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REVIEW

Unlocking the secrets of zombi pea: a pantropical orphan for a sustainable future

Srija Priyadarsini[1] · Alok Nandi[2] · Saurabh Singh[3] · Maniyam Nedunchezhiyan[4] · Pushpajeet Choudhari[5] · Ajoy Pattnaik[2]

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Abstract

Main conclusion **Zombi pea is a treasure trove for hunting genes to deliver climate-smart cultivars. The integrated power of genetic and genomic approaches could be fruitful in deciphering the genetic basis of climate resilience, domestication syndrome, and the utility of orphan crops for a sustainable future.**

Abstract The plant genetics, biology and physiology are significantly influenced by climate change in numerous ways, which ultimately threatens food and nutritional security. There is a need to diversify the food systems with climate-smart orphan crops and leveraging neoteric molecular, genetic, and genomic approaches to unlock the breeding potential of these orphans. Among the orphan legumes, Zombi pea is a genetic treasure trove for hunting genes to tackle the ghastly future. It is a potential future crop for food, nutrition, and sustainable agriculture. Recently, the progress on strengthening genomic resources of orphan legumes has gained momentum. Here, we provide an overview of current progress made in deciphering the domestication syndrome and identification of QTLs controlling biotic and abiotic stress resistance in zombi pea. The knowledge obtained so far about the genetic potential of zombi pea is likely the tip of the iceberg. Harnessing the biotechnological advancements in underpinning the potential of such orphan legumes is the key to developing a future roadmap for sustainable agriculture. This article emphasizes the need for integrating genetic and genomics approaches to unlock the true genetic potential of orphan legumes like zombi pea in addressing the challenges of climate change and achieving the United Nations' sustainable development goal of 'zero hunger'.

Keywords *Vigna vexillata* · Climate resilient · Genetics · Genomics · Breeding potential · Orphan crops

Introduction

Plant genetics and genomics are playing a crucial role in feeding the world by developing high yielding, climate resilient and nutritious crops. The world is already facing the threats of food and nutritional security in the era of climate change and population explosion. The recent Global Report on Food Crises (GRFC) released in 2024 revealed that in 2023, approximately 282 million people across 59 nations and territories faced acute hunger which depicts a global increase of 24 million as compared to 2022 (FSIN, Global Network Against Food Crises 2024, https://www.fsinplatform.org/grfc2024). This escalation in number of hungry stomachs is the result of food crisis which is attributed to conflicts between countries, extreme global climate change events and financial shocks. Globally, more than 36 million children under five suffered from acute malnutrition

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✉ Saurabh Singh
horticulturesaurabh@gmail.com

[1] Department of Vegetable Science, Odisha University of Agriculture and Technology (OUAT), Bhubaneswar 751003, India

[2] Department of Vegetable Science, Institute of Agricultural Sciences, Siksha 'O' Anusandhan (Deemed to Be University), Bhubaneswar, Odisha 751029, India

[3] Department of Vegetable Science, Rani Lakshmi Bai Central Agricultural University, U.P, Jhansi 284003, India

[4] Central Tuber Crop Research Institute (CTCRI), Regional Centre, Bhubaneswar, Odisha 751019, India

[5] International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Hyderabad, Telengana 502324, India

in 2023. Thus, the future food and nutritional security are under serious threat due to population explosion, global climate change, unprecedented conflicts and arable land scarcity (Tadele 2019). In order to address these issues, a paradigm shift from the existing strategies to transformative ones, that prioritize environmental sustainability, human nutrition and health equally, alternative crops, is necessary (Mabhaudhi et al. 2019). The current strategies to tackle these issues include innovative plant breeding programmes to develop climate resilient future crop varieties, genetic engineering and transgenic approaches, biofortification, crop pangenomes and recent revolution in genome editing tools (Pixley et al. 2023; Singh et al. 2024; Priyadarsini et al. 2025a). The scientists have warned that in the era of climate change there is huge possibility that pest and pathogen life cycles will shorten, their host range will spread, and species with ideal host may thrive in less suitable conditions. These drastic alterations would have negative impact on crop plants (Pixley et al. 2023; Harvey et al. 2023). In addition, the nutritional quality, protein content and other antioxidant properties are going to alter under increased temperature and greenhouse gas emissions, especially in C_3 crop plants (Soares et al. 2019; Kumari et al. 2023). The search for climate resilient future crops is one of the better alternative solutions to combat the threat of hunger and malnutrition. The hunt for alternative crops that are both nutrient-dense and appropriate for the changing agroclimatic circumstances of the future has been prompted by drastic shifts in global food habits, population explosion and climate change (Kumar and Bhalothia 2020).

Orphan or neglected, underutilized or minor or forbidden or promising or lesser-known crops have tremendous potential to tackle the issues of hidden hunger, malnutrition, climate change and food security (Mabhaudhi et al. 2019; Aditika et al. 2022). Owing to enormous potential of orphan or underutilized crops they can contribute to sustainable future in the era of climate change. Overdependence on certain dominant staple cereals like wheat, maize, rice is not enough to tackle the threats of food and nutritional security. Hence, it is imperative to do the comparative comprehensive analysis of nutritional profiling of underutilized crops with staple crops with respect to climate resilience under different agro-climatic conditions and diverse food systems (Mabhaudhi et al. 2019; Li et al. 2020; Ali and Bhattacharjee 2023). The orphan or underutilized crops are gaining popularity due to their potential to fight food and nutritional security in face of climate change. The orphan, underutilized, or neglected crops are those that have become less relevant during the past 500 years as a result of agronomic, biological, or societal reasons (Bermejo and Leon 1994). Besides being a cheap source of dietary proteins than meat, these potential crops can help in reclaiming problematic soils, carbon sequestration, abiotic stress tolerance and decline in emission of greenhouse gas (Stagnari et al. 2017; Chongtham et al. 2022). The wealth of orphan or underutilized legumes include different members such as Bambara Groundnut (*Vigna subterranean*), Yam bean (*Pachyrhizus erosus*), Adzuki Bean (*Vigna angularis*), Grass pea (*Lathyrus sativus*), Lima bean (*Phaseolus lunatus*), Cluster bean (*Cyamopsis tetragonoloba*), Marama bean (*Tylosema esculentum*), Sword bean (*Canavalia gladiata*), Jack bean (*Canavalia ensiformis*), Broad bean (*Vicia faba*), Hyacinth bean (*Lablab purpurues*), Winged bean (*Psophocarpus tetragonolobus*), African locus bean (Parkia Africana), African yam bean (*Sphenostylis stenocarpa*) and wild *Vigna* species (*V. vexillata, V. ambacensis, V. oblongifolia, V. luteola,*) (Samal et al. 2023; Kiran et al. 2024). These underutilized legumes are the reservoir of nutrients, bioactive compounds and protein, have adaptive nature to environmental stresses, and serve as important source of food, feed and fodder globally (Yao et al. 2012; Samal et al. 2023). The inclusion of these orphan legumes with stupendous and phenomenal potential in agricultural and food systems, and further their genetic enhancement for agronomic and nutritional attributes could be a sustainable step in achieving food and nutritional security in sustainable manner (Chongtham et al. 2022). However, these underutilized crops have attained little economic significance and poor attention by plant breeders, geneticists, decision-makers, merchants and consumers. The applications of innovative biotechnological tools like NGS techniques, genomics, genomic selection, genome editing and speed breeding will accelerate the domestication process, identification of domestication genes, genome-based characterization and breeding of novel varieties in orphan legumes (Huang et al. 2022; Kumar et al. 2023). In this review, we have made an effort to shed light on one of the unexplored gems among orphan legumes, that is 'zombi pea'. In our opinion, zombi pea under the genus '*Vigna'* is a stupendous future crop and it is imperative to consider it as one of the potential solutions to mitigate the challenges of food and nutritional security.

