for practical applications in crop production, very little is known about their genetic control, as noted by Dong and Wang (2015).

The objective of the present study is to review the evidence available for two domestication traits, namely pod shattering and seed size, in *Phaseolus* crop species, in order to gain insights into the magnitude of phenotypic changes associated with domestication and their genetic control. I will first review current evidence about domestication areas for these five *Phaseolus* species to establish how many independent domestication events were involved in the origin of *Phaseolus* crop species. Then, information available on phenotypic evaluations of these two key domestication traits in wild and domestic forms in *Phaseolus* beans will be reviewed. I finalize with a review of the information available on the genetic control of these two key domestication traits to establish whether or not there is evidence in the literature that support common genetic basis for these traits. This review is expected to stimulate further research into these matters.

2 Domestication Areas of *Phaseolus* Beans

Pinpointing crop domestication areas requires an interdisciplinary approach based on sources of evidence from fields such as archaeology, botany, and genetics. Plant remains that have been retrieved in archaeological sites, mainly in the form of carbonized remains, imprints of part plants on pottery, or plant remains preserved by desiccation in arid areas, provide information about where the earliest cultivation

activities for a crop occurred, the spread of a crop to other areas, and how early cultigens looked like (Zohary and Hopf 2000). However, archaeological evidence does not necessarily offer information on the wild progenitors from which domesticated plants derived, and comparisons of domesticated plants with their wild progenitors are key to understand the kind of changes (morphological, physiological, and genetic) that occurred during domestication.

Identification of domestication areas requires understanding of the genetic structure of the wild progenitor, along its range of distribution, and also of its domesticated counterpart. Areas of domestication are usually pinpointed by identifying the wild populations that are most closely related to the cultivated varieties. The reasoning behind this, as noted by Zohary and Hopf (2000), is that domestication is a very recent event (10,000 years ago) compared to evolutionary times of wild relatives. Therefore, most of genetic variations present in cultivated varieties have been mainly inherited from their wild progenitors. This means that establishing the genetic relationships among wild relatives and domesticated populations may reveal the wild stocks from which domesticated varieties arose, thus the domestication areas. This approach assumes that extant wild relatives have not appreciably changed in their genetic constitution and geographic distribution since the time of domestication. Advances in molecular marker technology have allowed, in many cases, delimitation of domestication areas when traditional approaches have not been successful. Below, I provide a summary of current knowledge on areas of domestication for the five *Phaseolus* crop species that is mainly based on molecular markers.

P. vulgaris, the common bean, occurs in its wild form from Northern Mexico to northern Argentina, where three gene pools have been recognized: the Mesoamerican, the Andean, and the Ecuadorian–Northern Peruvian one (Debouck et al. 1993; Gepts and Debouck 1991; Kwak and Gepts 2009). Common bean was domesticated at least twice: once from wild Mesoamerican populations and once from wild populations in the Andes of South America (Chacón et al. 2005; Gepts and Bliss 1986; Gepts and Debouck 1991; Kwak and Gepts 2009; Kwak et al. 2009; Nanni et al. 2011). For Mesoamerica, Kwak et al. (2009) proposed the Lerma-Santiago Basin in the state of Jalisco, Mexico, as the putative domestication area of Mesoamerican landraces based on data on 26 microsatellite loci (Fig. 1a). The evidence was based on the fact that all Mesoamerican varieties clustered in a single group, thus indicating a single domestication, and also that the wild populations most closely related to the domesticated cluster where those distributed on Rio Lerma-Rio Grande de Santiago Basin, in western-central Mexico. In contrast, Bitocchi et al. (2012) on the basis of sequencing of five DNA fragments concluded that common bean was domesticated in Oaxaca Valley in Mexico (Fig. 1a). This conclusion was reached on the basis of a close genetic relationship observed between two wild accessions from Oaxaca to a cluster formed by most of Mesoamerican domesticated accessions analyzed. For the Andean gene pool, Beebe et al. (2001) and Bitocchi et al. (2012), on the basis of AFLP and DNA sequence markers, respectively, proposed Bolivia–northern Argentina as a possible area of domestication for Andean landraces (Fig. 1a). These two studies found a close genetic relationship between wild accessions from this geographical region and Andean landraces. In contrast, Chacón et al. (2005) on

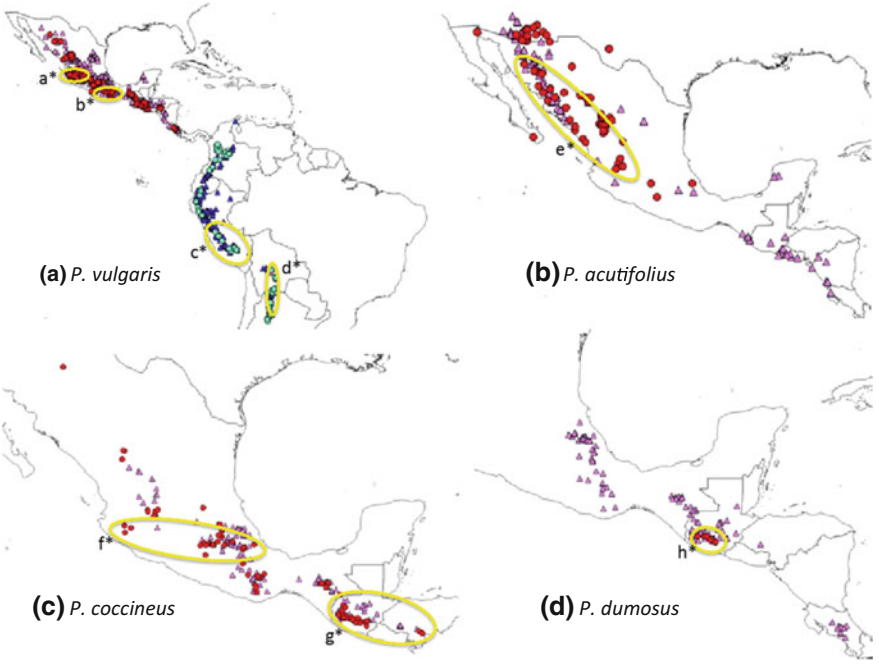

Fig. 1 Geographic distribution of wild relatives (red or light blue circles), landraces (pink or dark blue triangles), and putative domestication areas (areas highlighted in yellow) of four *Phaseolus* species. Putative domestication areas: for *P. vulgaris*: a* Lerma-Santiago Basin in the state of Jalisco, Mexico (Kwak et al. 2009), b* Oaxaca Valley in Mexico (Bitocchi et al. 2012), c* central-southern Peru (Chacón et al. 2005), d* Bolivia–northern Argentina (Beebe et al. 2001 and Bitocchi et al. 2012); for *P. acutifolius*: e* area spanning from north to south the states of Sonora, Sinaloa, and Jalisco in Mexico (Blair et al. 2012); for *P. coccineus*: f* Trans-Mexican Volcanic Belt (Guerra-García et al. 2017), g* area of Guatemala–Honduras (Rodriguez et al. 2013; Spataro et al. 2011); for *P. dumosus*: h* western Guatemala. See text for details

the basis of chloroplast DNA polymorphisms suggested central-southern Peru as the domestication area for Andean landraces (Fig. 1a), on the basis that the chloroplast DNA haplotype that was predominant among Andean landraces was found in wild accessions from this region. These two domestication events followed by diversification resulted in a large diversity of Mesoamerican and Andean eco-geographic races (Beebe et al. 2000, 2001; Singh et al. 1991).

