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REVIEW ARTICLE

A Review on Current Status and Future Prospects of Winged Bean (*Psophocarpus tetragonolobus*) in Tropical Agriculture

Patrush Lepcha [1] **· Ashley N. Egan** [2] **· Jeff J. Doyle** [3] **· N. Sathyanarayana** [1]

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Abstract Winged bean, *Psophocarpus tetragonolobus* (L.) DC., is analogous to soybean in yield and nutritional quality, proving a valuable alternative to soybean in tropical regions of the world. The presence of anti-nutritional factors and high costs associated with indeterminate plant habit have been major concerns in this crop. But occurrence of good genetic variability in germplasm collections offers precious resources for winged bean breeding. However, lack of germplasm characterization is hindering such efforts. From a genomic standpoint, winged bean has been little studied despite rapid advancement in legume genomics in the last decade. Exploiting modern genomics/breeding approaches for genetic resource characterization and the breeding of early maturing, high yielding, determinate varieties which are disease resistant and free of anti-nutritional factors along with developing consumer friendly value-added products of local significance are great challenges and opportunities in the future that would boost cultivation of winged bean in the tropics. We review past efforts and future prospects towards winged bean improvement.

Keywords Winged bean · Genomics · Biotechnology · Genetic resources · Molecular markers

Abbreviations

ANFs	Anti-nutritional factors
ISSR	Inter simple sequence repeats
KI	Kunitz type inhibitors
RAPD	Randomly amplified polymorphic DNA
SSR	Simple sequence repeats
WBA	Winged bean albumin
WCI	Winged bean chymotrypsin inhibitor

Introduction

Psophocarpus tetragonolobus (L.) DC., commonly called winged bean, Asparagus pea, or Goa bean, is a self-pollinated tropical legume classified within the phaseoloid clade of Leguminosae (Fabaceae). Winged bean has a twining habit, tuberous roots, longitudinally winged pods and both annual and perennial growth forms [1]. It has a diploid genome of 9 pairs of chromosomes (2n = 2× = 18; [2]) and an estimated genome size of 1.22 Gigabase pairs [3]. The plant grows in profusion in hot, humid, equatorial countries such as Indonesia, Malaysia, Thailand, the Philippines, India, Bangladesh, Myanmar and Sri Lanka [4].

Winged bean promises great economic and ecological significance to the tropical regions of the world, where soybean cultivation seems difficult. The fact that the most parts of the plant are edible at all stages of its life cycle coupled with its exceptional nutritional quality make it a promising candidate for increased, widespread use in protein deficient areas of the world, earning it titles such as '*one species supermarket*' and

Patrush Lepcha and Ashley N. Egan contributed equally to this work.

✉ N. Sathyanarayana
nsathyanarayana@cus.ac.in

1 Department of Botany, Sikkim University, 6th Mile, Tadong, Gangtok, Sikkim 737102, India

2 US National Herbarium (US), Department of Botany, Smithsonian Institution - NMNH, 10th and Constitution Ave NW, Washington DC 20013, USA

3 Section of Plant Breeding and Genetics, School of Integrative Plant Science, Cornell University, 412 Mann Library, Ithaca, NY 14853, USA

'*supermarket on a stalk*' [4]. If both seed and tuber yields are combined, winged bean can outperform many crop legumes that are conventionally grown in the tropics. It also nodulates more heavily than many other legumes [5], playing a significant role in soil improvement. In 1975, a clarion call to action for greater research into winged bean's potential for crop development was put forward by the United States National Academy of Sciences in a report entitled "*The Winged Bean: A High Protein Crop for the Tropics*" [4]. In the subsequent 15 years, a flurry of research efforts increased our understanding of this important legume, particularly in regards to its nutritive, anti-nutritive, protein, and chemical properties (Fig. 1).

However, thorough scrutiny of literature from this time suggests that these efforts in winged bean were not backed adequately by developments in breeding and genetic improvements, which seems to have pulled down its otherwise bright prospects. Today, after nearly four decades, much still needs to be done in terms of breeding and genetic improvement efforts in this crop, especially to develop broadly adopted, early maturing, high yielding varieties which are determinate, disease resistant and free of anti-nutritional factors. In order to mainstream winged bean cultivation, three areas need major focus: (a) the genetic improvement of winged bean requires, as a preliminary step, the characterization of whole germplasm collections in order to identify best donor lines and populations; (b) tracking the crop's domestication and evolutionary history is pivotal to future exploration and collection of genetic resources; and (c) like other underutilized legumes, winged bean suffers from a genomic gap since the advent of newer genetic technologies (1990 onwards; Fig. 1), which require exploring/exploiting newer opportunities thrown open by developments in genomic methods to strengthen breeding programs. In addition, development and commercialization of winged bean value-added products must be pursued vigorously to hit upon a much-needed economic boost through world-wide market for its products.

Here, we present a review of winged bean research to examine the current knowledge and past and present nutritional, agronomic, genomic and breeding status and advances in this crop, aspects dealt with the beginning sections of this review. In the later part, under a separate section - "Avenues for future focus" – we have flagged major issues and opportunities in this crop, discussed against the backdrop of developments in genomic research that would allow its development and cultivation on a broader scale in the tropics. We finish with thoughts concerning "Future prospects" for winged bean development.

