

Domestication Process of African Vigna Species

Subjects: Biodiversity Conservation

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Legumes are one of the most economically important and biodiverse families in plants recognised as the basis to develop functional foods. Among these, the *Vigna* genus stands out as a good representative because of its relatively recent African origin as well as its outstanding potential. Africa is a great biodiversity centre in which a great number of species are spread, but only three of them, *Vigna unguiculata*, *Vigna subterranea* and *Vigna vexillata*, were successfully domesticated.

Keywords: *Vigna* genus ; Introgression ; Hybridisation ; Domestication

1. Introduction

Legumes (Fabaceae) are considered one of the most important families of plants for human nutrition, especially considering the rapid growth rate of the world population ^[1]. However, almost all the efforts and resources invested in agriculture during the last century were focused on improving the yield, resistance and quality of a few specific staple crops. Neglected landraces are regarded as having interesting potential, and recent studies have demonstrated that some wild legumes can be an important target to develop modern functional foods because they possess various bioactive molecules that interact positively with human health ^{[2][3][4][5]}. Among these, members of the *Vigna* genus show a growing social and economic importance in several African regions, especially where the local population is not able to afford animal proteins ^{[6][7][8]}. Their seeds are rich in essential amino acids and contain a high concentration of minerals, lipids and vitamins ^{[9][10]}.

The genus *Vigna* (Savi, 1824), which belongs to the tribe Phaseoleae of the family Fabaceae, includes over 100 species ^[11] distributed in the tropical and subtropical areas of the world ^[12] grouped in five subgenera: *Vigna*, *Ceratotropis*, *Plectotropis*, *Lasiosporon* and *Haydonia* ^{[13][14][15]}. Phylogenetic findings propose the age of split between *Phaseolus* and *Vigna* genera at about 8–10 million years (Mya) and the age of split between *Ceratotropis* and *Vigna* subgenera at about 3–4 Mya ^{[13][14][15][16][17]}, but the genetic relationships between subgenera are particularly complex and far from being completely solved. Although most domesticated or semi-domesticated species are distributed in Asia, the greatest diversity of the *Vigna* genus is located in Sub-Saharan Africa ^{[14][18]}. *Vigna* subgenus, distributed in Africa, includes about 40 wild and 2 domesticated species, namely cowpea (also called black-eyed peas, chawli and kunde) (*Vigna unguiculata* L.) and Bambara groundnut (*V. subterranea* L.) ^[19] while *Ceratotropis* (Piper) Verdc., distributed in Asia, contains 21 wild and 7 domesticated species used widely for food and forage, namely mungbean or green gram (*V. radiata* L. Wilczek), black gram (*V. mungo* L. Hepper), moth bean (*V. aconitifolia* Jacq. Maréchal), rice bean (*V. umbellata* Thunb. Ohwi and Ohashi), adzuki bean (*V. angularis* L. Ohwi and Ohashi), creole bean (*V. reflexo-pilosa* Hayata), jungli bean (*V. trilobata* L. Verdc.). ^{[15][20][21][22]}. Moreover, three species belonging to *Plectotropis* (Schumach.) are distributed in Africa, including tuber cowpea (*V. vexillata* L.) ^[23]. Most of the African *Vigna* germplasm is based on wild plants and neglected or underutilized landraces, and many of these lineages are declining with a high risk of extinction. The recovery of wild accessions and research devoted to the phylogeny of the genus is therefore essential to prevent genetic erosion and the loss of *Vigna* diversity.

Plant domestication is widely recognised as an accelerated evolutionary process driven by a synergistic impact of human and natural selection, occurring in geographically restricted areas from wild progenitors. In legumes, the main modification is the loss of seed pod dehiscence or shattering ^{[24][25]}. The split at the dorsal and ventral sutures of the dry pod and successive release of the seeds occurs due to the desiccation of lignified cells in the pods ^[26]. The shattering habit is related to environmental aridity and persists in many varieties of domesticated *Vigna* species, thereby determining severe yield losses ^{[27][28]}. Additional implementations in *Vigna* domesticated species include an increase in seed or fruit size, change in seed colour, loss of seed dormancy, apical dominance and change in flowering timing ^{[29][30][31][32][33]}. These modifications were inherited more or less effectively in the various vine species currently cultivated, and this is the basis of the agrobiodiversity of this genus.