P. acutifolius, the tepary bean, is distributed as a wild plant in Southwestern United States and Northern Mexico, and according to previous studies, this species was probably domesticated only once in Mexico, in the states of Jalisco and Sinaloa on the basis of isozyme markers, in a region between Sonora and Sinaloa as suggested by phaseolin markers (although not a conclusive result) (Schinkel and Gepts 1988) or in a region between Jalisco, Sinaloa, and Sonora on the basis of the closer relationship between cultivars and wild accessions from this geographical region as shown by microsatellite (STR, short tandem repeats) molecular markers (Blair et al. 2012)

(Fig. 1b). A recent survey of SNP markers also showed that tepary beans were likely domesticated only once, although the authors could not precise the place of domestication (Gujaria-Verma et al. 2016).

P. coccineus, the runner bean, occurs in its wild form from Northern Mexico to probably not further south of Lake Nicaragua as claimed by Freytag and Debouck (2002) because this lake is a natural barrier for many floristic elements. Two subspecies have been recognized based on morphological characters: subspecies *coccineus* and subspecies *striatus*, the former including wild and domestic forms (Freytag and Debouck 2002). Previous studies have suggested at least two domestication events in Mesoamerica: one event in the area Guatemala–Honduras and the second event in Mexico (Rodriguez et al. 2013; Spataro et al. 2011) (Fig. 1c). Based on six chloroplast SSR markers, Rodriguez et al. (2013) found that domesticated accessions grouped in two clusters that also contained wild accessions. Although the authors suggested this pattern might indicate multiple domestications, they authors also suggested that a more focused study should address this question. On the basis of 12 SSR loci, Spataro et al. (2011) found that most of landraces resembled wild genotypes from the area Guatemala–Honduras. However, a recent genomic analysis of ten wild, three feral, and eleven domesticated populations of runner bean (242 individuals in total), with more than 40,000 SNP markers, suggested that this species was domesticated only once in Mexico, maybe in the area of the Trans-Mexican Volcanic Belt (TMVB) (Guerra-García et al. 2017) (Fig. 1c). This conclusion was based on the observation that domesticated individuals formed a monophyletic group and the results of an approximate Bayesian computation approach that supported the sce-

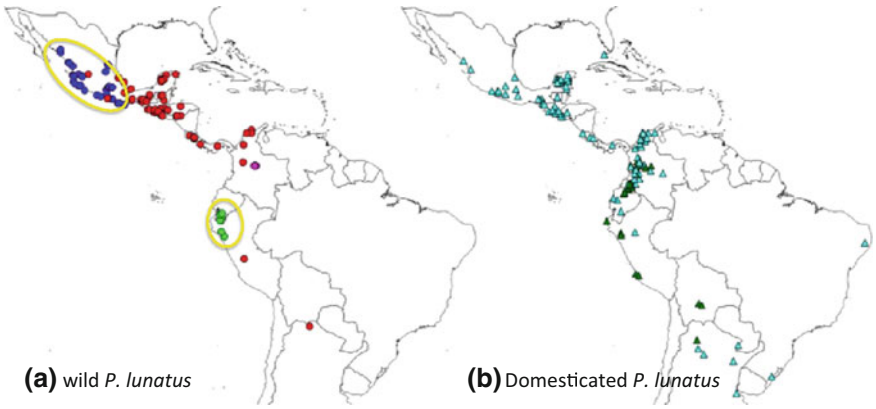

Fig. 2 Geographic distribution of **a** wild and **b** domesticated accessions of *P. lunatus* and putative domestication areas (enclosed in yellow). Wild accessions are shown as circles with different colors according to their gene pool: blue: Mesoamerican I, red: Mesoamerican II, bright green: Andean I, bright pink: Andean II. Domesticated accessions are shown in triangles of different color according to their gene pool: light blue: Mesoamerican, dark green: Andean. The putative domestication area for Mesoamerican landraces is central-western Mexico and for Andean landraces is the Andes of Ecuador–Northern Peru

nario where wild populations from TMVB were closely related to the domesticated populations.

P. dumosus, the year bean, is found in its wild state in western Guatemala and was domesticated in that place in line with evidence from isozyme patterns and linguistics (Schmit and Debouck 1991) (Fig. 1d). There are no other studies based on DNA molecular markers that provide additional evidence about the domestication of this species.

Wild populations of *P. lunatus*, the Lima bean, are geographically widespread from Northern Mexico to northern Argentina (Fig. 2a). Along its distribution range, wild Lima bean is structured into four non-overlapping gene pools: the Mesoamerican pool MI occurs at the northern end of the distribution range mainly in Northern and central-western Mexico, Mesoamerican pool MII is the most widely distributed and is found from southern Mexico to northern Argentina, the Andean gene pool AI is restricted to the western slope of the Andes of Ecuador–Northern Peru, and the