In addition to several potential wild species with value as food and nutrition, feed, green manure, and cover crop, the genus *Vigna* contains ten domesticated species (Takahashi et al. 2016). Zombi pea (*Vigna vexillata,* 2n = 22), a close relative of cowpea, is one of the phenomenal orphan legumes of genus *Vigna* and has pan tropical distribution (Priyadarsini et al. 2024, 2025b). One of the cultivated types of zombi pea is found in Indonesia which was brought under domestication with the selection of domestication genes governing reduced seed dormancy and non-shattering habit of pods (Marubodee et al. 2015). *Vigna vexillata* var. *macrosperma* is another domesticated form of zombi pea from Costa Rica (Marubodee et al. 2015). Zombi pea has also marked its footprint in the hilly Indian regions where the root tubers are consumed either raw or boiled (Arora and

Pandey 1996). Zombi pea plant parts are valued as vegetable, feed, fodder and seeds on drying as pulse. Zombi pea has medicinal and therapeutic properties, nutritional value as good source of protein and minerals. It is indeed a climate smart tuberous legume of future which accommodate genes governing resistance to biotic and abiotic stresses like cultivation in problematic soils (alkaline, saline, acidic), tolerance to waterlogged conditions, drought tolerance, salinity tolerance, resistance to insect-pests (bruchid resistance genes, *Maruca testulalis*, *Zabrotes subfasciatus*, and *Clavigralla tomentosicollis*) (Butsayawarapat et al. 2019; Amkul et al. 2019, 2023), resistance to viral menaces such as cowpea mottle carmovirus (CPMoV) (Ogundiwin et al. 2002) and powdery mildew (James and Lawn 1991). As compared to staple tubers like cassava, potato, sweet potato and yams, the protein content of zombi pea is significantly higher (Dachapak et al. 2018). The protein percentage is about three-fold to potato and yams, while six times more content than tapioca (Dachapak et al. 2018). Zombi pea is fairly high in other micronutrients like Cu, Fe, Zn and Mn (Kumar and Kumar 2016). Our group have previously provided the detailed analysis of nutritional profiling of zombi pea and how the plant density and deblossoming may alter the nutrient content in tubers as well as pods of zombi pea (Priyadarsini et al. 2024). Though this wonder crop has an array of astonishing applications, not much research work has been done to enhance its genetic makeup (Tripathi et al. 2020). During the past decade, unlocking the nutritional value and genetic potential of neglected crops has been regarded as one of the key tactics for enhancing global food security (Cheng 2018). Although, zombi pea is a carrier of relevant alleles making it a potential future crop, but limited genomic databases are available for this wonder crop. This review article examines the past, present and future of zombi pea in tackling the current issues of food and nutritional security. In the near future, the great strides in orphan legume breeding are possible by integrating genomics with efficient selection and phenotyping of crop germplasm (Varshney et al. 2009). We have also provided insights into future prospects of state-of-the-art genetic and genomic approaches in enhancing the wider adaptation of this orphan legume in agricultural and food systems. Exploring the potential of this unexplored gem could be a game changer to accomplish the United Nations sustainable development goal (SDG) 2 of ‘zero hunger’ by 2030.

Insights into origin, distribution and taxonomy

Zombi pea, a pan tropical herbaceous unexplored legume under the subgenus *Plectrotropis* of the genus *Vigna,* is widely distributed in wild form over the continents of Asia, America, Africa and Australia (Dachapak et al. 2017). Only a few pockets of Asia and Africa are the home to the cultivated forms of this miraculous crop. In the Indian subcontinent, it is distributed both in protected and partially disturbed environments in the hilly ranges of Peninsular and Himalayan regions. Based on the diversity studies, it is considered that the primary centre of origin and diversity of zombi pea is Southern Africa, while South-east Asia is secondary centres of diversity (Fig. 1) (Dachapak et al. 2017; Verma et al. 2022). Zombi pea has two cultivated forms, seed types and tuber types. Tropical regions of Africa are considered as place of domestication for seed types, while Bali and Timor islands of South East Asia (Indonesia) and North Eastern Hills of India are considered as the place of domestication for tuber types (Fig. 1) (Dachapak et al. 2018; Verma et al. 2022; Panzeri et al. 2022). The microsatellites (SSR) based genetic diversity analysis clearly demonstrated that the separate wild gene pools of zombi pea (*Vigna vexillata*) led to the domestication of these two types (Dachapak et al. 2017). Zombi pea is utilized as pulse and tuber crop by the native tribals of North Eastern regions of India (Asati and Yadav 2004; Dachapak et al. 2018). The seed type is considered as var. *macrosperma* and has evolved from wild zombi pea (wild *V. vexillata*) of East Africa, as it is fully cross compatible with wild zombi pea. The tuber type zombi pea is photoperiod sensitive. However, this type is not fully crossable with wild *V. vexillata* and domesticated var. *macrosperma*. Both these types are the result of diverse selection pressure imposed during course of evolution.