Current Knowledge Base of Winged Bean

Botanical Aspects and Uses *Psophocarpus tetragonolobus* belongs to subfamily Papilionoideae, tribe Phaseoleae and is closely associated with *Erythrina* L. and *Otoptera* DC. [6]. Based on morphological and palynological characters, Verdcourt and Halliday [7] classified 9 species into subgenus *Vignopsis* and subgen. *Psophocarpus,* the latter divided into sections *Psophocarpus* and *Unifoliolatae* A.Chev. ex Verdc. Recently, Nur Fatihah et al. [8] carried out a morphological cladistic analysis of all 9 species, classifying them into subgenera *Lophostigma, Longipedunculares,* and *Psophocarpus,* further split into sections *Psophocarpus* and *Vignopsis*, with *P. tetragonolobus* in the former. Eight of the 9

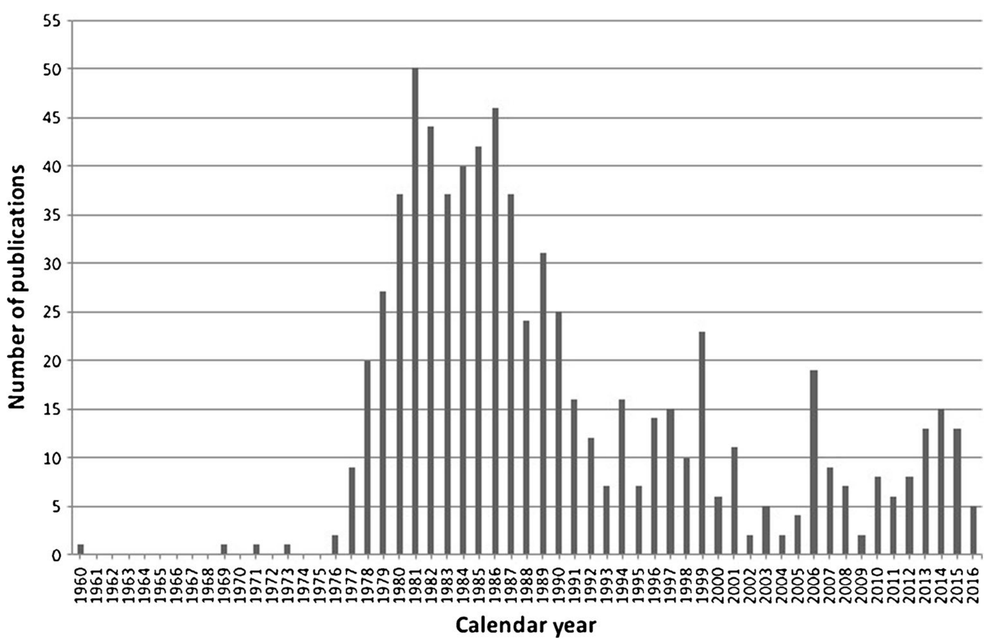

Fig. 1 Publication history of works centered on winged bean from year 1800 to present. Data gathered from an ISI Web of Science ALL database search with title search set to "*Psophocarpus tetragonolobus*" or "winged bean", pulling down 729 articles, beginning in 1960

species are endemic to West, Central and East Africa (Fig. 2). The ninth species, winged bean, is the only cultivated member of the genus and is distributed mostly in Asia (Fig. 2), but also introduced to other tropical areas [4].

Winged bean is predominantly a self-pollinated crop. However, up to 7.6% cross-pollination has been reported [9]. Even though winged bean is a perennial twining herb, it is mostly grown as an annual. The plant is 3–4 m tall and bears blue, bluish-white or purple flowers [4], borne singly or in threes on pseudoracemes (Fig. 3). Pods may reach 30–40 cm, containing 5–21 seeds. The pollen of winged bean is highly distinctive within the genus [10]. Pollen grains are spheroidal, with sizes ranging from 42.3–51.6 μm (polar axis) and 43.4–49.9 μm (equatorial axis). Some varieties produce starchy underground tubers that are 2–4 cm in diameter and 8–12 cm long [4].

With regard to uses, winged bean has been a minor food for diverse ethnic groups in Asia and Africa for centuries (Table 1) [11]. In India, immature pods are eaten as a raw vegetable [12] or pickled [7]. Elsewhere, the unripe seeds are used in soups and curries [11, 13], mature seeds are roasted and eaten like a peanut [13], and flowers are eaten and used to color dishes [4]. In Ghana, Burma and Papua New Guinea tubers are used in a range of culinary preparations [4]. It is also an ingredient for traditional Indonesian delicacies like *tempeh kecipir*, as well as in the preparation of snacks in Thailand [9].

The plant also reportedly possesses medicinal properties. In Malaya, roots are used as a poultice to treat vertigo and the leaves are used in the treatment of small pox [14]. In New Guinea, pods and tubers are considered roborant [15] and the pod extract is used to treat boils and ulcers [16]. Winged bean extracts show radical scavenging, antimicrobial and antioxidant activities [17–19]. A bioactive peptide with angiotensin-converting enzyme inhibitor activity has been reported from winged bean seed extracts [20]. Further active research endeavors into medicinal applications of winged bean should be pursued to gain a fuller understanding of its potential impacts.