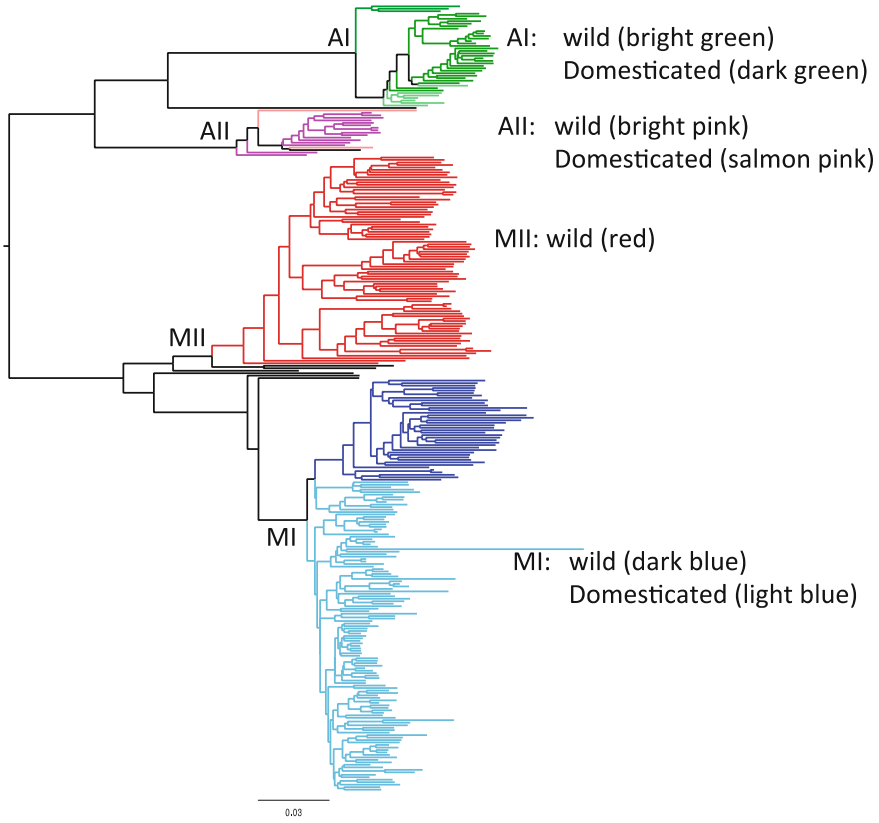

Fig. 3 Neighbor-joining topology, built on the basis of 317 accessions of wild and domesticated Lima bean and 19,387 SNP markers, showing the genetic relationships among accessions (data not published)

Andean gene pool AII is found in the central departments of Cundinamarca and Boyacá in Colombia (Fig. 2a) (Chacón-Sánchez and Martínez-Castillo 2017; Serrano-Serrano et al. 2010). The genetic relationships among these four gene pools are shown in Fig. 3. The genetic relationships along with the almost non-overlapping distribution of these four gene pools (Fig. 2a) suggest a strong phylogeographic structure. Lima bean was domesticated at least twice and independently (Fig. 2b) (Andueza-Noh et al. 2015; Andueza-Noh et al. 2013; Chacón-Sánchez and Martínez-Castillo 2017; Motta-Aldana et al. 2010; Serrano-Serrano et al. 2012). One domestication occurred from gene pool AI and gave rise to large-seeded Andean landraces known as "Big Lima." Another domestication occurred in central-western Mexico from gene pool MI and gave rise to small-seeded Mesoamerican landraces known as "Sieva" and "Potato."

3 Phenotypic Evaluations of Two Key Domestication Traits in *Phaseolus* Beans

3.1 Pod Shattering

The success of wild plants depends on their capacity to disperse their offspring and thus assure survival. Paradoxically, for domesticated plants, seed dispersal is an undesired trait that was either reduced or lost during their adaptation to novel agroecosystems not only during the domestication of *Phaseolus* beans but also during domestication of seed crops in general (Abbo et al. 2014; Harlan 1992). According to Harlan (1992), this trait is "crucial in establishing the disruptive selection that effectively maintains separation of the two kinds of populations" (wild and domesticated). This is because with shattering, seeds will escape harvest by humans and therefore will not contribute to the next cultivated generation; therefore, reduced fruit shattering is a trait that may show up in seed crops under unconscious or unintentional selection associated with harvesting (Harlan 1992).

In common bean, pod shattering is a trait that was not completely fixed during domestication. Wild populations are highly dehiscent and at maturity pod valves separate and twist dispersing the seeds a few meters away from the mother plant (Gepts and Debouck 1991). Some domesticated varieties of dry beans (e.g., some landraces of Nueva Granada race) still show some degree of pod shattering, especially when they are grown in dry environments (Acosta-Gallegos et al. 2007). Modern varieties known as snap beans, which have been bred to produce pods that are eaten as vegetables, are completely indehiscent (Gepts and Debouck 1991). In common bean, the twisting movement of pods has been attributed to the presence of fibers in pod walls and thus a reduced content of fibers would have been a selective advantage during domestication because retardation of seed dispersal facilitates harvest (Gepts and Debouck 1991).

Koinange et al. (1996) reported that pod shattering in a wild common bean genotype (accession G12873) was due to the presence of pod fibers in both the suture and pod walls, while pods of a domesticated non-shattering genotype (cultivar MIDAS, a snap variety) completely lacked these fibers (Koinange et al. 1996). Recently, Murgia et al. (2017) studied pod shattering in common bean in a population of 267 introgression lines derived from a cross between two contrasting parents, MG38 (a RIL with 55% wild background and high shattering) and the recurrent parent MIDAS. The authors analyzed pod shattering in the field, measured the chemical composition of the pods (total fiber content, lignin, cellulose, and hemicellulose), and carried out anatomical and histological analyses of pod valves. The authors found, as expected, that MG38 had 65% shattering pods while MIDAS was completely indehiscent, that MG38 had in the pod valves a higher carbon content (43.8% dry weight) than MIDAS (41% dry weight), that MG38 also had a higher fiber content in the pods (62%) than MIDAS (42%), and that MG38 always had higher contents of lignin, hemicellulose, and cellulose than MIDAS. Histological analyses revealed that in 20-day-old pods, shattering and non-shattering phenotypes showed striking differences in lignin deposition in the ventral sheath of the pod valves (lignification is more pronounced in shattering types), a trait that was highly correlated with carbon content (higher in shattering phenotypes and lower in non-shattering types). In the ventral sheath of the pod valves, MG38 (the shattering phenotype) showed a higher proportion of cells with thick secondary cell-wall formation compared to MIDAS (the non-shattering type) and this thickness tended to be reduced toward the dehiscence zone (a zone of easy fracture). In addition, MG38 showed a high degree of lignification in the inner cells of the pod walls (sclerenchymatic cells) compared to the absence of lignification in MIDAS. Murgia et al. (2017) discussed the histological differences between non-shattering and shattering types in common bean and soybean. In soybean, non-shattering types showed a higher degree of lignification in the dehiscence zone compared to the wild type (Dong et al. 2014), thus making the pod resistant to shatter, and also non-shattering types showed a lower degree of lignification in inner sclerenchyma cells of the pod wall, thus reducing valve twisting (Funatsuki et al. 2014). In contrast, there were no clear differences in the dehiscence zone in common bean; rather the differences between shattering and non-shattering phenotypes are in the degree of lignification in the ventral sheath of the pod valves and the presence/absence of lignification of the inner layer of sclerenchymatic cells of pod walls. These findings show clear histological differences in pod tissues associated with pod shattering between common bean and soybean, suggesting that different molecular mechanisms might underlie this trait in these two species. To establish whether similar or different mechanisms are responsible for pod shattering within the genus *Phaseolus*, a comprehensive method as the one proposed by Murgia et al. (2017) to phenotype pod shattering in *Phaseolus* beans should be implemented in a comparative framework. This method is very promising to disentangle the genetic architecture of this trait.