The genus *Vigna* is a vital plant taxon comprising about more than 200 species widely distributed in pantropical regions of Asia, Africa, Australia and America (Verma et al. 2022). The two most widely consumed genera among the legumes are *Vigna* and *Phaseolus*. Genus *Vigna* is further subcategorized into five subgenera namely, *Vigna, Plectrotropis, Ceratotropis, Lasiospron* and *Haydonia*. The domesticated and cultivated species of *Vigna* genus are confined to first three subgenera only (Harouna et al. 2018). The subgenus *Vigna* is referred as African Vigna, while the subgenus *Ceratotropis* is referred as Asian Vigna. The species under focus in this review, ‘*Vigna vexillata’,* is considered as an intermediate species between two subgenera, Asian and African *Vigna.* The molecular investigation further indicated that *Vigna vexillata* is closer to African Vigna (Zuluaga et al. 2021). In the genus *Vigna,* so far, 10 species are considered to be domesticated which includes Azuki bean (*Vigna angularis* var. *angularis*), Bambara groundnut [*Vigna subterranea* (L.) Verdc], Black gram [*Vigna mungo* var. *mungo* (L.) Hepper], Cowpea [*Vigna unguiculata* (L.) Walp.], Creole bean (*Vigna reflexo-pilosa* var. *glabra* = *Vigna glabrescens*), Minni payaru (*Vigna stipulacea*), Moth bean [*Vigna aconitifolia* (Jacq.) Marechal], Mung bean [*Vigna radiata* (L.) Wilczek], Rice bean [*Vigna umbellata* (Thunb.) Ohwi

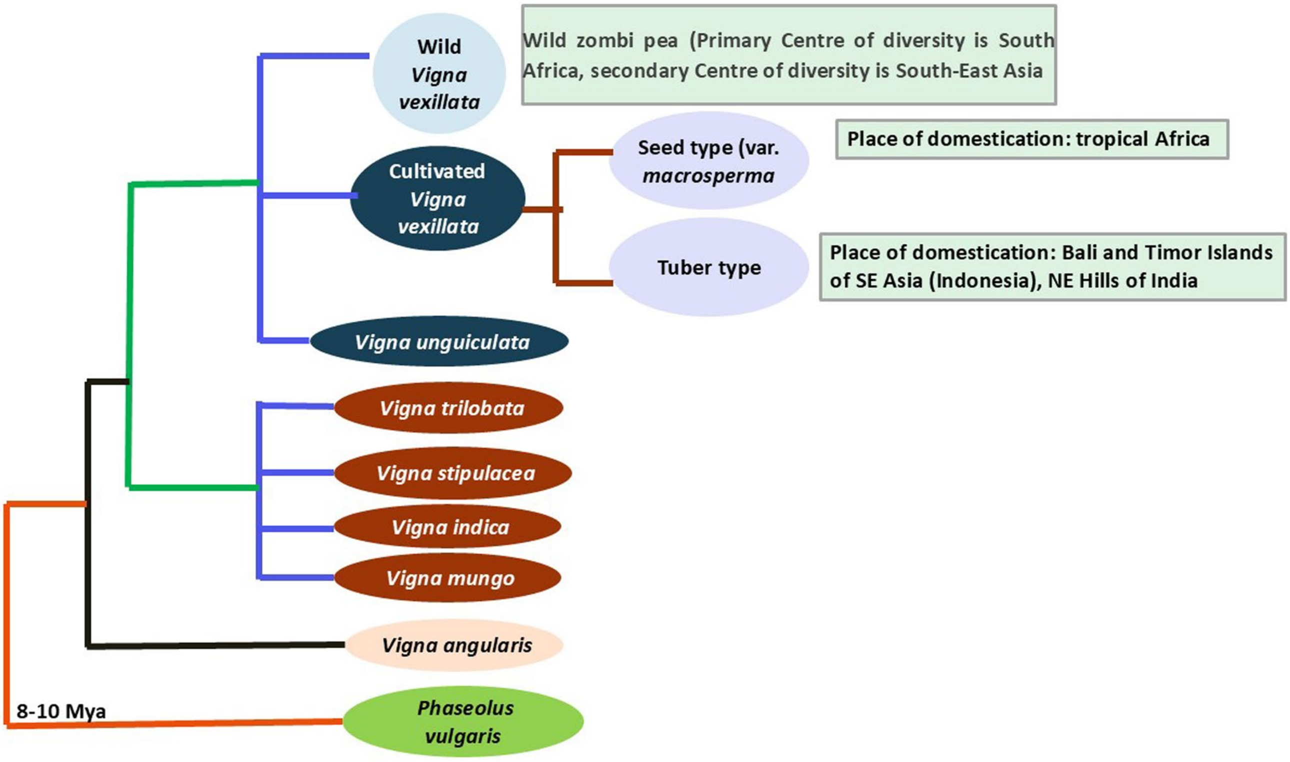

Fig. 1 The phylogenetic relationship and genetic lineage illustration. The primary centre of diversity for zombi pea is South Africa. Cultivated *Vigna vexillata* is of two types (seed type and tuber type). Seed type domesticated in tropical Africa, while tuber type domesticated in SE Asia. Cultivated *Vigna vexillata* shares high genomic similarity to cowpea (*V. unguiculata*). Zombi pea also has close relationship with other *Vigna* species. *Vigna vexillata* is distantly related to *V. angularis.* The genus *Vigna* diverged from *Phaseolus* about 8–10 million years ago (Mya) (Naito et al. 2022; Panzeri et al. 2022)

& Ohashi] and Zombi pea or Tuber cowpea (*Vigna vexillata*) (Takahashi et al. 2016; Harouna et al. 2018). The *Plectrotropis* subgenus is situated in between the *Vigna* and *Ceratotropis* subgenera. The *Plectrotropis* subgenus further consists of two sections, section *Plectrotropis* and section *Pseudoliebrechtsia.* Zombi pea is a highly polymorphic and potential species under the section *Plectrotropis* and eight taxonomic varieties have been described comprising *vexillata, macrosperma*, *ovata, lobatifloria, angustifolia*, *yunnanensis*, *dolichomena*, and *plurifora* (Verma et al. 2022). The *macrosperma* is cultivated type, while other seven are considered as wild types. The *Vigna vexillata* has genome synteny with *Vigna unguiculata* (Amkul et al. 2019).

