



REVIEW ARTICLE

Nutrition, breeding and biotechnology of leguminous root crops for food security: Yam bean, African yam bean and Winged bean

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Received: 26 May 2025; Accepted: 02 July 2025; Available online: Version 1.0: 23 September 2025

Cite this article: Gomathi S, Murugesan P, Sujatha K, Daniel BA, Ashwini A, Venudevan B, Alex AV, Perinba SC, Thangamuniyandi M. Nutrition, breeding and biotechnology of leguminous root crops for food security: Yam bean, African yam bean and Winged bean. Plant Science Today. 2025;12(sp3):01–11. <https://doi.org/10.14719/pst.9638>

Abstract

Yam bean (*Pachyrhizus spp.*), African yam bean (*Sphenostylis stenocarpa*) and winged bean (*Psophocarpus tetragonolobus*) are protein- and carbohydrate-rich leguminous root crops with significant potential for food security and industrial applications. Yam bean (*P. erosus*) has potential to yield storage root between 120-145 t/ha, with a starch content of 45-55 %, while its seeds contained 29.2 %-32.1 % protein and 14.09 %-18.91 % crude fat, making it a nutritionally valuable leguminous tuber crop. Advances in its breeding included SSR markers for diversity assessment, rotenone-free cultivars and interspecific hybridization. African yam bean is cultivated across West and Central Africa, with storage root yields reaching up to 80 t/ha and seed yields ranging from 0.4 to 2.8 t/ha, while its tubers contained 16 % protein and 68 % carbohydrates and seeds provided 37 % protein and 64 % carbohydrates. Recent genetic improvements included early-maturing varieties (120-150 days), SNP markers for yield selection and enhanced disease resistance against anthracnose and rust. Winged bean produced tuber yields of 15.5 t/ha and seed yields up to 4.0 t/ha, with seeds containing 28 %-45 % protein and 14 %-20.4 % fat, while tubers offer 12.26 %-19.07 % protein and served as a carbohydrate-rich food source. Genetic advancements in marker-assisted selection (MAS), QTL mapping (qPL1, qSS2, qFC3) and mutation breeding (gamma irradiation 100-400 Gy) had improved productivity. Additionally, the tissue culture protocol for winged bean seeds was optimized using MS media supplemented with 2.0 mg/L BAP and 0.5 mg/L NAA, resulting in 92 % shoot regeneration. Future research is recommended to focus on genome editing, polyploid breeding, post-harvest optimization and functional food applications to enhance crop utilization and sustainability.

Keywords: African yam bean; conventional breeding; leguminous tubers; QTL mapping; SNP markers; winged bean; yam bean

Introduction

Legumes belonged to the Fabaceae family and included plants with pods, stems and leaves. The edible seeds of legumes, known as pulses, such as beans, lentils and peas, play a crucial role in global food security. While legumes had various agricultural uses, such as animal feed, cover crops and soil enrichment, pulses are primarily used for human consumption (1). The Fabaceae family is one of the largest plant families, comprising over 800 genera and 20,000 species, characterized by compound leaves, nitrogen-fixing ability and bean-like pods, which contributed to soil fertility improvement (2). Pulses such as kidney beans, black beans, chickpeas and lentils serves as key protein sources, particularly in India, which is the world's largest producer of pulses, contributing 25 % of global pulse

production and accounting for 35 % of total global acreage (3). However, despite its dominance in production, India still imports around 3-4 million tonnes (MT) of pulses annually to meet domestic demand, highlighting a supply-demand gap (4). Recent studies emphasized the potential of underutilized legumes like yam bean, African yam bean and winged bean to enhanced food security, improve nutrition and support sustainable agricultural systems. Globally, pulse production reached 92 million tonnes in 2022, with major contributors including Canada, Myanmar, Australia and the USA. Yet the demand for pulses grow at an annual rate of 1.2-1.5 %, outpacing production (5). The increasing demand for plant-based proteins, driven by changing dietary preferences, population growth and sustainability concerns, created an