In spite of being a key domestication trait for *Phaseolus* beans, there is a great lack of studies comparing wild and domesticated populations for pod shattering (even for the common bean). For this reason, we have made a first attempt to analyze the

variation of this trait in a collection of 19 wild and 62 domesticated accessions of Lima bean (data from Paola Hurtado et al. not published). In brief, a total of 50 plants per accession were planted in one location in Colombia chosen to match the ecological conditions of their place of origin. Pods were harvested daily at physiological maturity and were placed in a desiccator during 48 h at 60 °C and constant airflow. A sample of 10 pods per accession was taken for measuring the minimum force (in Newtons (N)) required to fracture the pod in an AMETEK LS1 texture analyzer. In these accessions, about 50% needed a pod shattering force between 5 and 10 N, less than 5% required a force below 5 N, and less than 5% required a force beyond 15 N.

For investigating whether the biological status (wild or domesticated) was significant to explain variation in pod shattering force, a linear model was built and a Breusch Pagan test ($p=0.1147$) and an ANOVA test ($p=0.1525$) were applied; the results suggest that the biological status is not significant to explain variation in this trait and rather a phenotypic continuum is observed (data from Paola Hurtado et al., not published) (see Fig. 4a). This result is somehow unexpected given that pod shattering is one of the traits under disruptive selection during domestication. In contrast, gene pool of the landraces resulted to be significant to explain variation in this trait (Breusch Pagan test, $p=0.03$, ANOVA test, $p=1.7e{-}06$) (data from Paola Hurtado et al., not published). Mesoamerican (MI) landraces required less pod shattering force (average of 8.22 N) than Andean landraces (average of 13.91 N)

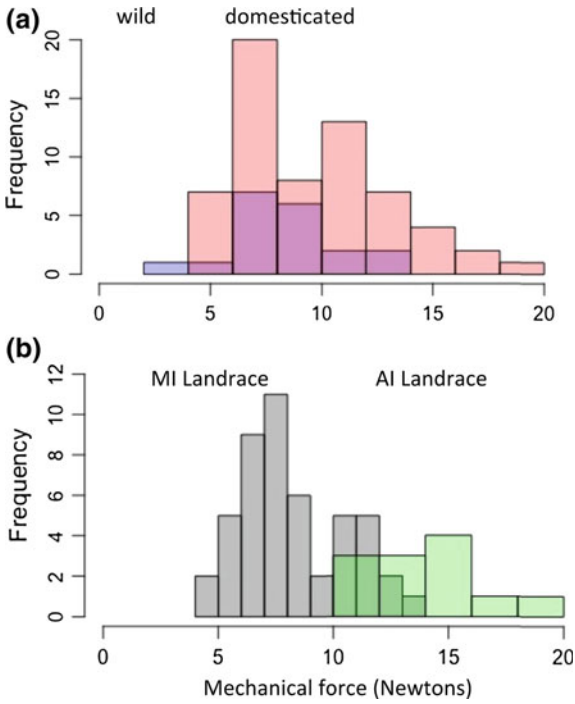

Fig. 4 Changes in pod shattering force (measured in Newtons) in the domestication of Lima bean based on data from Paola Hurtado et al. (not published). **a** Mechanical force applied to wild (blue bars) and domesticated (pink bars) accessions to break the pods. **b** Mechanical force applied to Mesoamerican (gray bars) and Andean (green bars) landraces to break the pods

(Fig. 4b). These results suggest that pod lignification patterns might be different for Andean and Mesoamerican landraces, a question of high interest that should be thoroughly investigated. Future studies in Lima bean should include more robust methods to evaluate this trait in order to investigate phenotypic convergence in both domestication events.

4 Seed Size

Increase in seed size during domestication may be an adaptation related to seedling competition (seedlings of the same species) in the cultivation field (Harlan 1992), because not only seeds that germinate first but also those that produce more vigorous seedlings (namely larger seeds) are more likely to contribute with progeny to the next generation. In cereals, increase in seed size is due to an increase in the endosperm (not in the embryo) with a tendency to elevate carbohydrate content and to lower protein content (Harlan 1992). In common bean, Singh et al. (2014) investigated whether the increase in seed size during common bean domestication was accompanied by an increase in starch or protein content. For this, a RIL population (168 individuals) derived from a cross between a wild parent and a domesticated parent from the Andean gene pool was analyzed using near-infrared reflectance (NIR). As in cereals, in this study the authors observed that seed size was positively correlated to starch content and negatively correlated to protein content.

In all *Phaseolus* crop species, wild relatives show smaller seeds than domesticated ones. In this section, 100-seed weight (in grams) data taken from the *Phaseolus* database at the International Center for Tropical Agriculture (CIAT) (http://genebank.ciat.cgiar.org/genebank/beancollection.do, consulted on April 7, 2018) will be compared among wild and domesticated accessions in each one of the five *Phaseolus* species to gain insights on how this trait has been affected during domestication. Only wild populations and landraces from the areas of origin of each crop species (see Figs. 1 and 2) were taken into account.

In common bean, Mesoamerican wild populations show seed sizes (measured as 100-seed weight) that go from 2 to 19 g, with an average of around 6 g, while Andean wild populations show ranges from 3.2 to 26 g, with average of around 12 g. Domestication increased considerably the variation in seed size in both domestication events (Fig. 5a). Seed weight in Mesoamerican landraces goes from 12 to 72 g, with average of 29 g, an average increase of 4–6 times in comparison with wild Mesoamerican ancestors (Fig. 5b). Seed weight in Andean landraces goes from 16 to 108 g, with an average of 48 g, an increase of about 4–5 times in comparison with wild Andean ancestors (Fig. 5c). So, it seems that in spite that Andean ancestors exhibit larger seeds than Mesoamerican ancestors, wild populations apparently responded to domestication in a similar way in the sense that a comparable increase in seed size (around 4–5 times) in both domestication events is observed.