Zombi pea is a potential gene source for sustainable food production in face of climate change, but meagre information is available regarding its genetic diversity. Based on morphological diversity analysis of zombi pea, Maréchal et al. (1978) suggested that this potential crop has its origin in Africa. Recently, Dachapak et al. (2017) also supported the hypothesis of East African origin of zombi pea by analysing allelic diversity of wild *Vigna vexillata* using SSR markers. *Vigna vexillata* is also consumed for its edible roots in Bali and Timor Islands of Indonesia (Dachapak et al. 2017). Damayanti et al. (2010) suggested that accessions from Bali are distinct from other African types as revealed by agro-morphological variation analysis. The phylogenetic analysis using DNA sequences of the nuclear DNA-ITS and chloroplast atpB-rbcL spacer regions, further supported that accessions grown in Bali are genetically distinct from the other accessions (Takahashi et al. (2016). These findings indicated that the zombi pea cultivated in Bali region domesticated independently (Dachapak et al. 2017). Limited reports are available on analysing molecular diversity in the germplasm of *Vigna vexillata.* The American and African accessions are distinct from each other as revealed by different sets of isozymes (Jaaska 2001), RAPD (Spinosa et al. 1998) and SSR markers (Dachapak et al. 2017). Further in-depth studies on genetic diversity analysis of wide range of germplasm from different pantropical regions using molecular markers would be instrumental in enhancing genetic gain and popularity of this orphan crop.

Breeding behaviour and hugging mechanism

Trifoliolate leaves and axillary inflorescences characterize the prostrate, spreading, brown-pubescent annual legume *Vigna vexillata* (Priyadarsini et al. 2024). It is a perennial herb that climbs or trails, having tuberous roots and sub umbellate inflorescences with two to six flowers that are typically on long peduncles. The axillary inflorescence is a solitary, 2–3 cm long, 2–4 pink or purple flowered on long peduncles at a peak (Al-Khulaidi et al. 2023). The flower's colour begins to fade at the last phase of the anthesis, and the pale yellowish standard that follows anthesis encloses the wings and keel (Hedström and Thulin 1986). Flowers are perfect, zygomorphic with 5 petals (1 standard, 2 wings and 2 keels) (Fig. 2). The stamens are in diadelphous condition [A1 + (9)], where 9 filaments are fused together and make a staminal column, while the 10th filament is free. The anthesis occur early morning and flowers remain open until midday. The pods can be eaten as a vegetable when they are immature. They grow to be roughly 18–20 cm long and produces 15–20 seeds. These are somewhat smaller than cowpeas and have a reddish-brown color. After boiling or roasting, the grains are either consumed raw or used to make dal. They have a somewhat different flavour from cowpeas. The zombi pea has moderately deep root system and is widely nodulose. After growing for two to four months, the primary roots produce tubers. Tubers are typically 12–13 cm long (Fig. 3). They are eaten after being boiled or roasted, and they are fleshy and simple to peel. In contrast to the Bali type, which exhibits viny and indeterminate growth patterns, photoperiod-sensitive, late flowering, and glabrous pods, the African type has determinate growth habits, hairy pods, and photoperiod insensitivity. The seed size in Asian type is comparatively bigger than African type. The propagation of zombi pea can be done by stem cutting and seeds. The tuber type is primarily cultivated for its fresh edible tuber roots, which have a protein content of up to 15%, about 5 times more content than in sweet potato (Dachapak et al. 2018). During early stages of crop growth, sufficient numbers of root nodules are formed by zombi pea plant and hence can be a potential source to enhance the fertility of newly developed areas (Priyadarsini et al. 2024). The zombi pea is beneficial as a cover crop to prevent soil erosion because it covers the land quickly. It is also an important green manure crop. The species can be a substitute crop for areas unsuitable for conventional tuber crops because it does well in marginal areas.

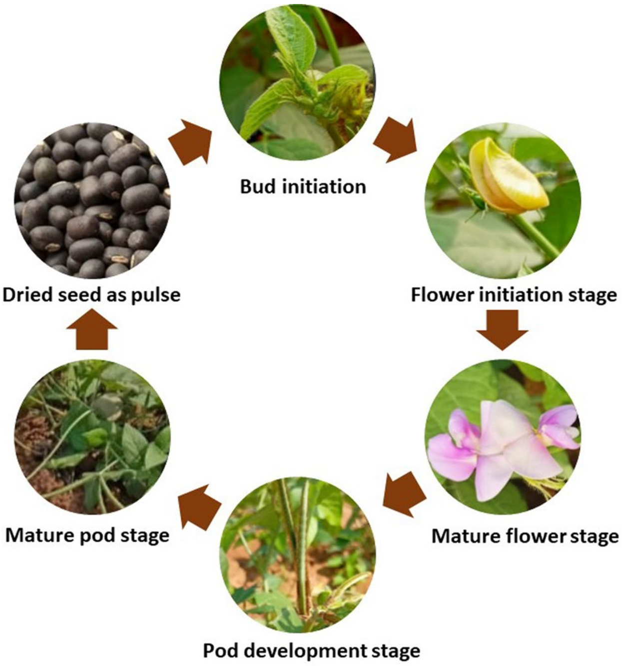

Fig. 2 Flower and pod development stages in zombi pea

The pollination interaction of zombi pea flowers and pollinator, Carpenter bee (*Xylocopa gualanensis* COCKERELL, Hymenoptera-Anthophoridae) revealed that mainly female bees forage on zombi pea flowers during early morning hours (Hedström and Thulin 1986). The bees forage on individual flowers for about 7–8 s. Occasionally, ants, stingless bees and small grasshoppers also visit the flowers of zombi pea. The bees land on the left-wing petal, seemingly using the lamellar structure at the base of the blade to provide them with support. The left-wing petal is pressed down with the weight of bees and during this process the keel-petal functions as a lever to rotate the interlocking left-hand keel-petal inward and downward. The bearded upper half of the style and the higher free parts of the stamens slide out of the stiff keel-beak due to pressure from the keel-petal's movement, which appears like "hugging" the bee over its dorsal region of the head and thorax (Hedström and Thulin 1986).

In zombi pea, both epigeal and hypogeal germinations have been documented. These germination behaviours correspond to their geographic origins (Dachapak et al. 2017). For instance, in a study, the accessions from America exhibited epigeal germination, while accessions from Africa and Australia exhibited hypogeal germination (Vanderborght 1989). Dachapak et al. (2017) also reported high seed diversity with respect to germination habits in zombi pea and documented both epigeal and hypogeal germination habits in the African accessions and while American accessions were homogenous for seed germination and exhibited epigeal germination.