Winged bean is suitable for cultivation in less fertile soils as it accumulates and fixes nitrogen with the help of bacterial symbionts [21]. It belongs to the cowpea cross inoculation group, nodulating with cowpea *Rhizobium* strains (EL, 32HI, LB756, etc.) in tropical and temperate environments [22], even in soils with no previous legume cropping [23]. As with other legumes, analysis of nitrogen and $\delta^{15}N$ values in nodules, roots and shoots showed that N accretion in winged bean critically depends on the *Rhizobium* strains colonized in root nodules [24]. Like other phaseoloid species, it is reported to be an ureide transporting plant, transporting fixed nitrogen from nodules as allantoin and allantoic acid [24].

Origin, Distribution and Cultivation Competing theories have been postulated to explain the origin of winged bean. A review by Zeven and De Wet [25] suggests four areas as probable centers of origin: (a) Indo-Malayan - due to a long cultivation history in eastern Assam, India; (b) Asiatic origin - which suggests winged bean was domesticated there from an unknown and now extinct endemic Asian progenitor; (c) Papua New Guinea - based on the large genetic variation found there; and (d) African center - due to similarities with African species. The African origin hypothesis has received much support due to observations that the morphology of *P. grandiflorus*, an African species, closely resembles winged bean [26]. Cytological and plant pathological evidence supports this [2]. It is possible that the progenitor of winged bean arose on the African side of the Indian Ocean and was carried east as a wild plant and then modified by human cultivation.

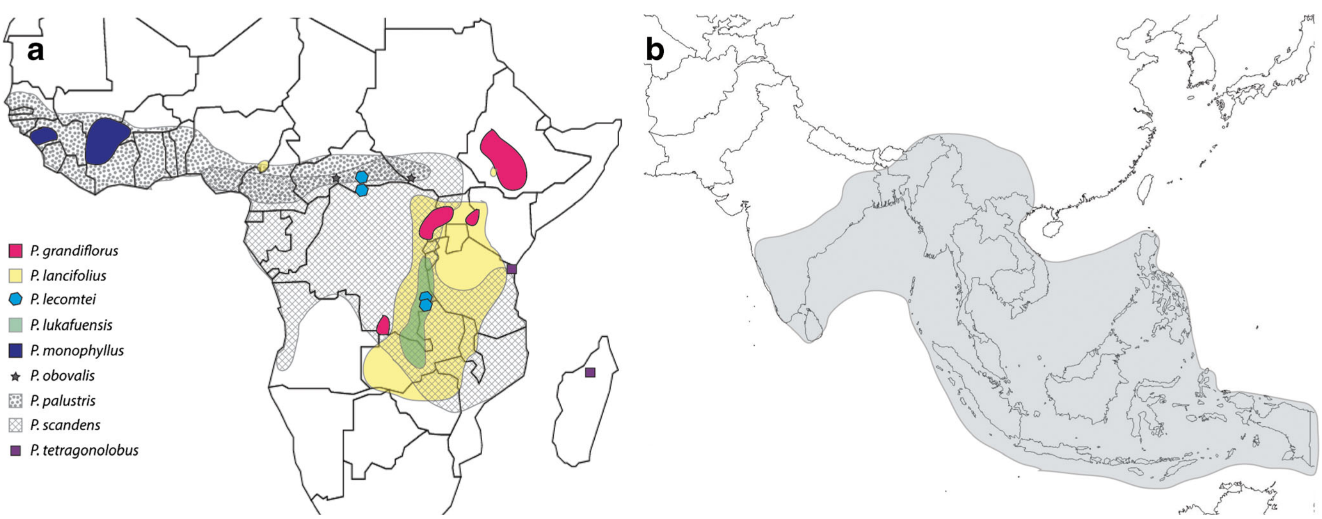

Fig. 2 Distribution of *Psophocarpus* in Africa (**a**) and of *P. tetragonolobus* in Asia (**b**). Distributions according to African Plant Database (http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php) and [4]

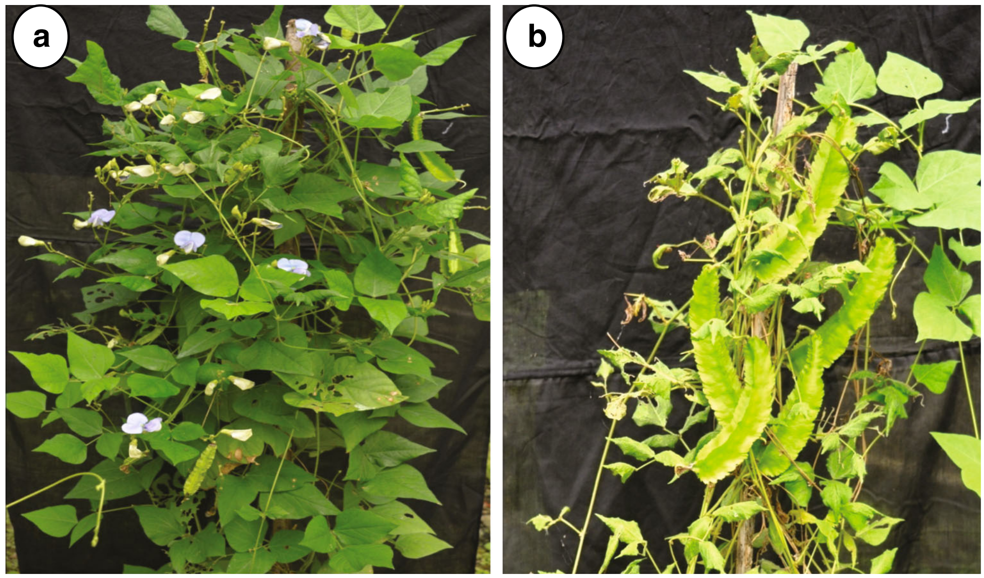

Fig. 3 Flowering (**a**) and fruiting (**b**) in *P. tetragonolobus*

Alternatively, it is possible that winged bean had a wider geographical distribution and was first domesticated in the Indian center or islands of Southeast Asia or Melanesia, as it is essentially a crop of Asia and the Western Pacific with considerable antiquity in these regions.