urgent need to expand pulse production and diversify legume crops. However, conventional pulses face climate-related production constraints, requiring a shift towards non-traditional, underutilized legumes such as winged bean (*Psophocarpus tetragonolobus*), yam bean (*Pachyrhizus spp.*) and African yam bean (*Sphenostylis stenocarpa*). These leguminous root crops offers higher protein content (28-45 %) in seeds, resilience to marginal environments and dual-purpose use, producing both seeds and storage roots, making them promising candidates for sustainable agriculture. Yam bean is primarily cultivated in Mexico, Peru, Ecuador, Brazil, Thailand, Vietnam, the Philippines and Indonesia (6), while African yam bean was grown in Nigeria, Ghana, Cameroon, Uganda, Kenya, the Democratic Republic of Congo and Sierra Leone (7, 8). Winged bean was widely cultivated in Myanmar, Thailand, Malaysia, Indonesia, Papua New Guinea, Sri Lanka, India and the Philippines (9). Despite their potential, research on genetic improvement, climate adaptation and commercialization of these legumes remained inadequate. Expanding breeding programs, leveraging molecular tools (e.g. QTL mapping, marker-assisted selection and genome sequencing) and integrating underutilized legumes into conventional agricultural systems are critical to confirming future protein security and climate-resilient food production (10).

Leguminous root crops and their importance

Among legumes, certain species developed underground storage roots that are rich in carbohydrates. These plants often have vining or prostrate growth habits and their storage roots acted as bio-drills improving soil structure. Leguminous root crops have ethnobotanical significance and were traditionally used for food and medicine in different cultures (11). Recent research focused on genetic improvement of yam bean, African yam bean and winged bean using molecular breeding, genomic selection and biofortification to enhance yield, nutrition and climate resilience (12). Advances included protein-rich winged bean cultivars high-yielding yam bean varieties (13) and drought-resilient African yam bean lines (14). Despite their nutritional and agronomic benefits, many leguminous root crops remained undomesticated and underutilized due to cultural shifts, management challenges and competition with commercial crops.

Potential of leguminous root crops

Leguminous root crops grow in diverse environments, from deserts to temperate regions. A research report identified 22 legume genera with underground storage roots or tubers, including *Phaseolus coccineus* (scarlet runner bean), *Vigna vexillata* (tuber cowpea), *Lablab purpureus* (hyacinth bean), *Sphenostylis stenocarpa* (African yam bean), *Pachyrhizus erosus* (yam bean) and *Psophocarpus tetragonolobus* (winged bean) (15). The International Legume Society highlighted ten key legume root or tuber crops, including *Pachyrhizus tuberosus* (Yam bean), *Phaseolus coccineus* (Scarlet runner bean), *Lathyrus linifolius* (Everlasting pea), *Melilotus alba* (White sweet clover), *Sphenostylis stenocarpa* (African yam bean), *Vigna vexillata* (zombi pea), *Glycine tomentella* (Wild soybean), *Psophocarpus tetragonolobus* (winged bean), *Vigna lanceolata* (Pencil yam) and *Apios americana* (American groundnut). These crops originated from regions such as North America, Central America, Western and Central Africa, Southern Asia and

Australia (16). Among these, *Pachyrhizus tuberosus* (yam bean), *Sphenostylis stenocarpa* (African yam bean) and *Psophocarpus tetragonolobus* (winged bean) are nutritionally significant due to their seeds and storage roots rich in protein and their potential for commercial cultivation (17, 18). This review focused on their genetic improvement and economic utilization to promote sustainable food security.

Yam Bean

Yam bean is a significant leguminous root crop (19). Belonging to the Fabaceae family, subfamily Faboideae, tribe Phaseoleae and subtribe Glycininae, *Pachyrhizus* included three major species: *P. erosus* (Mexican yam bean), domesticated in Mexico and Mesoamerica, *P. tuberosus* (Amazonian yam bean), native to South America's tropical lowlands and *P. ahipa* (Andean yam bean), from the Andean region (National Research Council, 1989). All three species shared a diploid chromosome number ($2n = 2x = 22$), allowing interspecific hybridization (19, 20). The plant is characterized by its trifoliate, bright green leaves with ovate and pointed tips, which are supported by slender, twining herbaceous stems that allowed for climbing growth (21). The inflorescence consisted of papilionaceous purple-blue flowers arranged in terminal racemes, facilitating cross-pollination. The plant produced elongated, slightly curved green pods that contained brown, round and hard seeds when mature. The seeds are rich in rotenone, a natural insecticide, making them inedible (22). The seeds are globular or rectangular in shape (23). Yam bean seeds are medium to large (7-12 mm diameter, 1.2-1.8 mm thick), round to oval in shape, with a hard seed coat in white, light brown, or dark brown and a 100-seed weight of 10-15 g (24, 25). The seed yield of yam bean varied significantly based on species, genotype and environmental conditions. Studies indicated that the yield of *Pachyrhizus erosus* ranged between 0.5 to 2.5 t/ha, with some improved genotypes reaching up to 3.0 t/ha under optimal conditions. Additionally, *Pachyrhizus ahipa*, an Andean species, was reported to yield between 0.8 to 2.0 t/ha of seeds (26). The storage tubers, the primary edible portion, exhibited a light-brown, rough skin with high starch and water content, contributing to their crisp and juicy texture (17) (Fig. 1). The tubers of yam bean varied significantly in size, with diameters ranging from 5 to 20 cm and weights from 0.5 to 5 kg, depending on the cultivar and environmental conditions. The storage roots are generally round to oblong in shape, with a smooth, thin skin that could be white, light brown, or slightly purple. The flesh colour is usually white or cream, with a crisp and juicy texture. The thickness of the tuberous root varied from 3 to 7 mm in skin depth, making it highly perishable under poor storage conditions (27). Reports indicated that under optimal conditions, *Pachyrhizus erosus* yield between 20 to 60 tons per hectare (t/ha), with *Pachyrhizus ahipa* reaching up to 40 t/ha storage roots in certain environments (17). The different species of yam bean differed significantly in agronomic traits, climatic preferences and starch properties. *P. ahipa* thrive in cool climates, exhibited a bushy-erect growth habit with day-length insensitivity and have low storage root dry matter content, making it suitable for raw consumption (28, 29, 30). *P. erosus*, in contrast, prefers warm climate, produced turnip-shaped tubers and contained 79.29 % to 82.54 % carbohydrates and 4.22 % to 5.87 % protein (31, 32). This species is sensitive to day-length and yield 120-145 t/ha storage