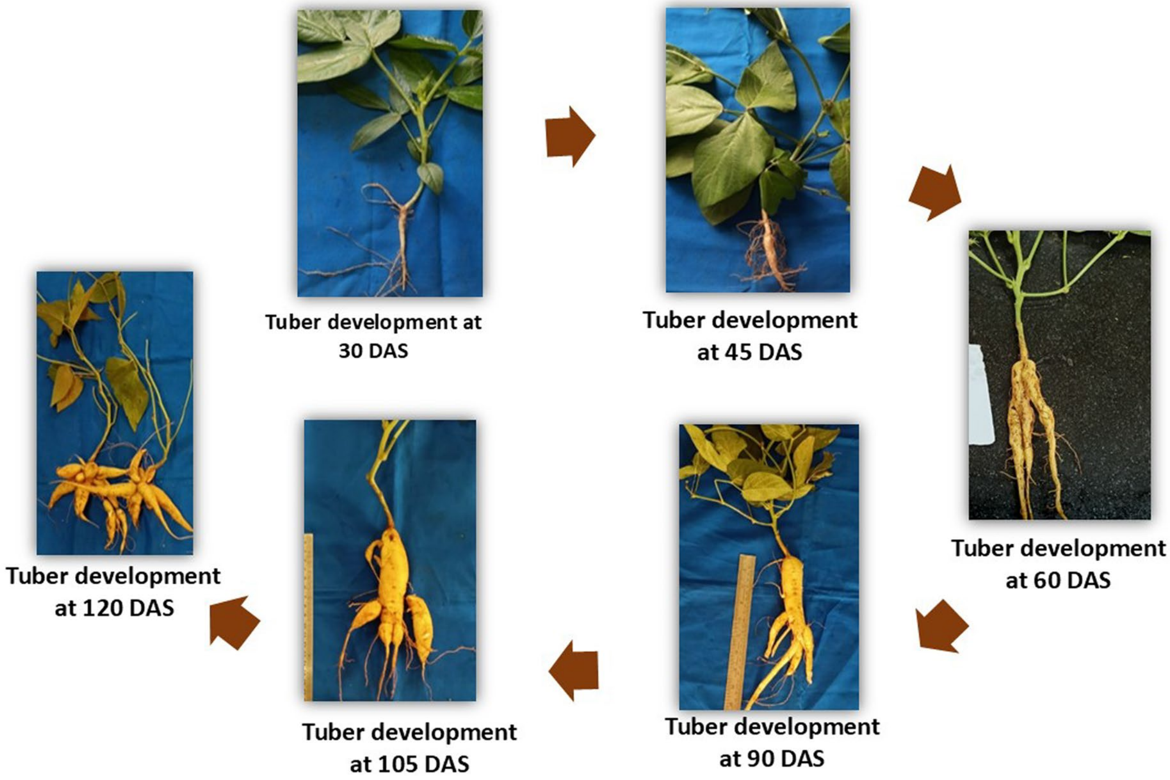

Fig. 3 Tuber development stages in zombi pea. DAS: days after sowing

Status of genomic resources

Some progresses have been made in the sequencing of the genomes of orphan crops, and a number of genome-sequencing projects have been launched with this goal, such as the African Orphan Crops Consortium (AOCC) (http://africanorphancrops.org) have been generated in the last one decade (Ye and Fan 2021). The AOCC selected 101 orphan crops which are micro-and-macro nutrient dense and in which there is a need to develop genetic resources for crop improvement relevant to African agriculture (Hendre et al. 2019). Among the *Vigna* species the genome sequence of three members viz. cowpea (*Vigna unguiculata*), adzuki bean (*Vigna angularis* var. *angularis*) and mung bean (*Vigna radiata)* is available in public domain (Kang et al. 2014, 2015; Yang et al. 2015; Lonardi et al. 2019). The *VigSatDB*—the genomic resource database based on three *Vigna* species (cowpea, adzuki bean and mung bean) for SSR mining has been developed recently by Jasrotia et al. (2019). If the genomic database of all the major *Vigna* species is used to develop such web-based database, it will be a potential genomic resource for genetic improvement of *Vigna* species in face of climate change. The potential future crop species of genus *Vigna*, zombi pea (*Vigna vexillata*) has enormous capacity to confront the prevailing challenges of food and nutritional security. Due to its marvellous properties to stand in the filed under the situations when other staple crops like rice, wheat, potato have failed, the orphan crops like zombi pea have gained the popularity as insurance or famine crops (Shorinola et al. 2024). Despite being a gold mine of genes for resistance to biotic and abiotic stresses, nutritional quality and climate resilience, little is known about the genetics and limited genomic resources are available in this neglected orphan crop. Based on comparative genomics, macro and micro-syntenic relationships have been revealed among *Vigna* species including zombi pea, cowpea, azuki bean and mung bean (Dachapak et al. 2018; Amkul et al. 2019). The diploid chromosome numbers ($2n = 2x = 22$) also same among these *Vigna* species. The genome of common bean and other *Vigna* species is highly conserved (Muñoz-Amatriaín et al. 2017). Zombi pea also shares common phenotypic characteristics with cowpea and both have African origin (Kitch and Shade 1993). The cowpea and zombi pea belong to different subgenera, but due to high genome conservation, the cowpea genome sequence information can be effectively utilized for generation of genomic resources, gene identification and genome analysis (Dachapak et al. 2018). The genetic linkage map of zombi pea have been created using SSR and RAD markers (Marubodee et al. 2015). Amkul et al. (2019) created the high-density genetic linkage map of 6,529 SNP (single nucleotide polymorphism) markers in zombi pea based on