Geographically, India forms the westernmost limits while Papua New Guinea constitutes the eastern most border of winged bean distribution (Fig. 2b). In this range, winged bean is grown in Sri Lanka, Bangladesh, Burma, Indonesia, Malaysia, Thailand, and the Philippines [1]. It is introduced to Madagascar and several African countries [27]. In Papua New Guinea, it is grown extensively in the highlands and in north coast provinces for the tuber, which is highly prized for flavor and nutritional value [28]. In other countries, it is grown mostly as a minor garden crop along rice field borders, hedges, or fences. Winged bean is usually cultivated by planting the seeds in and around homesteads in small plots. It takes 4–5 months to mature, although harvesting of green pods can take place earlier. Papua New Guinean crops indicate that under conditions of minimum management, seed yields may range from 800 to 1,400 kg dry seed/ha, while tuber yields vary from 5,533 to 11,754 kg/ha [28].

Nutritive Value Winged bean is particularly well known for nutritious seeds, tubers, pods, foliage and flowers. Crude protein content of winged bean seed (33.82%) is higher than cowpea (22.5%), pigeon pea (22.4%) and lima beans (23.3%), and similar to soybeans (35%; Table 2) [29, 30]. Winged bean produces immense amount of protein in leaves (5–8% by weight), tubers (17–19%) and seeds (32–37%) [11, 31]. The amino acid content reported also reveals similar trends [11]. However, as in the case of other leguminous plants, sulphur-containing amino acids are limiting in winged bean. Winged bean seeds are rich in carbohydrates (23–40%) [4, 32, 33]. Minerals like K, P, S, Ca, Mg, Na, Fe, Mn, Zn, B, Ba, Sr, Cr and Cu and vitamins including retinol (Vitamin A), thiamin (Vitamin B1), riboflavin (Vitamin B2), niacin (Vitamin B3), pyridoxine (Vitamin B6), folic acid (Vitamin

Table 1 Yield data and food use of winged bean [11]

Plant part	Greatest yield reported (kg/ha)	Composition per 100 g fresh weight	Place consumed	Food preparation
Pods	34,000–35,500	1.9–4.3 g protein	S.E. Asia, Sri Lanka, P.N.G.[a], Ivory Coast	Steamed, fried, soups, salads
Tubers	5,500–11,700	3.0–15.0 g protein	Burma, P.N.G.	Steamed, roasted, boiled
Seeds	2,000–5,000	29.8–39.0 g protein 15.0–20.4 g oil	Indonesia, P.N.G, Ivory Coast	Parched, in tempeh, flour added to traditional dishes
Leaves	–	5.0–7.6 g protein	Sri Lanka	Steamed, salads
Flowers	–	2.8–5.6 g protein	P.N.G.	Steamed, salads

[a] Papua New Guinea

Table 2 Nutrient/minerals/physico-chemical properties of winged bean seeds [29]

Nutrients/minerals/ physico-chemical properties	Winged bean (concentration/ amount)	Nutrients/minerals/ physico-chemical properties	Winged bean (concentration/ amount)
Moisture (%)	9.22 ± 0.18	Calcium (mg/kg)	889.86 ± 0.63
Total ash (%)	4.91 ± 0.01	Sodium (mg/kg)	1,972.34 ± 0.69
Fat (%)	17.51 ± 0.35	Potassium (mg/kg)	4,219.30 ± 0.81
Crude fiber (%)	12.23 ± 0.13	Peroxide value (meg/kg)	11.41 ± 0.30
Crude protein (%)	33.83 ± 0.61	Saponification value (mgKOH/g)	190.34 ± 0.64
Carbohydrate (%)	22.30 ± 0.82	Unsaponification matter (g/kg)	16.36 ± 0.64
Magnesium (mg/kg)	2,238.18 ± 0.04	Acid value (mgKOH/g)	0.71 ± 0.01
Zinc (mg/kg)	36,476 ± 0.64	Iodine value	144.57 ± 0.53
Copper (mg/kg)	90.79 ± 0.72	Refractive index at 25 °C	1.47 ± 0.01

B9), ascorbic acid (Vitamin C) and tocopherol (Vitamin E) are also present in adequate quantity as recommended for the human diet [32, 34, 35]. In general, there is broad similarity between mineral and vitamin contents of winged bean and soybean. However, the content of thiamin, riboflavin and niacin in winged bean exceeds that of soybean and other beans [35].