In runner bean (*P. coccineus*), wild populations (that occur only in Mesoamerica) have a wide range in seed size that go from 0.6 to 37.9 g, with an average of

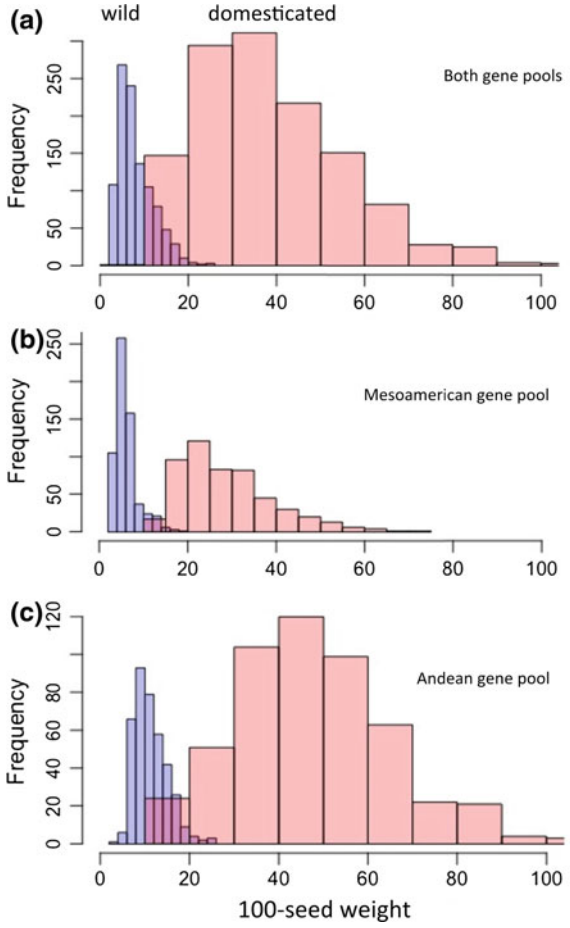

Fig. 5 Changes in seed weight in the domestication of common bean. Blue bars: wild populations. Pink bars: domesticated populations. **a** Wild and domesticated populations of common bean from both gene pools (Mesoamerican and Andean). **b** Wild and domesticated populations from Mesoamerican gene pool. **c** Wild and domesticated populations from Andean gene pool

around 14 g. In this species, domestication also increased variation in seed size and domesticated populations exhibit an average increase of about 5–6 times (Fig. 6a) in relation to their wild ancestors, with sizes that go from 20.1 to 199.5 g, with an average of around 89 g (see Fig. 6a). It is interesting to note that runner beans show the largest variation in seed size among all five domesticated species.

Tepary bean (*P. acutifolius*) shows the smallest seeds of all five species, in wild and domesticated types. Wild populations that occur mainly in central-northern Mexico and Southwestern United States contain seed sizes between 1.6 and 8.2 g, with an average of 3.34 g (Fig. 6b). Domesticated tepary beans show seed sizes with a non-overlapping distribution with wild tepary beans, with a range that goes from 9.2 to 27.2 g and an average of 15.28 g, which represents an increase of about 3–6 times. It is worth noticing that among the five species, tepary bean is the only one that shows a clear-cut difference in seed size among wild and domesticated forms, which may

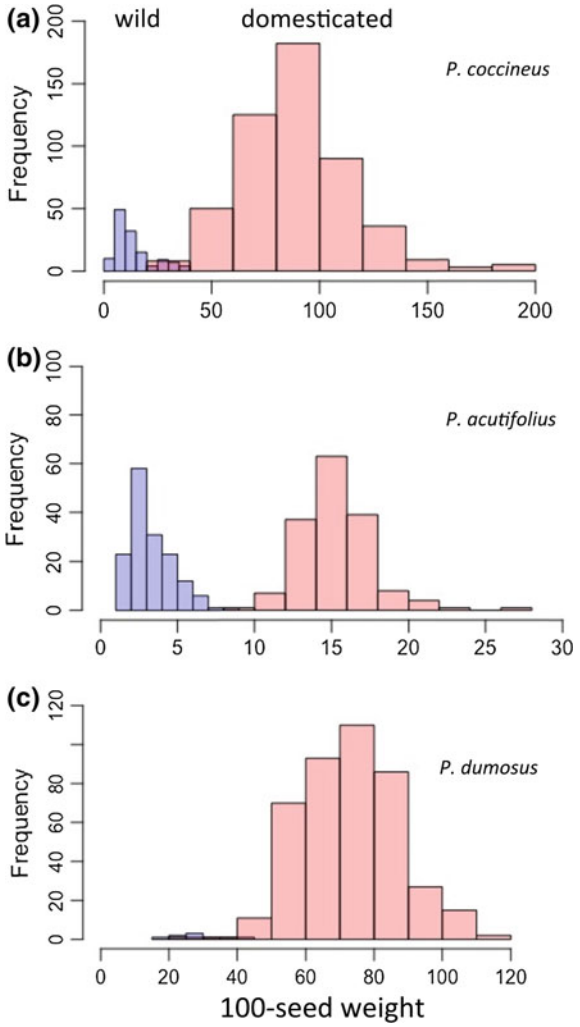

Fig. 6 Changes in seed weight in the domestication of three *Phaseolus* species. Blue bars: wild populations. Pink bars: domesticated populations. **a** *P. coccineus*. **b** *P. acutifolius*. **c** *P. dumosus*

suggest that in this species seed size was a crucial domestication trait as defined by Abbo et al. (2014).

For year bean (*P. dumosus*), according to seed size data available at CIAT (only nine accessions for the wild), wild populations show seed sizes from 19 to 42.8 g (even larger than in *P. coccineus*), with an average of 29.42 g. Domestication increased seed size about 2–3 times only, and domesticated seeds go from 26 to 116.2 g, with an average of 73.32 g (Fig. 6c).