SLAF-seq marker analysis and elucidated the genetics of bruchid resistance in zombi pea. These genomic resources have been exploited in mapping of genes/QTLs governing various morphological traits, resistance to biotic and abiotic stresses and understanding genetic basis of domestication of zombi pea (Dachapak et al. 2018; Amkul et al. 2019; Butsayawarapat et al. 2019). Based on the DNA sequences of the nuclear rDNA-ITS and chloroplast atpB-rbcL spacer regions, the phylogenetic positions of different *Vigna* species were determined, which highlighted the utility of wild *Vigna* species including *Vigna vexillata* (Takahashi et al. 2016). Recently, using PacBio long-reads, the genome sequence of 12 *Vigna* species including wild *Vigna vexillata* (JP256321) was documented by Naito et al. (2022). This accession of zombi pea, 'JP256321' is tolerant to flooding and acidic soil conditions (Naito et al. 2022). They reported a genome size of 715,000,000 bp for *Vigna vexillata* accession 'JP256321' and annotated 28,035 genes (Naito et al. 2022). The transposable elements (TE) contributed 50% in the genome size of *Vigna vexillata* (Naito et al. 2022). The creation of robust genomic resources in underutilized orphans like zombi pea will facilitate elucidation of population structure, gene flow, candidate gene mapping, genetic linkage mapping and phylogenetic relationships (Diakostefani et al. 2024). The plastid and nuclear genome assembly analysis of five different minor legumes comprising sword bean, jack bean, zombi pea, Kersting's groundnut and moth bean enabled the identification of microsatellite markers (Diakostefani et al. 2024). A total of 16 polymorphic SSR markers derived from plastid and nuclear genome were identified in zombi pea by Diakostefani et al. (2024). Wide genome size variation occurs in orphan legumes. The estimated genome size of *Vigna vexillata* var. *macrosperma* line 'TVNu240' is 802 Mb, while the estimated genome size of TVNu-341 (*Vigna vexillata* var. *vexillata)* is 792 Mb (Diakostefani et al. 2024). The plastid genome of 149,321 bp was reported in zombi pea. In addition to molecular markers like SSRs, whole genome sequence data, even when merely combined into partial drafts, can provide researchers vital genetic information. To leverage the zombi pea genomics, the selection of genetic material for the generation of genomic resources must comply with the demand from the breeders and farmer's point of view. For instance, selection of germplasm lines to create reference genome assemblies must embodies the desirable traits adapted to local environment (Shorinola et al. 2024). Likewise, Bredeson et al. (2022), as part of their greater yam genome sequencing project, sequenced a breeding line that is commonly employed as a parent in the greater yam genetic improvement program and carries resistance to anthracnose, a significant disease in this crop. Similar trends can be replicated while generating reference genome and genomic resources in zombi pea. The state-of-the-art biotechnological tools like NGS, TILLING, allele mining and association mapping has enabled the discovery of gene based functional markers in related *Vigna* species. Considering the immense importance of underutilized crops like zombi pea to numerous indigenous populations, genomics initiatives cantered around these crops must be employed to enhance research capabilities in these regions. To create a more comprehensive understanding of crop adaptability and metabolic phenotypes at the cell, organ, plant, and species levels, the genomics of orphan crops like zombi pea must be integrated with plant physiology and biochemistry (Moghaddam et al. 2021; Edwards et al. 2023). In the genomics era, numerous adaptive genes or alleles have been proved climate resilient in majority of the staple of orphan crops. The genomics has become more accessible in the recent past and exploring the zombi pea crop genome is of significant importance in the hotter and drier future.

Comparative genetics and genomics deciphering domestication syndrome

The plant domestication is the most vital biological evolutionary phenomenon which has significantly influenced the human history. Human life still depends upon the crop plants that underwent domestication process from their wild progenitor species primarily about > 10,000 years ago (Ross-Ibarra et al. 2007). In addition to genetic architecture, mode of reproduction, breeding behaviour and ecology of crop plants, the economic and cultural value of plant species for humans has significantly altered the domestication process (Pratap et al. 2023). Among the crop plants, the legume crops are the essential component of agricultural food systems. The legume crops are of significant value in the agricultural systems due to their nitrogen fixation ability and restoring soil fertility besides being an important source of protein and energy to humans. The underutilized orphan legumes are treasure trove of genes for nutrition, biotic and abiotic stresses, hence have substantial potential to strengthen food security in the era of climate change (Kumar et al. 2023). Zombi pea is one of the potential future crops among the leguminous orphans (Priyadarsini et al. 2024, 2025b). Over the past few decades, domesticated species have been the focus of molecular studies to identify genes associated with major agronomic traits as well as traits related to domestication. In the post-genomics era, the genomics associated state-of-the-art tools like genome-wide association studies (GWAS), candidate gene mapping, whole-genome resequencing, transcriptomics, quantitative trait locus (QTL) mapping, functional genomics, genome editing and metabolomics, have propelled the molecular investigation of domestication syndrome across the crop plants (Dachapak et al. 2018; Singh et al. 2024).

The morpho-physiological alterations that occurs during transformation of wild forms to domesticated forms is called as ‘domestication syndrome’ (Dachapak et al. 2018). The domestication of crop plants is an evolutionary process of selective breeding which is the outcome of human and natural selections (Purugganan 2019). Plant architecture, growth habit, increase in size of edible organs like seed and pod size, minimization of seed dormancy and photo insensitivity are potent syndrome traits in *Vigna* species (Isemura et al. 2007). The genetics and genomics of zombi pea domestication is relatively obscure. In addition, unravelling the genetic basis of zombi pea domestication is quite fascinating as the two domesticated types of *Vigna vexillata* has been proposed to be evolved from same or different wild types of zombi pea involving different processes of domestication (Dachapak et al. 2017). The QTL mapping has been employed successfully in unravelling the domestication genetics of majority of the *Vigna* species. Enriching the understanding of genomic regions governing domestication syndrome is of significant value to harness the potential of wild germplasm for genetic improvement of crop plants. In this context, QTLs determining domestication syndrome in zombi pea has been demonstrated in different studies (Fig. 4). Dachapak et al. (2018) used the F_2 mapping population originated from a cross between cultivated (JP235863) and wild (AusTRCF66514) forms of *Vigna vexillata* to map the QTLs governing genetics of zombi pea domestication. From this F_2 mapping population, a linkage map comprising 11 linkage groups (LGs) was developed utilizing 145 simple sequence repeats (SSR), 117 RAD-seq, and two morphological markers. The composite interval mapping based QTL analysis for 22 domestication related traits in zombi pea revealed 37 QTLs for 18 traits (Dachapak et al. 2018). A total of 8 QTLs were identified for tuber size (5 QTLs for tuber width and 3 QTLs for tuber weight). The QTLs for tuber width, *Tbw1.1, Tbw2.1, Tbw3.1, Tbw4.1* and *Tbw8.1,* are located on linkage groups, 1, 2, 3, 4 and 8, respectively. The QTLs controlling tuber weight, *Tbwt2.1, Tbwt4.1* and *Tbwt8.1,* are located on chromosome numbers, 2, 4 and 8, respectively (Dachapak et al. 2018). It is noteworthy that the major QTLs for tuber related traits (*Tbw8.1* and *Tbwt8.1*) are located on linkage group 8, and this tuber trait is the most distinctive domestication trait which distinguishes tuber type zombi pea of Bali region of Indonesia from other cultivated forms of *V. vexillata.* In the genus *Vigna,* the other species forming tuberous roots are, *V. marina,* and *V. lobatifolia.* Albeit, to elucidate the regulatory mechanisms behind tuber formation in zombi pea, the comparative genomics with major tuber forming crops such as, potato, sweet potato, cassava and yams, would be instrumental. The comparative analysis of domestication-related QTLs of *Vigna vexillata* with related species like *Vigna angularis, Vigna unguiculata, Vigna umbellate* and *Vigna radiata,* revealed that some of the QTLs for seed size, leaf size and pod size are conserved between Zombi pea and