Lipid constitutes the third major component after protein and carbohydrates in winged bean seed, with 94% of lipid available in free form and the reminder chemically or physically complexed with proteins or carbohydrates [33]. In mature seeds, total lipid content is estimated to be 14–25% [35, 36], with the unsaturated fatty acid component constituting 54–75% of this content [33, 37]. Major fatty acids in seeds are stigmasterol (66.4%) and β-sitosterol (25.1%). The lipid quality is enriched by the presence of mono- (38.6%) and poly-unsaturated fatty acids (36.9%) without trans-fatty acids, meeting the edible standard [33]. Winged bean seed contains oil in the range of 15–20.4% [4]. Khor et al. [38] noted that winged bean oil contains 30–40% saturated and 60–70% unsaturated fatty acids. About 10–20% of the saturated fatty acids contains behenic acid and about 50% of the unsaturated fatty acids consist of oleic and linolenic acids. Winged bean oil was found to have more saturated fatty acids and unsaponifiable matter than peanut and soybean oils, indicating that perhaps for edible purposes, winged bean oil is less preferable (Table 3). However, a recent study of physicochemical properties of winged bean seed oil found that the hexane extracted fatty oil, which is the most common industrial extraction process, agrees with all the edible characteristics as well as fatty acid compositions. Primarily, elaidic and parinaric acid, which are known anti-nutritional trans-fatty acids were absent in the hexane fraction and the fatty oil contained very little percentage (0.25%) of non-fatty acid compounds. Further, the oil is fit for edible purposes after refining by standard procedures such as the alkali-degumming method [33]. Another study has also found winged bean oil superior to soybean oil due to its high oxidative stability, solid fat content, and good thermal conductivity, making it good for frying food [39].

Table 3 Comparison of fatty acids contents of winged bean oil vis-à-vis other selected common food oils [11]

Food lipid	PUFA[a]	Mono-unsaturated FA[b]	Saturated FA	P/S[c] value
1. Corn oil	53	32	11	4.8
2. Soybean oil	59	20	15	3.9
3. Peanut oil	29	47	18	1.6
4. Chicken fat	26	38	32	0.8
5. Egg yolk	12	49	32	0.4
6. Pork fat	09	49	38	0.2
7. Beef fat	03	44	48	0.06
8. Coconut oil	Trace	07	86	–
9. Winged bean	30.7	39	30.3	1.0

[a] Polysaturated fatty acid

[b] Fatty acid

[c] The ratio of PUFA to saturated FA

Anti-Nutritional Factors With all the positive nutrition offered by winged bean, anti-nutritive factors (ANFs) also exist and have been extensively studied, including trypsin inhibitors, chymotrypsin inhibitors and hemagglutinins. Kortt [40] recorded differences in seed trypsin and chymotrypsin inhibitor activities, with trypsin inhibitor activity (mg trypsin inhibited per g of bean) found to be lower in Malaysian (average 23.4, range 22–24) and Indonesian (average 28, range 27–29) as compared to Papua New Guinea (average 36, range 31–42.5) or Myanmar (average 33, range 28–40) varieties. Trypsin inhibitor activity in winged bean ranges from 11,300 IU/g of bean sample [23] to 74,700 IU/g of sample [34], showing wide variation depending on cultivar. Kortt [40] found winged bean exhibits higher chymotrypsin inhibitor activity (30–48 mg chymotrypsin inhibited per g of bean) compared to trypsin inhibitor activity. So far, three Bowman-Birk-type inhibitors and nine Kunitz type inhibitors (KI) have been characterized from winged bean seeds [*e.g.*, 40–42], although recent winged bean transcriptome analysis of KI genes suggest many more [3]. The complete amino acid sequence of winged bean albumin-1 (WBA-1) determined by Kortt et al. [42] revealed homology with KI. Determination of the crystal structure of a double-headed α-chymotrypsin inhibitor [43] led to an understanding of the mechanism of inhibition of the protein against a chymotrypsin. Two putative KI genes (*WCI2* and *WCI5*) have been isolated of which *WCI5* is new to the *WCI* family and is exclusively expressed in winged bean seeds and showed inhibitory effects on proteinase activity and *Helicoverpa armigera* larval growth [44, 45].

Often, toxicity of the winged bean seed is attributed to its hemagglutinin content. Jaffe and Korte [35] detected hemagglutinin activity of +3 with normal rabbit erythrocytes and +5 with pronase-treated erythrocytes and showed that raw beans fed to rats caused considerable mortality in two weeks. A related study reported hemagglutinin activity in 27 varieties ranging from 77 hemagglutinin units/g to 154 hemagglutinin units/mg [46]. According to Kortt [46], three basic proteins isolated from winged bean (psophocarpin B1, B2 and B3) showed similar amino acid composition to soybean lectins. Two types of hemodimeric glycoprotein lectins (hemagglutinins) viz. basic lectin (WBA-I) and acidic lectin (WBA-II) have been characterized from winged bean [47] and have been shown to interact with and agglutinate various blood types differently [48]. Nonetheless, most trypsin and chymotrypsin inhibitors as well as hemagglutinating agents found in winged bean are heat–labile and are consequently destroyed by the application of moist heat. When defatted winged bean flour was autoclaved, about 30–40% of the trypsin inhibitor activity and 15% of the chymotrypsin inhibitor activity was inactivated, while hemagglutinin activity decreased 75–96%. Autoclaving for 30 min completely destroyed trypsin and chymotrypsin inhibitors and hemagglutinating agents, but rendered 50–66% of insoluble protein [35].