Generally, the current existing crops show lower resistance to biotic and abiotic stress compared to wild relatives, and often they have reached their full yield. The selection of desirable traits and breeding processes to improve crop productivity have caused the depletion of diversity and the increase in the frequency of deleterious genetic variants that are fixed in the genomes of crops [34][35][36]. These constraints have a serious impact on agriculture, limiting the possibility to grow such crops under more extreme environmental conditions. Thanks to this residual genetic diversity and also to studies performed on *Vigna* species, most of the accessions are well adapted to a wide range of extreme environmental conditions, such as sandy beaches, arid lands and wetlands, harbouring tolerance and resistance genes towards biotic and abiotic stresses. These genetic traits are used for developing new stress-tolerant crops [37][38][39][40][41][42][43]. By contrast, less is known about the effects of domestication on the nutritional value of seeds [7] even if recent studies have reported that cultivated legumes show a lower carotenoid and protein content in seeds compared with the wild relatives [44][45]. Where, when and how many times the domestication process of African *Vigna* crops occurred continues to be debated among researchers. Although archaeological remains of *Vigna* indicate that the domestication process in Africa was started recently compared to other field crops [46][47]. Modern evolutionary models proposed for other crops suggest that the predomestication phase may have lasted several thousands of years [48][49]. Generally, the centres of origin are also recognized as centres of diversity, and thus these areas require special precautionary measures of conservation [50]. Although for many crops the single-origin model is usually the most parsimonious, the hypothesis that provides multiple origins starting from independent founder lineages seems well suited for the crops of *Vigna* originated in Africa [51][52]. Moreover, despite whether and to what extent introgression influences the domestication process is still underexplored, some studies already show that gene flow between cowpea and its wild relatives may occur. Pervasive introgression can also intensify the feralisation process, promoting the crops to return to a wild environment and causing serious problems for the conservation of biodiversity [53].

2. *Vigna unguiculata* (L.) Walp.

V. unguiculata, which was considered an orphan crop for several decades, has recently become one of the most important legumes in the world. Its name derives from Latin and means “with a small claw”, referring to the size of the claw of the petals [54] or commonly named as “cowpea” because of its use as fodder for cows [55] and black-eyed pea/bean for the black hilum. This crop is largely cultivated, especially in semiarid regions of Africa and Asia where other crops fail to grow [10]. Currently, on a global scale, about 15 million hectares are dedicated to *V. unguiculata*, with an annual production of 7 million Mg and an average yield of 0.6 Mg ha⁻¹ [56]. The most interesting environmental traits of this species are represented by the generalized low agrochemical input requirements. In fact, this crop shows relatively high adaptation to drought, especially in comparison to other legumes [57] and can fix up to 200 kg N ha⁻¹ [58] with a positive soil N balance of up to 92 kg ha⁻¹ [59]. Nevertheless, several abiotic and biotic constraints (i.e., low soil fertility, pests, diseases, parasitic weeds, and nematodes) limit the yield [43][60][61]. Moreover, low productivity is often associated with the use of traditional and unimproved varieties, still widely cultivated in Africa [62]. This crop has a fundamental role in human nutrition, showing seeds rich in proteins and essential amino acids (i.e., tryptophan and lysine), carbohydrates, folic acid and minerals. Recent studies carried on a large sampling have shown high variability in protein and mineral concentrations, suggesting that some lineages could be potential sources of genes useful to produce new varieties [63][64][65][66].