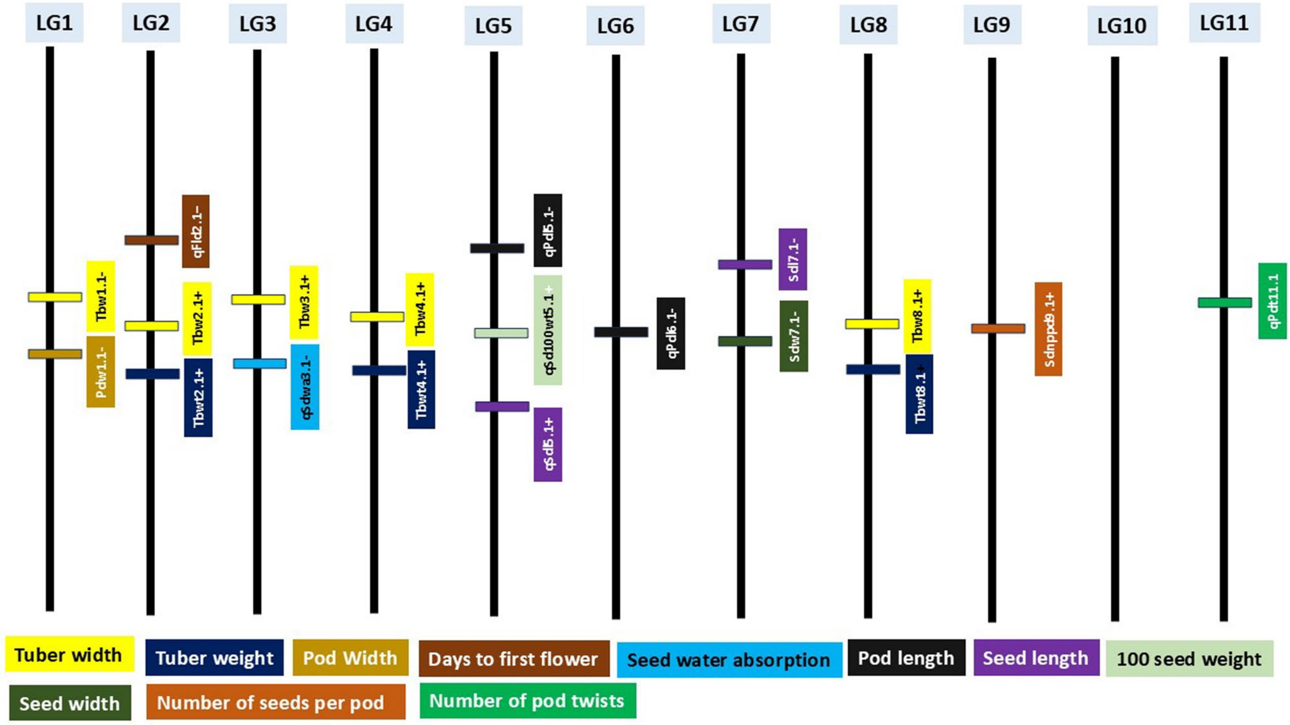

Fig. 4 Pictographical representation of major QTLs for domestication related traits in zombi pea (Dachapak et al. 2018; Amkul et al. 2020)

cowpea (Dachapak et al. 2018). There have been numerous genomic rearrangements occurred in *Vigna vexillata*, as evident by comparative analysis of *Vigna vexillata* linkage map with those of the other *Vigna* species (Dachapak et al. 2018). Recently, Amkul et al. (2020) investigated the genetic basis of 13 domestication related traits in zombi pea using F_2 mapping population derived from the cross of cultivated (var. *macrosperma*) (TVNu 240) and wild (var. *vexillata*) (TVNu 1623) accessions. The domestication related traits under study included shattering of pods, number of days to flowering, thickness of stem, seed dormancy, days to harvesting, number of branches per plant, stem length, length of pods, leaf area, seed related traits like 100-seed weight, seed size (seed length and seed width) and number of seeds per pod (Amkul et al. 2020). For the 13 domestication related traits, 62 QTLs were mapped and for each trait about 1–11 QTLs were designated (Amkul et al. 2020). The linkage group 5 (LG5), corresponding to chromosome 5 of cowpea, contained the major QTLs for stem length, number of branches, days to flowering, length of pod, seed traits (100-seed weight, seed length and number of seeds per pod). While, the linkage group 11 and 3 contained the major QTLs for pod shattering and seed dormancy, respectively. Thus, the genetics of domestication related traits such as seed dormancy and pod shattering, varies between these two African species, zombi pea and cowpea (Amkul et al. 2020). During the domestication process, the seed dormancy has reduced in cultivated zombi pea. The seed dormancy is regulated by a major QTL, '*qSdwa3.1*', which explained 22.2% of phenotypic variation (Amkul et al. 2020). The candidate gene analysis detected calmodulin-binding protein-like gene, '*Vigun03g339300*' as candidate gene for seed dormancy related QTL, '*qSdwa3.1*' (Amkul et al. 2020). While, in the cowpea, a close relative of zombi pea, the major QTL related to seed dormancy is identified as '*Sdp1.1+*', that explains 40% of total phenotypic variation and is located on chromosome number 3 (Kongjaimun et al. 2012).