Phytate is another important anti-nutrient commonly found in legume seeds. Phytates are antioxidants that bind to some dietary minerals, interfering with their availability [49]. Phytate content in winged bean is estimated to be between 6.1–7.5 mg of phytate phosphorus/g of bean, equal to that of soybean. Like many beans, winged bean possesses free phenolics, tannins, phytic acid, flatulence factors, saponins, and hydrogen cyanide. Some of these, especially tannins and phenolic compounds, nonspecifically inhibit enzyme activity and form a complex with food proteins, reducing their quality [50]. Estimates of winged bean tannin content varied from 0.03–7.5 mg of D-catechin/g of bean [49], much lower than other legume species. Even with all this, the levels of phytates, etc., are not significantly high to cause adverse effects. Considering that most of these ANFs are destroyed by boiling or autoclaving [49], properly processed winged bean could be safely used as a major plant protein source.

Pests and Diseases Like most plants, winged bean is affected by insect pests, fungal and viral diseases, and pathogenic nematodes. *Hemiptera, Thysanoptera, Diptera, Coleoptera, Lepidoptera* and *Orthoptera* species are reported as pests on winged bean. *Maruca testulalis* (bean pod borer) and *Helicoverpa armigera* (cotton bollworm) target pods and flowers. *Leucoptera psophocarpella* (winged-bean blotch miner) extensively damages leaves, whereas *Mylabris afzelii* and *M. pustulata* damage flowers [51]. Caterpillars of *Aphis craccivora* (black bean aphid), *Henosepilachna signatipennis* (ladybird), *Ophiomyia phaseoli* (bean fly), *Lampides boeticus* (pea blue butterfly), *Nezara viridula* (southern green stink bug), *Podalia* spp., *Polyphagotarsonemus latus* and *Tetranychus urticae* are other pests that reportedly damage shoots, leaves and flowers [52]. Infestations of root-knot nematodes on winged bean have been shown, with *Meloidogyne javanica*, *M. incognita* and *M. arenaria* identified as major pathogenic nematodes, causing ~70% tuberous root loss [52]. Major viral diseases identified include necrotic mosaic virus which affects 9% of the total young plants in the field, ring spot mosaic virus which causes approximately 10–20% yield loss and leaf curl disease which has appeared only at Kpouebo, Ivory Coast [9, 51–53]. A new endornavirus, provisionally named Winged bean endornavirus 1, was recently discovered [54]. Five major fungal diseases have been reported from winged bean: false rust (*Synchytrium psophocarpi),* dark leaf spot (*Pseudocercosa psophocarpi),* powdery mildew (*Oidium* sp.; *Erysiphe cichoracearum*), collar rot (*Macrophomina phaseolina*, *Fusarium semitectum*, *F. equiseti*, *F. moniliforme*, *Rhizoctonia solani*) and choanephora blight (*Choanephora cucurbitarum*) [9, 53, 55]. Detailed symptoms and management of some of these pests and diseases are well described [52], but in the absence of comprehensive solutions, it is vital to screen germplasm through a uniform evaluation process to identify insect and disease resistant lines and enable marker assisted breeding programs to develop resistant varieties and cultivars [9].

Cytogenetics, Breeding and Biotechnology Cytological studies of the *Psophocarpus* genus showed a basic chromosome number of x = 9. Thus, *P. tetragonolobus* and all other species were confirmed to have 2n = 2× = 18 [56]. She et al. [57] examined finer karyotypic details of winged bean chromosomes using banding patterns and fluorescent *in situ* hybridization with the aid of 45S and 5S ribosomal RNA gene probes, illustrating the utility of these methods for species identification and differentiation.

Development of early maturing, high yielding, dwarf, erect, and non-shattering pod bearing plants with reduced anti-nutritional factors constitute major breeding objectives in winged bean. Unlocking the genetic diversity housed in global germplasm collections is therefore critically important. Morphometric evaluations showed good diversity for a number of traits in germplasm collections, including variation in leaf size and shape and pod color in Asiatic germplasm [58]. Genetic studies revealed dominance of purple over green for stem color, calyx color and pod wing color and rectangular over flat pod shape [59]. Eagleton et al. [60] showed variation in flowering habit. Good variability for nutritional and biochemical traits such as protein and oil content have also been shown [23].

Considerable effort has gone into developing superior winged bean varieties via mutation-breeding. For example, successful experiments resulted in a single, erect stem mutant, a multiple branched bushy mutant, and a mutant with long pods [61]. By gamma irradiation, three bushy mutants [62], an early-flowering mutation [63] and chlorophyll variants [64] were recovered, as well as seed coat color, low tannin-producing, and nodulation mutants [65]. Hakande [66] successfully induced a spectrum of mutations and identified about 22 desirable morphological and chlorophyll mutants. Unfortunately, the majority of mutant lines recovered so far have been reported to be sterile.

Considerable success has been had in developing micropropagation techniques in winged bean. Micropropagation using protoplast culture with 2-mercaptoethanol supplemented enzyme solution was successful [67]. Genetic stability of *in vitro* regenerated plants was tested by Koshy et al. [68] using RAPD markers. They found that callus-derived plants showed less fidelity vis-à-vis plants regenerated from shoot tip culture, axillary bud proliferation and cotyledon culture. Direct somatic embryogenesis from leaf explants was achieved via MS media combined with different hormonal concentrations [69]. Induction of callus and shoot proliferation from leaf, petiole, node and epicotyl explants has been demonstrated [70]. In an attempt to standardize gene transfer, Gill [71] integrated plasmid-encoded neomycin phosphotransferase (NPT-II) into the plant genome via epicotyl-derived protoplasts, but transformed calli could not be induced for shoot regeneration.