The high number of wild subspecies found exclusively in Africa strongly supports the idea of an African origin. However, intraspecies phylogeny remains far from being completely elucidated [67]. The centre of origin of the species is probably located in the southernmost regions of Africa, where most subspecies are found and where most genetic diversity could be still hidden [68]. Several taxonomic revisions based on morphological and molecular traits permitted to identify 10 perennial and 1 annual subspecies, the latter split into two varieties: ssp. *unguiculata* var. *unguiculata* (domesticated cowpea) and ssp. *unguiculata* var. *spontanea* (Schweinf.) Pasquet., also known as subsp. *dekindtiana* sensu Verdcourt non Harms [69][70][71][72][73][74][75][76]. Besides the domesticated cowpea, the *dekindtiana* group includes some obligate short-day wild forms, well adapted to arid environments. While the var. *spontanea* grows especially around cultivated fields and roadsides, and it is recognized as the progenitor of domesticated cowpea [75][77][78][79], the subspecies *alba*, *pubescens*, *tenuis*, *stenophylla* and *dekindtiana* are perennial plants [75][76]. The development of new molecular tools to discriminate among wild, weedy, and cultivated accessions is considered a modern and fundamental target, particularly needed for disentangling the complex taxonomic relationships among subspecies and to discriminate between true wild plants and ferals.

Although little is known about the domestication process, some scientists have hypothesized that ancient cowpea progenitors, such as the modern wild forms, were adapted to dry habitats and grew spontaneously south of the Sahara Desert [80]. These plants were gathered, cultivated and dispersed by men near the villages, but they were unsuited for

cultivation. Although they did not show high yield, the wild lineages were spread in the humid zones thanks to their pods that remained closed for the humid atmosphere. Through several generations of cultivation, new mutants have arisen, showing interesting domestic traits, including resistance to shattering. Subsequently, humans have selected and helped spread these landraces by exchange and trade activities. Since the oldest archaeological records of domesticated forms found in central Ghana are dated around 1500 BC, the domestication process likely started before that period (**Figure 1**) [47][81]. However, the precise origin is widely debated, and two independent domestication centres in West and East Africa are proposed by different researchers [68][74][79][82][83][84][85][86].