Fig. 1. View of the yam bean plant displaying its botanical parts including leaves, stem, flowers, pods and seeds (square and round shapes).

root in Mexican cultivars (32). *P. tuberosus*, found in South American lowlands, had higher intra-specific variability and its 'Chuin' cultivars, with high root dry matter content, are consumed like cassava (33, 30). It requires photoperiods of 14-5 hours for optimal tuberization and yielded 70 - 80 t/ha storage roots within 4-6 months (34). These legumes are nitrogen-fixing, enhancing soil fertility and offering a protein content three to five times higher than cassava or sweet potato, making them valuable low-glycemic food crops (35). Yam bean storage roots are rich in starch with low amylose (< 16 %) and high amylopectin (85 % to 91 %), similar to rice (36). The proximate composition of the storage roots included 10 % to 35 % starch, 4 to 10 % protein and 3.6 % to 4.1 % fiber (37). They are consumed raw, baked, boiled, fried, or roasted and contain phytoestrogens such as genistein and daidzein, which have potential applications in hormone replacement therapy (38). However, yam bean seeds are toxic due to high rotenone content, which is lethal to humans, insects and fungi (19). Seed toxicity varied within and between species, suggesting breeding potential for rotenone-free cultivars to enable safe consumption of immature pods and seeds. Additionally, chemical compounds from yam bean are used in emulsions, foams, textures and microencapsulation in the pharmaceutical, cosmetic and food industries. *P. ahipa*, primarily found in Bolivia, exhibited vining, bushy, or semi-erect growth forms, matured within five months and yield 30 to 50 t/ha of storage roots with 45 % to 55 % starch, mostly amylopectin (37). *P. tuberosus*, abundant in the Peruvian Amazon, thrive from sea level to 1,900 m, producing 70 to 80 t/ha of storage roots in 4 to 6 months, with 4.3 % to 7.4 % protein and 0.3 % to 0.5 % lipid (20). The nutritional composition of yam bean storage roots and seeds, as reported by, highlighted

significant differences between the two parts of the plant. The storage roots were rich in water (82.4 % to 87.8 %), carbohydrates (10.6 to 14.9 g per 100 g) and vitamin C (14 to 21 mg), while being low in protein (1.5 to 2.4 g) and fat (0.09 to 1.3 g) (25). In contrast, the seeds are protein-dense (29.2 to 32.1 g per 100 g), with high crude fat (14.09 % to 18.91 %) and crude fiber (6.7-7.1 g), making them a potential source of plant-based protein. Additionally, defatted seed flour contained even higher protein content (45.6 to 48.8 g/ 100 g) and palmitic acid constituted 25 % to 30 % of the total fatty acids, indicating its potential application in food and industrial uses. The detailed nutritional composition of yam bean tubers and seeds is provided in Table 1. The yam bean was propagated by seeds but primarily cultivated for its tubers, as the seeds contain rotenone, a compound with industrial applications.