In Lima bean, wild populations show seed sizes that go from 4 to around 33 g with an average of 11.2 g (Fig. 7a). In this species, two major gene pools exist: the Mesoamerican and the Andean. The seed weight of Mesoamerican gene pool ranges

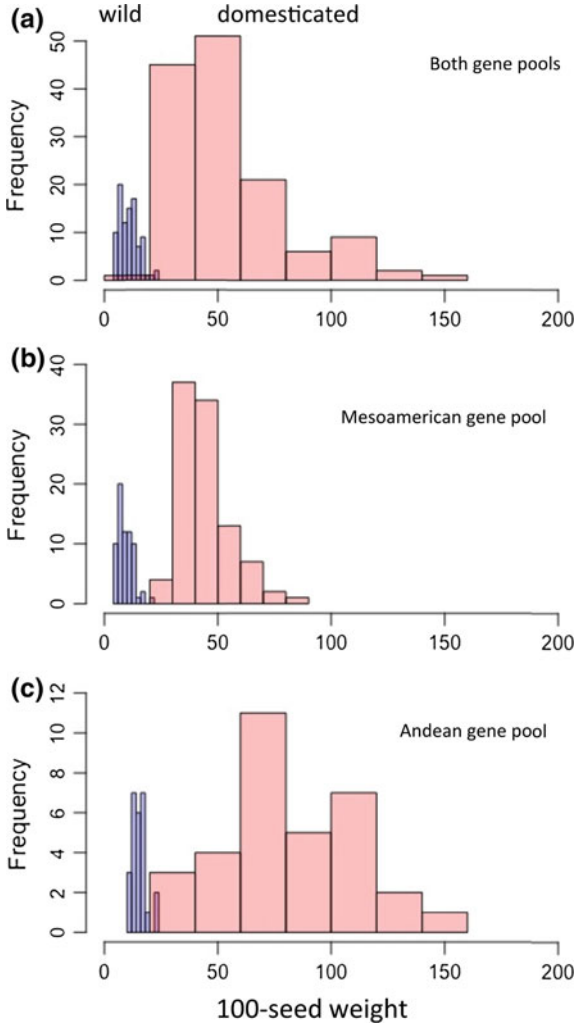

Fig. 7 Changes in seed weight in the domestication of Lima bean. Blue bars: wild populations. Pink bars: domesticated populations. **a** Wild and domesticated populations of Lima bean from both gene pools (Mesoamerican and Andean). **b** Wild and domesticated populations from Mesoamerican gene pool. **c** Wild and domesticated populations from Andean gene pool

from 4 to about 21, with an average of around 9.4 g. In the Andean wild gene pool, seeds are heavier and their weights go from 11 to 24 g with an average of 15.4 g. Lima bean landraces have seeds whose weight go from 21 to around 144 g, with average of 56 g. As mentioned before, this species was domesticated in Mesoamerica and the Andes. Mesoamerican landraces (gene pool MI) show seed sizes that go from 21 to 107 g, with average of around 44 g. The increase in seed size for Mesoamerican landraces in comparison with their wild relatives has been of around 5 times (Fig. 7b). On the other hand, Andean landraces show seeds that weight from 32 to 144 g, with an average of around 84.2 g, almost doubling the size of Mesoamerican landraces. In

comparison with the wild Andean ancestor, Andean landraces have increased their size about 5–6 times in average (Fig. 7c).

In summary, it appears that domestication in these five species did not affect seed size in the same way; in some species like *P. dumosus,* increase in seed size was only 2–3 times, while in the other species the average increase was up to 6 times. In all species examined. there are clear differences in seed size between wild and domestic forms, although different degrees of overlap were observed. Very little is known about what nutritional changes have accompanied the increase in seed size in domesticated populations (except for common bean), a subject that should be further investigated. Another important question to solve is whether the same genes underlie changes in seed size among these five domesticated species, a subject that will be revised below.

5 Molecular Genetics and Genetic Architecture of Pod Shattering

Arabidopsis thaliana has been the model plant to study the cascade of genes involved in pod shattering. This plant possesses a dry fruit called silique that shatters at maturity through the dehiscence zone (DZ) to disperse the seeds (Estornell et al. 2013). DZ is constituted by a thin layer of cells that differentiates at the valve/replum margin of the fruit; the separation of these cells allows the detachment of the valves from the replum, and seeds are dispersed (Ferrándiz et al. 2000). Two genes that are at the top of the regulatory cascade that control fruit shattering in *Arabidopsis* are the closely related MADS-box genes *SHATERPROOF* (*SHP1*) and *SHATERPROOF2* (*SHP2*) (Liljegren et al. 2000) that control cell differentiation in DZ. Acting downstream of the *SHP1/2* genes are the genes known as *INDEHISCENT* (*IND*) and *ALCATRAZ* (*ALC*)—the former codes for an atypical bHLH protein that specifies the differentiation of cells in the DZ, and its mutation in *Arabidopsis* results in indehiscent fruits (Liljegren et al. 2004), and the second encodes a myc/bHLH protein, necessary for the formation of a non-lignified specialized cell layer within the DZ and its mutation prevents dehiscence of the fruit (Rajani and Sundaresan 2001). On the other hand, *FRUITFULL* (*FUL*), a MADS-box gene, is required for the expansion and differentiation of fruit valves, is a negative regulator of *SHP1/2* and restricts the expression of *SHP1/2* and *IND* to the DZ (Ferrándiz et al. 2000). The constitutive expression of FUL produces indehiscent fruits because of the conversion of DZ cells into valve cells (Ferrándiz et al. 2000). The *NST1* gene (*NAC SECONDARY WALL THICKENING PROMOTING FACTOR 1*) acts downstream of *SHP1/2* and is expressed in the lignified layer of cells in the DZ, and its mutation results in indehiscent fruits because the cells of the valve margins lose lignification (Mitsuda and Ohme-Takagi 2008). Finally, for silique dehiscence to take place, the action of enzymes known as endo-polygalacturonases (PGs) that degrade pectin to promote cell separation is indispensable. The genes *ARABIDOPSIS DEHISCENCE ZONE POLYGALAC-*

TORUNASE1 (*ADPG1*) and *ADGP2* encode for PGs that are expressed specifically in DZ (Ogawa et al. 2009). It has been demonstrated that *IND* is necessary for normal expression of *ADPG1* in DZ (Ogawa et al. 2009).

In legume crops (chickpea, lentils, soybean, common bean, Lima bean, etc.), indehiscent pods appeared in all domestic forms apparently as a result of selection associated with harvesting (Harlan 1992). The question to investigate here is whether or not the same genes and molecular mechanisms explain the observed phenotypic convergence. In the last few years, some evidence has appeared on this subject but is still very poor. In soybean, for example, Dong et al. (2014) showed that loss of seed dispersal in domesticated soybean is caused by the excessive lignification of fiber cap cells (FCC) in the abscission layer that prevents pod shattering. The thickening of FCC secondary walls is controlled by a gene known as *SHATTERING1-5* (*SHAT1-5*), a homolog of *AtNST1/2*, which is expressed at much higher levels in domesticated soybean compared to wild soybean due to the loss in the former of a repressive *cis*-regulatory element at the 5' promoter region. While in soybean Dong et al. (2014) concentrated their efforts in the study of the genes responsible for differences in binding strength of the pod among wild and domestic forms, Funatsuki et al. (2014) studied the genes responsible for the generation of dehiscing forces in the pod. These authors identified a major QTL that encodes a protein called *Pdh1*. The gene *PDH1* is expressed in the inner sclerenchyma of pod walls at the beginning of lignin deposition, and this gene is associated with an increase in the torsion of dried pod walls that promotes pod dehiscence. In domesticated soybean, a functional protein of this gene is not produced due to a premature stop codon (Funatsuki et al. 2014).