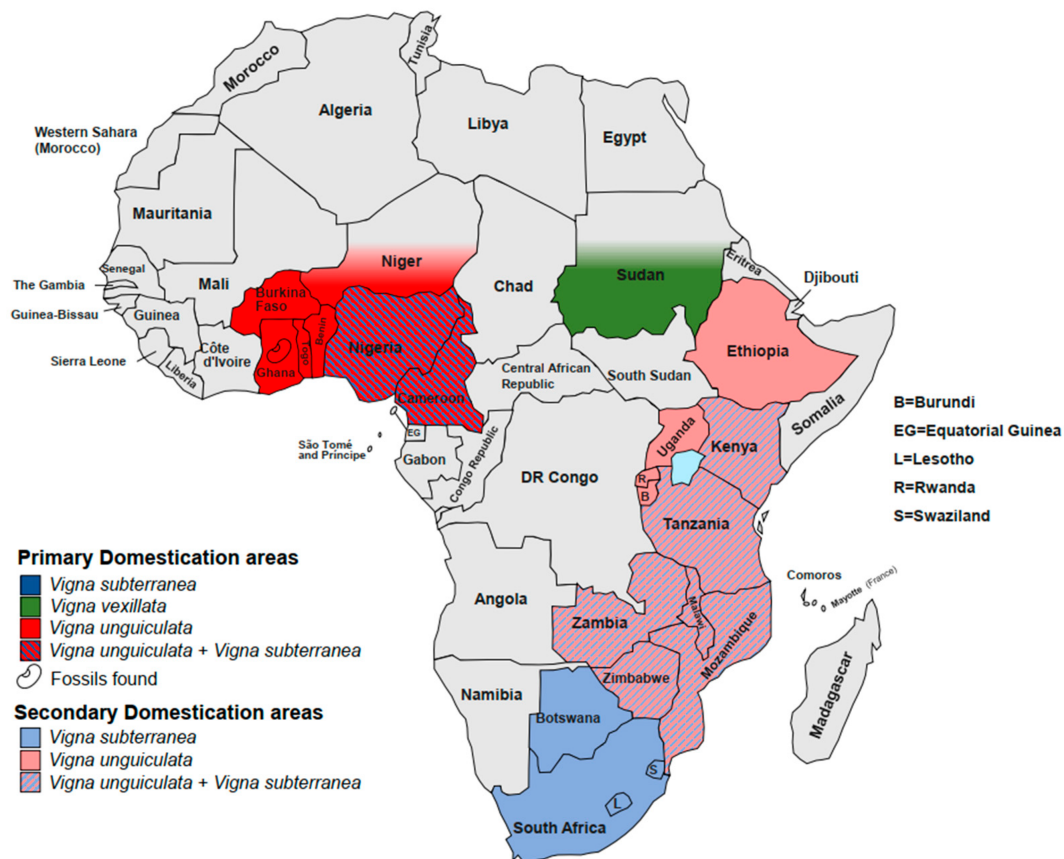


Figure 1. Primary and secondary domestication sites in Africa.

Morphological and DNA markers support the idea that domestication occurred only once, but analyses on whole genomes provide evidence for more independent domestication events in Africa and diversification events out of Africa [51][87]. Analyses of genetic variability are generally applied to identify the origin of species and the groups of accessions that show high variability in certain geographic areas and are interpreted as the most ancient populations. Although cowpea from West Africa showed a high genetic variability [88], cultivated accessions grown in East and West Africa were shown to be most closely related to the respective local wild lineages [52][89], thereby indicating that domestication could have occurred in both regions. Outside Africa, cultivated cowpea was exposed to different ecological conditions, including new biotic and abiotic stresses that probably have contributed to shaping the genetic structure of landraces. When cowpea moved through Asian regions (especially in Thailand, China, the Philippines and India), it encountered environments with more humidity and less brightness where the drying of pods and grains was hindered. Some accessions were selected for the use of the immature pods to produce a peculiar form of vegetable called yardlong bean (*V. unguiculata* ssp. *unguiculata* cv. *sesquipedalis*) [51][90][91]. Although Chinese accessions show lower genetic diversity compared to African cowpea, signals of genetic bottlenecks lead to the conclusion that a limited number of relatively recent selection events occurred; however, where the selection process arose is still unknown [92]. Moreover, other cultivar groups (e.g., ‘Textilis’, ‘Biflora’ or ‘Cylindrica’, ‘Melanophthalmus’) are classified by morphological traits [75][93]. Still, additional genomic analyses should be performed to confirm the genetic relationships and understand how and where these accessions originated [67][85][88][94][95].

3. *Vigna subterranea* (L.) Verdc.

Vigna subterranea, also named Bambara groundnut, is an indigenous African grain legume. Its common name derives from the groundnut (*Arachis hypogaea* L.) due to the hypogean pods’ growth, whereas the “Bambara” name is derived from a Malian tribe [96]. Despite its potential in terms of nutritional value and resistance to biotic and abiotic stresses [97][98], Bambara is cultivated mainly in small farms or in families as a subsistence crop [99], and naturally grows in semi-arid

regions in Africa. Regarding the origin of the species itself, the domesticated or semi-domesticated *Vigna subterranea* var. *subterranea* was most likely generated from its wild counterpart *Vigna subterranea* var. *spontanea* using both morphological and isozyme data [100][101].