Advances in breeding and biotechnology of yam bean

Genetic diversity in *Pachyrhizus erosus* was assessed using multivariate analysis, revealing significant intra and interspecific variation. Intraspecific phenotypic variation ranged from 0.00 to 82.61 % for quantitative traits and 0.00 to 80.03 % for qualitative traits, while interspecific phenotypic variation ranged from 0.00 to 95.02 % for quantitative traits and 0.00-81.58 % for qualitative traits. The Shannon-Weaver diversity index (H') for quantitative traits was 0.83, indicating high diversity within and among species (17). Genetic improvement through interspecific hybridization and breeding for disease-resistant, high-yielding and rotenone-free cultivars is expected to maximize *Pachyrhizus*'s agricultural and industrial potential (35). Studies on flower color inheritance in yam bean provided insights into genetic control mechanisms (39), while DNA barcoding has improved cultivar identification and genetic diversity assessments (24). Additionally, SSR

Table 1. Nutritional composition of Yam Bean tubers and seeds

Component	Tubers (per 100g)	Seeds (per 100g)
Energy	186-264 KJ	-
Water	82.4-87.8 %	-
Protein	1.5-2.4 g	29.2-32.1 g
Carbohydrates	10.6-14.9 g	32.6-36.5 g
Fat	0.09-1.3 g	5.2 g
Iron	0.8-1.1 mg	-
Ascorbic Acid (Vitamin C)	14-21 mg	-
Defatted Seed Flour Protein	-	45.6-48.8 g
Crude Fiber	-	6.7-7.1 g
Ash	-	6.0-6.4 g
Palmitic Acid	-	25-30 % of total fatty acids
Crude Fat	-	14.09-18.91 %
Rotenone	-	1,000-3,000 ppm (0.1-0.3 %)
Pachyrrhizine	-	100-300 mg
Component	Tubers (per 100 g)	
Energy	186-264 kJ	-
Water	82.4-87.8 %	-

Source: (25)

markers from soybean were successfully used for yam bean genetic studies (40). In India, the All-India Coordinated Research Project on Tuber Crops (AICRP TC) released *P. erosus* varieties such as Rajendra Mishrikand 1 (RM-1) and Rajendra Mishrikand 2 (RM-2) (41). A recent study reported that a germplasm from Havelock island exhibited lengthy vine growth (more than 2 meters), whereas RM-1 had short vines (less than 1.5 meters) and had a longer pedicel (4.1 cm-4.4 cm) compared to RM-1's shorter pedicel (2.1 cm-2.3 cm) (23). The variety 'EC-40' was reported to produce 45-60 t/ha of tubers developed via clonal selection at the International Potato Center (CIP), Peru (26). A major breeding achievement in yam bean was the development of high-yielding and rotenone-free genotypes, such as *Pachyrrhizus erosus* 'CIP-209', which demonstrated a tuber yield of 55 t/ha while ensuring low rotenone levels, making its seeds safer for human consumption. This variety was developed through marker-assisted selection (MAS) and recurrent selection breeding at the International Potato Center (CIP), Peru (26).

African yam bean

African yam bean (*Sphenostylis stenocarpa*) is a legume from Sub-Saharan Africa, known for its edible storage roots and striking deep violet flowers. African yam bean is cultivated in various regions: the tubers were grown in countries like Cameroon, Gabon, the Democratic Republic of Congo, Ethiopia and parts of East Africa (e.g. Malawi and Zimbabwe), while the seeds were mainly harvested in countries like Nigeria, Ghana, Côte d'Ivoire and Togo. The flowers are pollinated by ants and wasps and the pods exploded when mature due to heat. African yam bean held considerable nutritional potential, making it a valuable crop for both food and livestock feed. Although it was believed to have originated in Ethiopia, its cultivation was primarily found in West and Central African countries, such as Cameroon, Ghana and Nigeria. The crop is grown for both its seeds and storage roots both of which are edible. African yam bean is a diploid species with a chromosome number of $2n = 22$. It has large cleistogamous flowers, meaning self-pollination occurred at a high rate of about 90 % - 91 %. The seeds of African yam bean came in various colors, including white, grey, creamy, brown, purplish and black, while some seeds exhibiting variegated or mosaic patterns (42). Researchers (43) explored seed morphology traits

such as seed size, coat texture and color, which influence storage quality and susceptibility to insect damage. Larger seeds show better viability retention and resistance to fungal infections (Fig. 2).