The first study that addressed the genetic architecture of several morphological and physiological traits of the domestication syndrome in *Phaseolus* beans is the one that Koinange et al. (1996) carried out in common bean. Among the traits the authors studied were seed dispersal (that was measured as presence or absence of pod suture fibers and pod wall fibers), seed dormancy, growth habit, gigantism (pod length and 100-seed weight), earliness, photoperiod sensitivity, harvest index, and seed pigmentation. The presence of pod suture fibers and pod wall fibers was determined visually by breaking the pod beak and pod wall, respectively. The authors built a population of 65 F8 recombinant inbred lines (RILs) derived from the cross between a wild (G12873, Mesoamerican origin) and a domesticated accession (cultivar Midas, a wax snap bean of Andean origin), chosen to show the broadest range of domestication syndrome traits. The authors also built a linkage map with 83 DNA and biochemical markers to identify quantitative trait loci (QTL) governing domestication-related traits. For seed dispersal, measured as lack of suture fibers, the authors detected a single locus (*St*) on linkage group (LG) 2, and for the lack of pod wall fibers, they also detected a single locus in the same linkage group that was either tightly linked to *St* or identical to *St* (pleiotropy) (Table 1). These results suggest that the genetic control of pod shattering in common bean might be simple; however, this result might be due to the way this trait was measured.

Recent attempts to identify the causal gene underlying *St* in common bean have been reported. Gioia et al. (2013) adopted a candidate-gene approach to identify the gene in *St* responsible for pod dehiscence in common bean, selecting *IND* as a

Table 1 QTLs for pod shattering and seed weight detected in crosses between wild × domesticated, domesticated × domesticated, or in a set of wild and domesticated accessions

Domestication attribute	Trait	Linkage group	QTL or gene or linked marker	R^2 (%) per locus	R^2 (%) per trait	Reference
Pod shattering (wild × domesticated cross)	Pod suture fibers	2	*St*	–	–	Koinange et al. (1996)
	Pod wall fibers	2	*St*?	–	–	
Gigantism (wild × domesticated cross)	100-seed weight	1	D1492-3	18	57	Koinange et al. (1996)
		7	*Phs*	27		
		7	Uri-2	16		
		11	*D0252*	15		
		1	QTL1	–	42.3	Guzmán-Maldonado et al. (2003)
		2	QTL2	–		
		3	QTL3	–		
		4	QTL4	–		
		4	QTL5	–		
		2	sw2.2 Popayan	16	–	Blair et al. (2006)
		2	sw2.2 Darien	17		
		7	*Phs* Popayan	7		
		7	*Phs* Darien	6		
		8	sw8.1 Popayan	5		
		8	sw8.1 Darien	8		
		8	sw8.2 Popayan	8		
		8	sw8.2 Darien	6		
		11	sw11.1 Popayan	8		
		11	sw11.1 Darien	9		

(continued)

Table 1 (continued)

Domestication attribute	Trait	Linkage group	QTL or gene or linked marker	R^2 (%) per locus	R^2 (%) per trait	Reference
Gigantism (domesticated × domesticated cross)	100-seed weight	4a	BC500.400	18	44	Park et al. (2000)
		5	Q05.850	10		
		6	Y07.1200	9		
		3	G03.1150	9		
		8	D12.700	5		
		7	J09.950–1.0	3		
		4b	BC406.450	5		
		8	BC457.400	4		
Gigantism GWAS	100-seed weight	1	3 genes	–	–	Schmutz et al. (2014)
		2	1 gene	–		
		3	10 genes	–		
		4	2 genes	–		
		6	2 genes	–		
		7	42 genes	–		
		8	9 genes	–		
		9	3 genes	–		
		10	2 genes	–		
		11	1 gene	–		

R^2: percent of phenotypic variance explained by QTL or trait
–: lack of information

potential candidate due to its key role in *Arabidopsis*. For this, the authors identified by sequence comparison the homologue in common bean (*PvIND*) of the *AtIND* gene. The authors sequenced this gene in a collection of 77 wild and 80 domesticated accessions of common bean and three related species (*P. acutifolius*, *P. coccineus,* and *P. lunatus*). In addition, 105 accessions of common bean were scored for the presence of fibers in pod sutures and pod walls with the same method reported by Koinange et al. (1996). For mapping this candidate gene, the authors developed two RIL populations (BAT93 × Jalo EEP 558 and Midas × G12873). This candidate gene was mapped to chromosome 2, and although it was located close to the *St* locus, these two loci did not show cosegregation. In addition, the authors did not find any SNP within the sequence of *PvIND* associated with pod shattering. These results showed that *PvIND* does not play a role in pod shattering in common bean. As noted by Dong and Wang (2015), the role of *IND* in valve margin cell lignification might be

specific to the Brassicaceae clade and other *AtIND* homologues in common bean should be investigated. Another study that implemented a candidate-gene approach was the one reported by Nanni et al. (2011) who sequenced in a set of wild and domesticated accessions of common bean, the homologue of *AtSHP1* in common bean, called *PvSHP1*. The authors found that this gene mapped to chromosome six and was not related to pod shattering.

As it can be seen, in spite of being a key trait for domestication of *Phaseolus* beans, almost nothing is known about its genetic control; therefore, to unravel the genetic basis of pod shattering in *Phaseolus* beans, more research is needed as noted by Dong and Wang (2015), especially in fiber cell differentiation and regulation of secondary cell-wall deposition given that fibers are mainly composed of sclerenchyma cells with well-developed secondary cell walls. To carry out studies in *Phaseolus* beans comparable to those reported in other legume crops, it will be very important to understand the differences in pod anatomy and functional mechanisms governing pod shattering among species and accordingly develop phenotyping methods to score this trait (the methods reported by Murgia et al. (2017) are very promising), taking into account specific tissues from which to take samples (in the case of expression analyses) and the time of sampling (pod developmental stage).