The origin of this species is hypothesised to be in Mali, in the Timbuktu region [102], but the precise centre of origin is still unknown. In fact, there is no evidence of wild lineages in Mali [103]. Dalziel, Begemann and Goli [104][105][106] analysed a lot of morphologic traits such as seed morphology, seed pattern diversity and other diversity indices (number of days to maturity, pod length, number of stems per plant and internode length). They found that the most diversity is located in an area that spans from Jos Plateau and Yola Adamawa (Nigeria) to Garoua (Cameroon). Somta and Olukolu [107][108] evaluated the phylogeography of several accessions spread in Africa. The markers used (i.e., SSR and DaRT) showed a cluster with higher diversity in the area between Nigeria and Cameroon. The researchers confirm the area of origin while suggesting a possible subsequent introduction of Western domesticated accessions in East Africa (**Figure 1**). In contrast, Aliyu et al. [97], in an overview of the past two decades of genetic diversity analysis, also proposed that the Southern African region could constitute a divergent time-spaced domestication event. However, the researchers suggest that these hypotheses need further examination.

In terms of genetic diversity, Bambara has a peculiar behaviour. In fact, many researchers studied Bambara's genetics with different techniques to clarify how wide the genetic pool is and how homogeneous the single landraces are. Molosiwa et al. [109] evaluated genetic distances between 24 landraces with phenotypic and genetic markers (i.e., SSR and DaRT). The main results report that landraces are different to each other, suggesting the existence of great allelic diversity among the various populations. At the same time, though, single landraces tend to be very homogeneous, and in three generations of inbreeding became pure lines. This is due mainly to its self-pollinating nature [110] but also small farmers, who, by breeding the same landraces, also acted as selection drivers [111][112]. Molosiwa [113] selected 12 SSR markers and 5 Bambara accessions to evaluate the potential for creating pure lines, finding that these accessions at the second cycle of selection completely have lost the heterozygosity.

All these findings suggest that Bambara has incredible genetic potential. The genetic screening through the different lineages and the consequent discovery of peculiar sites of interest could be the basis for an improvement of crop programs. Moreover, the use of pure lines in agriculture is fundamental not only for the optimisation and standardisation of agricultural practices but also for the development of breeding programs. Currently, there are no reports of ongoing improvement or breeding programs for this species. The extremely wide pool of wild and domesticated accessions can be used to create ideal crops that can better withstand climate change as well as being able to grow with low agronomic inputs.

4. *Vigna vexillata* (L.) A. Rich.

Widely distributed in Africa, Asia, America and Australia, *V. vexillata* (Zombi pea) is one the least known and underutilized *Vigna* crops. Likewise, *V. unguiculata*, Zombi pea shows a high morphological diversity probably determined by geological, ecological, climatic and anthropomorphic constraints that also determined exceptional patterns of genetic variability [19][74]. Eight varieties including *vexillata*, *angustifolia*, *ovata*, *dolichomena*, *yunnanensis*, *pluriflora*, *lobatiflora* and *macrosperma* are recognized [12][19][23][114][115]. Var. *macrosperma* shows typical traits associated with domestication syndrome such as bush-like habit, early flowering and higher seed yield [116][117]. Moreover, loss of seed dormancy and various degrees of pod shattering were detected in different crop accessions while the wild seeds remained intrinsically dormant [118][119]. Several researchers reported that two forms were domesticated independently (i.e., seed type and tuber type), and some evidence lines suggest that the seed type was domesticated in Sudan, whereas the tuber type was domesticated in India (**Figure 1**) [120][121][122][123][124]. However, molecular analyses were performed on a limited number of accessions and loci [124], and the phylogenetic intra-specific delimitation has resulted in much more complexity than that of other *Vigna* crops [125]. Thus, modern genomic analyses are needed to resolve the genetic relationships and confirm the origin of the two forms.

Several studies have also shown that the Zombi pea is the result of a long adaptation process to different environmental stress, including acid, alkaline, saline, drought and wet soils [115][117][126][127][128]. Moreover, since some accessions were found to be resistant to different viral diseases and parasite insects, widely recognized as major pests of cowpea, this species is an important harbour of resistances to various biotic stresses, particularly useful to improve modern *Vigna* crops [129][130][131][132][133][134].

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