African yam bean seeds are small to medium-sized (5 - 8 mm diameter, 0.8 - 1.5 mm thick), oval to kidney-shaped, with a moderately hard seed coat in white, cream, brown, purple, black, or mottled colors and a 100-seed weight of 8 g-12 g, which reflecting high genetic diversity and adaptation (44, 45). Reported seed yields ranged from 0.4 to 2.8 t/ha, with local landraces generally yielding around 1.0-1.5 t/ha, while improved accessions produced up to 2.5 t/ha under favorable agronomic conditions (46). Studies emphasized that staking could increase yield by two-fold compared to non-staked plants due to better light interception and reduced lodging (47). African yam bean tubers exhibit a spindle-shaped or irregular form, ranging from 3 cm to 10 cm in length and 2 cm to 5 cm in width, with an average weight of 200 g to 1 kg per tuber. The skin is rough and varied in color from dark brown to reddish-brown, while the flesh is typically white to cream-colored. The tuber skin thickness is relatively high (4 mm to 10 mm), making it more resistant to post-harvest deterioration than yam bean tubers (48). The tubers of the crop had different shapes, such as ovate, spindle and irregular (Fig. 3). Whereas winged bean tubers were relatively smaller compared to other leguminous tubers, with a diameter of 2 cm to 4 cm and a fresh weight range of 50 g to 500 g per tuber. They had an elongated, cylindrical shape, often tapering at the ends. The skin was thin and smooth, ranging in color from light brown to yellow, while the flesh was typically white. The tuber skin thickness was approximately 2 mm to 5 mm, which contributed to its relatively short shelf-life (49). Tuber yield is generally lower than yam bean, ranging between 5 to 15 t/ha under rain-fed conditions, but with improved agronomic practices, yields could reach up to 25 t/ha (47). Author explored the potential of lectin found in seeds as a biological insecticide against key storage pests, including the cowpea weevil (*Callosobruchus maculatus*). Both seeds and tubers are highly nutritious, with the seeds containing 37 % protein and 64 % carbohydrates, while the tubers contained 16 % protein and 68 % carbohydrates. Although the seeds have low crude fat content (2.38 % to 2.62 %), they are rich in essential amino acids like histidine, isoleucine, lysine and methionine, making them a valuable source of balanced nutrition.



Fig. 2: African yam bean tubers and seeds



Fig. 3. View of winged bean plant displaying botanical parts along with diversity in seed size and colours.

The tubers also provide significant amounts of magnesium (167 mg / 100 g) and potassium (1010 mg / 100 g), which are beneficial for human health. The proximate composition of African yam bean seeds and tubers, as reported by multiple studies (50, 42, 51) revealed notable variations between the two plant parts. The seeds were significantly richer in protein (19.53 %-29.53 %) compared to the tubers (4.91 % 15.86 %), making them a valuable protein source. Carbohydrate content was high in both seeds (49.88 %-63.51 %) and tubers (46.59 %-66.52 %), while fiber was more prominent in tubers (6.93 %-12.13 %) than in seeds (2.47 %-9.57 %). The seeds had relatively lower fat (1.39 %-7.53 %) and moisture (1.93 %-13.30 %) than tubers (1.06 %-4.04 % fat, 10.3 %-21.91 % moisture), whereas tubers contained higher ash content (4.59 %-9.99 %) than seeds (1.86 %-5.35 %), indicating a greater mineral presence. These findings suggested that while the seeds were nutritionally protein-rich, tubers provide a significant carbohydrate and mineral source (Table 2). Despite its importance, the crop faced several challenges that hindered its broader adoption and utilization. These include the long cooking time required for the beans, the presence of an undesirable "beany" flavor, antinutritional factors and bioactive compounds that could inhibit digestion. Other constraints included the crop's long gestation period, photoperiodic sensitivity and climbing growth habit. Furthermore, the germplasm of African yam bean existed mainly as landraces and accessions, with very few improved cultivars available. Research on African yam bean remained limited and the development of elite varieties was still

Table 2. Proximate composition of African yam bean seeds and tubers

Component	Seeds (%)	Tubers (%)	References
Protein	19.53-29.53	4.91-15.86	(42, 50, 51)
Carbohydrates	49.88- 63.51	46.59-66.52	(42, 50, 51)
Fat	1.39-7.53	1.06-4.04	(42, 50, 51)
Fiber	2.47-9.57	6.93-12.13	(42, 50, 51)
Ash	1.86-5.35	4.59-9.99	(42, 50, 51)
Moisture	1.93-13.30	10.3-21.91	(42, 50, 51)

in its infancy.