Molecular Markers and Genomics Winged bean has received little attention in terms of molecular breeding and genomic research, with few studies having used DNA markers for genetic analyses. Mohanty et al. [72] analyzed 24 winged bean accessions and determined that ISSR markers were superior to RAPD markers. Chen et al. [73] used ISSR markers to assess genetic diversity among 45 winged bean accessions and reported a narrow genetic base in their germplasm collection. Chapman [74] sequenced a seedling transcriptome from the winged bean genotype *Ibadan Local-1* and reported mining of ~1900 microsatellite and ~1800 conserved orthologous set loci. In a parallel effort to stimulate genomics assisted breeding programs in winged bean, Vatanparast et al. [3] sequenced transcriptomes of multiple tissues from two Sri Lankan winged bean genotypes from United States Department of Agriculture germplasm accessions *PI 639033* and *PI 491423* and reported large-scale marker development, identifying over 5,000 single nucleotide polymorphisms and ~13,000 SSR markers between their Sri Lankan and Chapman's Nigerian genotypes. Most recently, Wong et al. [75] developed 9,682 genic SSR markers via transcriptome sequencing from Malaysian accessions and validated 18 SSRs across 9 accessions.

Gene Expression and Regulation Understanding the regulation of gene expression during growth and differentiation is critical to produce cultivars with new abilities by genetic engineering. Preliminary efforts on structural and functional characterization of gene families involved in resistance against insects and pathogens have revealed important insights. Habu et al. [76] reported that winged bean chymotrypsin inhibitor (WCI) proteins are encoded by a multigene family and accumulate abundantly in seeds, tuberous roots and less so in stems, a finding confirmed by transcriptomics [3]. Inhibitory effects of these proteins on larval growth make their genes promising candidates for enhancing plant defense against *Helicoverpa armigera* [44]. Three Kunitz type chymotrypsin inhibitor genes (*WCI-3b, WCI2* and *WCI5*) have been isolated, with *WCI5* exclusively expressed in seeds [44, 76]. Studies on the winged bean chitinase gene *ChitWI,* which confers antifungal properties in many crop plants, revealed that the acidic class III chitinase was strongly expressed in roots [77] where it may be involved in root development. Vatanparast et al. [3] reported a phylogeny of 48 soybean trypsin inhibitor (STI) gene family sequences obtained from Sri Lankan and Nigerian winged bean transcriptomes. Their study found that the Kunitz-type inhibitor (KTI) gene family has expanded extensively in the winged bean lineage relative to other legumes.

Avenues for Future Focus

Origin of Domestication Knowledge concerning a crop's domestication history provides pivotal insights into its genetic past and future potential, especially in relation to wild relatives, species that act as natural reserves of diverse gene pools upon which to draw for genetic engineering and improvement. The current mystery behind the origin of domestication of winged bean presents a problem with regard to its genetic past. Our current understanding of the relationships among *Psophocarpus* species is based mostly on morphology [7, 8]. Sampling these species to generate a molecular phylogeny can provide insight into the relative genetic distance of the cultivated species from its wild relatives and perhaps shed light on its putative progenitors. Such a comparison would also enable us to determine the relative loss of genetic variation in the cultivated species, a phenomenon that often accompanies domestication. Further, comparing the cultivated winged bean with its wild relatives would enable discovery of 'domestication genes', thus providing insight into genomic loci of interest for further research and development.

Genomics-Assisted Trait Development Development of winged bean cultivars with desirable agronomic traits has no doubt been stymied by the relative lack of genetic resources for this orphan crop. Given the recent efforts in genomics and transcriptomics of winged bean and other legumes, the genetic resource base now exists to facilitate such efforts, unlike past research. Today, relatively inexpensive, widely available genomic technologies have the potential to spur research on winged bean forward like no era before. Next generation sequencing coupled with comparative genomic analyses, mapping, and synteny studies offer powerful methodological tools towards identification of functional SNPs and length variants associated with agronomically important traits in winged bean. In legumes, so far altogether six species: *Cajanus cajan* (833 Mb), *Cicer arietinum* (738 Mb), *Glycine max* (1112 Mb), *Lotus japonicus* (472 Mb), *Medicago truncatula* (373 Mb) and *Phaseolus vulgaris* (588 Mbp) have been entirely sequenced [78]. The information generated from these projects in terms of the estimated number of genes (28,269–48,680) and transcripts (25,640–243,067) plus ongoing or additional genome sequence efforts in *Pisum sativum* (4450 Mb), *Lupinus angustifolius* (924 Mb), *Trifolium pratense* (440 Mb), and *Arachis hypogea* (2800 Mb) can serve as references for sequencing efforts in winged bean. Further, a consensus genetic map using SSR, SNPs and gene-based markers covering over 20,141 cM and 11 linkage group for legumes has been reported [79]. In addition, an exhaustive database of marker repositories (SSRs, SNPs, and indels) is made available for common bean [80] and soybean [81]. These new tools will be useful in accelerating molecular breeding programs in winged bean. With such resources available, a thorough study of synteny between soybean and winged bean will be highly useful for comparative genomic and genome selection studies in this species. With genome sequencing becoming increasingly affordable, efforts should be put towards deep sequencing the genome of winged bean to enable large scale analyses of gene content, linkage mapping, evolution of repetitive elements, and association mapping.