6 Genetic Architecture of Seed Weight

Very few studies in *Phaseolus* beans have addressed the identification of genes involved in changes in seed weight during domestication. In the study of Koinange et al. (1996) mentioned above, four QTLs were detected for seed weight that explained 57% of phenotypic variation: one QTL in LG 1, two QTLs in LG 7, and one QTL in LG 11 (Table 1). In LG 7, the nearest marker associated with one of the detected QTLs for seed weight was the Phaseolin (*Phs*, the major seed storage protein) locus.

Another study that analyzed QTLs associated with seed weight in a cross between wild and domesticated genotypes of common bean was the one of Guzmán-Maldonado et al. (2003). In that study, 120 $F_{2:3}$ lines derived from a cross between the cultivar Bayo Baranda (race Durango, Mesoamerican origin, 100-seed weight of 43.9 g) and a wild genotype (G22387, Mesoamerican origin, 100-seed weight of 4.7 g) were analyzed for 100-seed weight and other seed characters. This cross was therefore informative for detection of QTLs for the Mesoamerican domestication event. Five QTLs were significantly associated with seed mass that together explained about 42.3% of variation: one in LG1, one in LG2, one in LG3, and two in LG4 (Table 1).

An additional study that analyzed QTLs associated with seed weight in a cross between wild and domesticated genotypes was reported by Blair et al. (2006) in a $BC_2F_{3:5}$ population derived from a cross between a wild genotype (G24404, Andean origin, the donor parent, average 100-seed weight of 16 g) and an Andean cultivar (ICA Cerinza, the recurrent parent, average 100-seed weight of 53 g). This cross was

therefore informative about QTLs associated with seed size in the Andean domestication event. A total of five QTLs associated with seed weight were consistently detected in the two locations where populations were grown (Darién and Popayán in Colombia). These QTLs were located in LG 2 (one QTL), LG 7 (one QTL), LG 8 (two QTLs), and LG 11 (one QTL) (Table 1). The QTL in LG7 was linked to the *Phs* locus, as was also reported by Koinange et al. (1996).

Other studies in common bean have investigated QTLs contributing to seed weight but from crosses between domesticated genotypes, not between wild and domesticated genotypes; therefore, QTLs detected in these studies may differ from those acting on the domestication syndrome. For example, Park et al. (2000) analyzed 63 RILs derived from a cross between two domesticated genotypes of Andean origin ('PC-50' and XAN-159) for seed characters including 100-seed weight (PC-50: 100-seed weight 35.2–45.1 g, XAN-159: 100-seed weight 17.8–24.7 g), seed length, and seed height. For seed weight, the authors found five QTLs in linkage groups 3, 4, 6, 7, and 8 that together explained about 44% of variation in this trait (Table 1). In this study, one of the seed weight QTLs detected in LG7 was linked to the *Phs* locus, a similar finding to that reported by Koinange et al. (1996).

Schmutz et al. (2014) published the first reference genome of common bean and in the context of this genome carried out a genome-wide association analysis (GWAS) to detect genes associated with the increase in seed size during domestication in Mesoamerica. They found 15 genes associated with improvement of Mesoamerican cultivars, including multiple members of the cytokinin synthesis whose orthologs in *Arabidopsis* are known to be involved in seed size. These 15 genes were found in chromosomes 1 (one gene), 3 (five genes), 4 (one gene), 6 (one gene), 7 (two genes), 8 (one gene), 10 (one gene), and 11 (three genes). The authors also carried out a GWAS to identify genes associated with domestication of common bean in Mesoamerica and were able to locate 75 candidate genes that included the 15 improvement genes described above. These 75 candidate genes were located in chromosomes 1 (three genes), 2 (one gene), 3 (ten genes), 4 (two genes), 6 (two genes), 7 (42 genes, 33 of which are in a sweep window 9.662–10.662 Mb), 8 (nine genes), 9 (three genes), 10 (two genes), and 11 (one gene).

It is interesting to note that while the earliest studies identified rather few genes for seed weight, the study of Schmutz et al. (2014) that implemented a genome approach was able to detect much more genes in almost all chromosomes (except in chromosome 5), which suggests a polygenic control for this trait. Due to its polygenic nature, in order to advance in the detection of genes that control seed size among the five domesticated species in the *Phaseolus* genus, a genomic perspective should be implemented in future studies.

7 Conclusions

We can conclude that the five domesticated *Phaseolus* species offer the opportunity to evaluate the genetic basis of the domestication syndrome in at least seven independent

domestication events. Wild ancestors and areas of domestication for all these species have been identified which enable correct comparisons in future studies. In all these species, phenotypic convergence is observed in pod shattering and seed weight, as adaptations during domestication. The question that arises here is whether this phenotypic convergence may be explained by parallel or convergent evolution. The phenotypic evidence revised here for seed weight suggests that these species have responded in a similar way during domestication in the sense that domesticated forms show larger seeds than their wild ancestors, but there are evident differences in the magnitude of seed size increase and the degree of phenotypic overlap among wild and domestic forms. In this last aspect, only in *P. acutifolius* a clear pattern of disruptive selection with no overlapping phenotypic distributions among wild and domestic forms was observed; in the other four species, a rather phenotypic continuum is present. For pod shattering, evidence is very scarce. Evaluations of this trait among wild and domestic forms have been carried out in common bean and Lima bean only. This trait is expected to be under disruptive selection; however, the studies show that this trait has not been fixed among domesticated forms, and some landraces still show a high degree of pod shattering, sometimes overlapping wild forms. Very little is known about the genetic control of these two domestication traits in *Phaseolus* beans, and the few studies have been carried out only in common bean. In common bean, two loci (or only one with pleiotropic effects) have been detected in linkage group 2, but so far the genes underlying these loci have not been identified. A major limitation is the way this trait has been phenotyped, but recent advances have been reported. For seed weight, recent studies using a genomic perspective show a highly polygenic nature, with QTLs present in all chromosomes (except in chromosome 5). Future studies should involve more sophisticated approaches for the phenotyping of these traits, especially pod shattering, and genomic tools to detect loci involved in their control; only in this way we could answer the question of how the observed phenotypic convergence arose, either by parallel or convergent evolution.

Funding The present study was partially funded by Colciencias, Colombia, under contract number 009-2015 and project code 1101-658-42502.

Acknowledgements Thanks are due to the Genetic Resources Unit of CIAT, especially to Dr. Daniel Debouck and Dr. Peter Wenzl, for providing the Lima bean seed material used in this study and for all their support in the phenotypic characterization of pod shattering in Lima bean. Thanks are also due to Paola Hurtado for sharing unpublished pod shattering data in Lima bean.

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