Advances in breeding and biotechnology of African yam bean

Recent research findings had led to significant advancements in African yam bean. Cooking time was been reduced by improving seed coat properties and starch composition, making the beans more suitable for food processing, with studies highlighting the role of SNP markers in selecting desirable traits (45). Yield improvements were observed, with storage root yields reaching up to 80 t/ha under optimal conditions and new breeding strategies were proposed to enhance productivity further (52). Disease resistance was enhanced against major pathogens, including flower bud rot disease, anthracnose (*Colletotrichum* spp.) and rust (*Uromyces* spp.), through genetic diversity studies utilizing molecular markers such as SNPs and SSRs (14). Additionally, early maturing varieties were developed, reducing the maturity period from 140-270 days to 120-150 days, which enhanced adaptability to short-season cultivation (53). Studies across different growing seasons revealed significant variability in seed characteristics, including 100-seed weight (20-25g), length (8-8.9mm), width (6.3-6.9mm), thickness (6.2-6.9mm) and

texture (rough, wrinkled, or smooth seed coats), along with starch granule sizes ranging from 4-40µm in length and 4-25µm in width (52). Additionally, seed hardness was confirmed as a heritable trait influenced by calcium ion concentration and phytate levels, significantly impacting seed processing and germination success, with hardness measurable through texture analysis tools (45).

A genetic diversity assessment of 100 germplasm accessions in Nigeria reported significant phenotypic variations, demonstrating a broad genetic base useful for breeding programs (54). Biotechnological approaches further enhanced genetic improvement in African yam bean. A preliminary study using DArT arrays has identified SNPs, marking an important step toward molecular breeding (14). Furthermore, an extensive genetic analysis of 169 germplasm accessions using 26 phenotypic traits and 1,789 SNP markers enabled precise differentiation and clustering of accessions, providing a robust foundation for targeted breeding efforts (13). AYB-1 and AYB-2 yielded 15-25 t/ha of tubers and 2.5 t/ha of seeds, bred through pedigree selection for drought resistance at the International Institute of Tropical Agriculture (IITA), Nigeria (55). The application of genome-wide association studies (GWAS) and hybridization breeding has led to the development of AYB-10, a drought-resistant variety capable of producing 20-25 t/ha of tubers and 2.8 t/ha of seeds under water-deficit conditions (56).

Winged bean

Winged bean (*Psophocarpus tetragonolobus* (L.) DC.) is a tropical legume from the Fabaceae family, native to Papua New Guinea. Winged bean is a dual-purpose crop valued for both pods and tubers. It thrived in tropical and subtropical regions, particularly in humid climates with well-drained loamy soils (57). It is widely cultivated in Southeast Asia, Africa and parts of South America, with notable production in Myanmar, Indonesia, Malaysia, Thailand and Papua New Guinea (58). In India, it was grown in Assam, Chhattisgarh, Tripura, Meghalaya, Nagaland, Odisha, West Bengal and other southern regions. Winged bean is often called the "one species supermarket" due to its highly nutritious pods, seeds, leaves, flowers and tubers, all of which are edible (59) (Fig 3).

Winged bean is a highly adaptable and nutritious crop that produced fresh pods, dry seeds and tubers, with its roots rich in proteins, heat shock proteins (*Hsps*), amino acids and antioxidant metabolites that enhance stress tolerance and drought resistance (58). Winged bean seeds are protein-rich (28 %-45 %) and contained 14 %-19 % oil, making them nutritionally comparable to soybean (58). Winged bean seeds are medium to large (6-11 mm diameter, 1.4-2.1 mm thick), round to slightly oblong, with a thick and very hard seed coat in dark brown, reddish-brown, black, or speckled colors and a 100 -seed weight of 12 g-18 g (60, 57, 61). The seed yield of winged bean was highly variable, ranging from 1.0 to 3.5 t/ha, with reports of exceptional genotypes achieving up to 4.0 t/ha under optimal conditions (62). Its high protein content (up to 37 %) made it a valuable alternative to traditional legumes. The yield potential depended on staking, genotype and agro-climatic conditions, with staked plants exhibiting higher productivity compared to those left to trail on the ground (63). The tubers contained 12 %-19 % protein and 1 %-4 % fat, while immature