Transcriptomics offers additional ability to analyze differential gene expression within tissues to aid in deciphering gene networks and regulatory pathways, provides genetic resources upon which to choose loci for targeted enrichment to enable large-scale nuclear and chloroplast marker development for phylogenetic or population genetic analyses, and enables a relatively complete, one-time sequencing of the expressed complement of a genome [82]. Recently, this work has begun with several studies sequencing transcriptomes from different areas of cultivation [3, 74, 75, 83]. The power of transcriptomics to further winged bean breeding efforts for traits of interest is exemplified by the research of Vatanparast et al. [3] who characterized the trypsin gene family in winged bean and by Singh et al. [83] who investigated differential gene expression in low- *vs.* high-condensed tannin containing cultivars, discovering over 1,000 differentially expressed contigs. These studies highlight genetic loci that may be potentially useful for genetic engineering or development of more suitable cultivars for human or animal consumption.

Agronomic Trait Development The genetic resources now available through transcriptomes and sequenced genomes of other crop legumes provide a base upon which to study and improve agronomically important traits. Winged bean transcriptomes can now be harnessed for trait-gene discovery, assessment of ecotype diversity, and many other trajectories of inquiry. As noted above, winged bean is known to suffer from a number of pests, viruses, and fungal pathogens. An investigation into the complement and evolution of disease resistance genes within the winged bean genome, as well as its wild relatives, may aid in the genetic engineering of resistant crop cultivars. Likewise, comparative transcriptome analyses across a morphologically or chemically diverse cultivar set drawn from across the range of winged bean might allow association mapping of traits important for agronomic development, such as the breeding of self-supporting cultivars or tolerance to different environmental growth conditions. Such efforts could potentially contribute to the development of a pivotal tropical crop resource in the genetic improvements of the "supermarket on a stalk".

Exploring Potential beyond Current Uses Development and commercialization of value added products is one other aspect that is likely to drive future demand for winged bean. Several such products as well as functional foods were developed earlier in an attempt to explore new opportunities for this crop. Winged bean Tofu, tempeh, snack foods, curd, weaning foods, coffee substitute, etc., were tested on a commercial scale in Thailand, Indonesia, and Ghana [11]. A few reports [50] indicate that processed oil from winged-bean seed has good nutritional quality and suitable for cooking, especially fried foods. However, these efforts have met with little success due to major drawbacks in large-scale production and processing of raw materials as well as commercialization. That said, efforts to commercialize winged bean products are still continuing as evidenced by recent patents. For example, in 2013, a Chinese company filed a patent for a method for high yield protein extraction from winged bean, with the aim that this product could then be used as an additive for commercial endeavors (patent CN 103275171A). Thus, parallel efforts are needed to diversify these products based on local needs and to establish an enabling policy environment and funding opportunities to move forward the efforts on value added product development and their commercialization.

Future Prospects

In the face of global climate change and growing demand for healthy, nutritious food sources, legumes as a whole are not being utilized to their full potential [84], winged bean among them. The exceptional nutritional quality along with tropical adaptation makes winged bean a promising candidate for cultivation in the tropical areas of the world. Winged bean has been cultivated by indigenous communities in Asia for centuries where it functions as an important protein source in local markets. The Food and Agriculture Organization of the United Nations (FAO) has noted that availability of legumes in Asian regions is low, and that winged bean is one of several legumes that is under-exploited [85]. Given its previous cultivation history in the tropics, its considerable nutrition quality, and continued development of resources for research, winged bean has the potential to become a global food security crop.

Despite the considerable information on taxonomy, cytology, nutritional analysis and other topics discussed above, research still needs to be done to realize winged bean's full potential for the dynamic needs of tropical agriculture. Past research efforts were hampered by a lack of genetic resources and knowledge upon which to build, critical infrastructure that can spur research efforts. Recent advancements, especially in the areas of transcriptome sequencing, marker discovery, tissue culture protocol development, etc., provide a foundation upon which to make genetic and genomic advances. By integrating related genomic resources such as the soybean and common bean genomes with multiple sequenced transcriptomes of *Psophocarpus*, winged bean is now poised to benefit from comparative genomics. Inferences concerning the evolution of genome-wide gene content and expression can be made, along with easy creation of molecular markers for phylogeny, genetic diversity assessment, population structure analyses, linkage mapping, and many other endeavors that would help to increase our understanding and utilization of this species.

As a tropical vine, winged bean production is currently limited by the need for structural support and most cultivars are day-length sensitive, features that limit yield [51]. And, as discussed above, winged bean contain some anti-nutritive properties, for example, trypsin and tannin content. However, we are confident that future genetic studies using site-directed mutagenesis and other breeding techniques can overcome these challenges to produce viable cultivars adaptable to a variety of conditions and needs.

We reiterate the clarion call to action to researchers worldwide to build upon our current knowledge and new genetic and genomic resources to answer key questions concerning the origin of the cultivated winged bean, trait specific-characterization of germplasm, identification of genes and molecular markers underlying the key agronomic and chemical traits and contribute to the development of genetic and physical maps. This new wealth of information and resources will accelerate crop improvement efforts in winged bean and thus lead to varieties with improved yield and quality. Establishment of an enabling policy and funding environments through governmental and non-governmental organizations will be critical to push forward research and development efforts. Yet, the nutritional potential of this legume demands such efforts. We have no doubt that renewed research efforts, particularly those employing genomics technologies, will thrust winged bean forward and help turn this orphan legume crop into one of worldwide impact.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflicts of interest.

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