Pods had 1 %-3 % protein, along with vitamins and minerals (64). Winged bean seeds and tubers exhibited distinct nutritional profiles, with seeds being notably rich in protein (28 - 45 % dry weight) and fat (14 %-20.4 %), while tubers contained lower protein (12.26 %-19.07 %) and minimal fat (0.6 %-1.2 %), making them a valuable alternative energy source (65, 64, 58). Carbohydrates were more abundant in tubers (34 %-40 %) compared to seeds (26.81 ± 6.88 %), whereas fiber and ash content were generally higher in seeds (10.24 ± 5.49 % and 4.16 ± 0.41 %, respectively) than in tubers (3.5 %-5.0 % and 2.5 %-3.0 %), indicating their dietary significance (65, 64). Additionally, moisture content varied across both plant parts, ranging from 3.76 %-9.09 % in seeds and 1.40 %-7.81 % in tubers, further influencing their storage and processing potential (65, 64). The tubers also have high starch content with low amylose, similar to rice, making them suitable for food processing (64). (Table 3). Additionally, the seeds contained bioactive compounds such as flavonoids, tannins and polyphenols, with kaempferol as the dominant flavonoid (65). These properties made winged bean proteins ideal for emulsification, foaming and gelling, expanding their potential applications in the food industry (66). Recent reviews consolidated the nutritional and functional applications of winged bean, emphasizing its biochemical richness, food processing potential and industrial value (16). Fresh tubers weighed between 80 g-230 g in the first year, increasing to 369 g -392 g per plant in the second year. The pods were typically 30 cm long, with each plant producing 60-78 pods in the first year before declining in subsequent years. Mature seeds weighed about 38.5 g per 100 seeds and the highest seed yield occurred in the first year, averaging 327 g per plant (58). For optimal yield and better crop management, winged bean is best cultivated as an annual rather than a perennial (57). In Papua New Guinea, where tubers were highly valued, selective pruning of shoot tips and flowers enhanced tuber development, leading to higher protein-rich tuber yields (67). Genetic studies indicated significant variation in pod and tuber yield, with certain accessions yielding up to 23.6 t/ha for pods and 15.5 t/ha for tubers (58). Winged bean accessions such as W099 and W018 exhibited consistently high yields, making them ideal for commercial cultivation. Tuber yield varied significantly among different varieties, with reported yields ranging from 10 to 35 t/ha and in some improved genotypes, up to 50 t/ha under optimal soil and climatic conditions (62). The crop's biological nitrogen-fixing ability also enhanced soil fertility, making it a valuable sustainable agricultural resource (57). Additionally, recent studies have explored alternative uses of winged bean tubers as animal feed, demonstrating that they can replace cassava in ruminant diets without adversely affecting ruminal fermentation and digestibility (68). Despite its limited expansion due to restricted breeding programs and limited

genetic improvement efforts, recent advancements in molecular characterization and marker-assisted breeding were expected to accelerate the development of high-yielding and stress-tolerant varieties (69). However, winged bean had breeding challenges, including its long maturation period, indeterminate growth habit and presence of anti-nutritional factors such as trypsin inhibitors and hemagglutinins (65). Activity was measured between 77 to 154 hemagglutinin units per gram of seeds. These compounds could interfere with protein digestion and cause agglutination of red blood cells, respectively. However, heat treatments such as boiling, roasting, or autoclaving can significantly reduce or eliminate these anti-nutritional factors (70). Moreover, advancements in molecular breeding, genetic characterization and tissue culture are paving the way for the development of improved varieties with shorter growth cycles, higher yields and reduced anti-nutritional factors (63). Trypsin inhibitor activity varied widely, with reported values ranging from 11300 to 74700 IU per gram of seeds.

Advances in breeding and biotechnology of Winged bean

To enhance winged bean production, research recommended cultivating high-yielding varieties such as PT-1, PT-2, PT-3, W018 and W099, which demonstrated superior adaptability in both upland and lowland environments. Dual-purpose varieties like 'Jati Belanda' and 'UB-1' were also notable for their enhanced pod and storage root productivity (60, 71, 72). It was reported that the traditional winged bean variety 'Ratchaburi' yielded 7.42 and 5.69 T/ha of storage roots in the 2021-2022 and 2022-2023 seasons, respectively, while improved varieties W018 and W099 produced significantly higher yields, reaching up to 22.4 and 19.3 T/ha (72, 73). These varieties such as W018, W099 and PT-3 were cultivated post-monsoon and early winter, where optimal soil moisture and moderate temperatures enhanced productivity. Genetic studies using RAPD and ISSR markers have revealed a broad genetic base among cultivated accessions, supporting targeted breeding programs (74). Induced mutation breeding using gamma irradiation (100 - 400 Gy) and colchicine polyploidy treatments (0.01 %-0.05 %) has led to 30 %-40 % higher biomass production, 42.6 % increased storage root starch content (compared to 35.2 % in non-mutated plants) and a 15 % rise in seed protein content, thereby improving nutritional quality and productivity (63, 75). Tissue culture advancements have optimized plant regeneration, ensuring genetic stability in elite genotypes. The most effective tissue culture protocol involved Murashige and Skoog (MS) media supplemented with 6-benzylaminopurine (BAP) at 2.0 mg/L and naphthalene acetic acid (NAA) at 0.5 mg/L, achieving a 92 % shoot regeneration rate within 12-15 days. Micro-propagation further accelerated breeding, producing 50 plantlets per explant within four weeks (76). Molecular breeding efforts have leveraged Genotyping-by-Sequencing (GBS) and RNA-Seq to identify 48 novel SNP markers linked to drought resistance, high tuber yield and improved seed coat characteristics (77). Molecular variance analysis has showed that 95 % of genetic diversity existed within accessions, suggesting a high degree of genetic variation (78). QTL mapping has pinpointed key loci controlling essential agronomic traits, including qPL1 (pod length), qSS2 (seed size) and qFC3 (flower color). Marker-assisted selection (MAS) using this locus has improved seed yield by 17.8 % and tuber yield by

Table 3. Proximate composition of winged bean seeds and tubers

Component	Seeds (% dry weight)	Tubers (% dry weight)	References
Protein	28-45	12.26-19.07	(58, 64, 65)
Fat	14-20.4	0.6-1.2	(58, 64, 65)
Carbohydrates	26.81 ± 6.88	34-40	(58, 64, 65)
Fiber	10.24 ± 5.49	3.5-5.0	(58, 64, 65)
Ash	4.16 ± 0.41	2.5-3.0	(58, 64, 65)
Moisture	3.76-9.09	1.40-7.81	(58, 64, 65)

22.4 %, demonstrating the effectiveness of genomics-driven breeding. Furthermore, AMMI model analysis has revealed that 84.10 % of genotype-by-environment interaction (GEI) variability was explained by the first two components, aiding in the selection of stable, high-yielding genotypes for commercial cultivation (65). Hybrid cultivar 'Tpt-5', which was QTL-mapped for high tuber yield and disease resistance, led to a yield increase of 30 %-50 % compared to traditional landraces, reaching up to 48 t/ha. It was developed using mutation breeding and molecular-assisted selection at the Asian Vegetable Research and Development Center (AVRDC), Taiwan (62).

Research gaps and future research needs

Despite their nutritional and agricultural potential, leguminous root crops remained underutilized due to limited genomic resources, long maturation periods and the presence of anti-nutritional factors. More extensive whole-genome sequencing, GWAS and transcriptomic studies are needed to accelerate marker-assisted selection and gene editing for early maturity, high yield and reduced anti-nutritional compounds (26, 79). Interspecific hybridization and polyploid breeding could have improve tuber starch quality, pest resistance and yield stability (80). Additionally, tissue culture and micro-propagation techniques required further optimization for efficient mass propagation of elite genotypes (63). Research on drought and salinity tolerance mechanisms is necessary to expand their cultivation in climate-stressed regions (14). Moreover, post-harvest losses due to storage issues, limited processing technology and low consumer awareness need to be addressed through advanced food processing techniques and market expansion strategies. Integrating functional food research to explore bioactive compounds and nutraceutical applications can further enhanced their industrial and pharmaceutical value (81). By combining genomic innovations, agronomic optimization and value-added product development, these legume tubers are positioned as viable alternatives for food security and sustainable agriculture worldwide. To enhance the domestication and cultivation of yam bean and African yam bean in non-traditional areas, germplasm exchange programs, international collaborations and breeding strategies tailored for diverse agro-climatic regions are crucial.

Conclusion

Yam bean, African yam bean and winged bean are nutritionally valuable and highly adaptable leguminous storage root crops with significant potential for food security and sustainable agriculture. These crops provide both storage root and seeds rich in protein, carbohydrates and essential nutrients while improving soil fertility through biological nitrogen fixation. Advances in breeding, including conventional selection, mutation breeding, tissue culture and molecular approaches such as Genotyping-by-Sequencing (GBS), QTL mapping and marker-assisted selection (MAS), enhance yield potential, stress tolerance and nutritional quality. Despite these advancements, widespread cultivation remained limited due to challenges such as long maturity periods, low consumer acceptance due to anti-nutritional factors and restricted genetic improvement programs. Expanding research and commercialization efforts can established these underutilized legumes as viable supplementary crops along with other crops like cassava,

sweet potato and soybean, promoting resilience in global food systems.

Acknowledgements

We are grateful to Department of Seed Science and Technology, Agriculture College and Research Institute, (TNAU), Madurai, for providing financial support throughout the research activities and manuscript preparation. Authors acknowledge Director, ICAR-CTCRI and ICAR, New Delhi for support through institute research project.

Authors' contributions

All authors contributed equally to data collection, analysis, drafting the original manuscript, editing and reviewing. All authors read and approved the final manuscript

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical issues: None

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Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

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Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.