The major QTL for pod shattering was identified as '*qPdt11.1+*' with 17.6% of phenotypically explained variation. This QTL consists of two genes *Vigun11g053700* and *Vigun11g054200,* encoding UGE1 and glycosyltransferase GT14, respectively. In cowpea, three major QTLs have been reported controlling pod shattering. Hence, the gene loci regulating pod shattering and seed dormancy in zombi pea and cowpea are different. Seed size is an important domestication trait in legume crops, and is a polygenic trait. The major QTLs for seed size in zombi pea, '*qSd100wt5.1+*' (seed weight) and '*qSdl5.1+*' (seed length), were reported to be located on same linkage group, LG5. The candidate genes for these QTLs were identified as *Vigun05g139100* and *Vigun05g140300* respectively. Pod length is another key domestication trait in legume crops. The major QTL, '*qPdl5.1-*' located on LG5 explaining 38% of total trait variation, regulates pod length in zombi pea (Amkul et al. 2020). The candidate gene analysis selected pectate lyase 1 encoding gene '*Vigun05g125800*' as candidate gene for this QTL. The pectate lyase is a pectin degrading enzyme and is speculated to enhance pod length in zombi pea. In French bean as well, pectic polymers have been reported to play role in increasing pod length (Stolle-Smits et al. 1999). For days to flowering in zombi pea, two major QTLs were reported, *qFld2.1* – and *qFld5.1,* on LG2 and LG5, respectively. The candidate gene analysis revealed that WRKY transcription factor (TF), *Vigun02g051100,* and zinc-finger protein, *Vigun02g052800*, are the putative candidate genes of these QTLs, respectively (Amkul et al. 2020). The WRKY TFs regulates various biological functions in plant system, for instance, *SoyWRKY15a* gene that encodes WRKY15, is linked with changes in seed size in soybean during the process of domestication (Gu et al. 2017). The cultivated zombi pea produces more seed numbers per pod than wild type, wherein Amkul et al. (2020) reported major QTLs for seed numbers per pod on LG3, LG5 and LG7. Thus, the comparative genome analysis with closely related reference genome of cowpea facilitated the determination of candidate genes for domestication traits related QTLs (Amkul et al. 2020). The genome of zombi pea is highly conserved with other related *Vigna* species like rice bean, azuki bean, cowpea and mungbean (Amkul et al. 2020). Its genome is also conserved with other legumes like French bean and soybean (Amkul et al. 2019). The gene encoding MALE STERILE 5 protein, '*Vigun05g126900*' gene was identified as candidate gene for major QTL related to seed numbers per pod, '*qSdnppd5.1-'.* In contrast to wild zombi pea, the cultivated type has undergone drastic phenotypic changes during the process of domestication. Dissecting the genetic basis of domestication is critical for diversifying the agricultural system to tackle the issues of reducing global food security. In seed type zombi pea and tuber type zombi pea, there may be multiple signalling pathways which are activated or deactivated in these types resulting formation of tubers in tuber type. For instance, in potato, the multiple signals regulate tuber formation such as the upregulation of *StSP6A* leads to early tuberization in potato under long days and overexpression of *StBEL5* mRNA causes higher tuber yield in potato. During the process of tuber initiation, the mRNA *StBEL5* causes signal induction in the leaf and amplification occurs in the stolon region where interaction of *StSP6A* and flowering locus protein induces tuberization (Hannapel et al. 2017). Thus, the in-depth comparative genomics with non-tuberous legumes could be instrumental in underpinning the genes and regulatory pathways that have been altered significantly or either absent, thereby leading to tuber formation in zombi pea.

The comparative genomics analysis with major root and tuber crops may be helpful in elucidating the unique evolutionary pathways of tuber production in tuberous legumes like zombi pea and staple tubers like sweet potato, carrot, potato and yams. While there may be variation between zombi pea and tuber crops like sweet potato, carrot and potato with respect to underlying genes involved in tuber formation, but the regulatory pathways and gene families may have the similarity regarding this phenomenon across the crop species. It could be attributed to the fact that many molecular pathways of plant growth and development including tuberization are conserved in plant species during the course of evolution (Mathura et al. 2024). In zombi pea three QTLs have been reported controlling tuber weight with PVE of 15% (Dachapak et al. 2018; Amkul et al. 2020), while in potato a few QTLs controls tuber weight with PVE of 20% (Hara-Skrzypiec et al. 2018). In potato negative relationship exists between tuber weight and leaf area, while in zombi pea, the cultivated alleles of tuber width, leaf width and leaflet width are reported to be located on same LG3, which could be attributed to pleiotropic effect of a gene (Dachapak et al. 2018; Amkul et al. 2020). Further, it is noteworthy that independent evolution of tuber type and seed type zombi pea in separate geographical locations, and the current genetic studies, indicates independent evolution of tuberization in tuber type zombi pea instead of divergence from a common ancestor with other staple tuber crops. Additionally, it is well evident that auxins, gibberellins and cytokinin like phytohormones, and related gene network regulates storage root development in plant species (Kondhare et al. 2021). The comparative understanding of crosstalk between plant growth regulators, environmental factors and storage organs of zombi pea and tuberous crops may shed light into molecular mechanism of this process. Further, in-depth comparative genomics of tuber formation in zombi pea and other major tuberous crops like potato, sweet potato, carrot etc. may help in understanding the unique regulatory pathways or genes involved in tuber formation in zombi pea.

Zombi pea: a treasure trove for hunting genes

The orphan or underutilized or insurance or minor crops are reservoir of genes to adapt to changing climate and these stupendous crops can help marginal agricultural systems become more resilient (Mabhaudhi et al. 2019). Additionally, orphan crops offer a large gene pool for future agricultural advancement in niche marginal environments (Ye and Fan 2021; Kamenya et al. 2021; Kumar et al. 2023). Exploring the genetic potential of such orphan crops could be instrumental in addressing the issues for food and nutritional security (Massawe et al. 2015; Talabi et al. 2022). Since nutri-dense underutilized crops are already a part of the regional food systems, it is likely that they are socially acceptable. Among the orphan legumes, zombi pea is a future smart food crop with enormous potential to tackle the ghastly future in face of climate change (Fig. 5). The inclusion of zombi pea in locally adapted areas and as an important component of diverse crop cycles can improve the food security without increasing the area under cultivation (Waha et al. 2020). Zombi pea carries the potential genes to win the battle against abiotic stresses in face of climate change. The wild and cultivated zombi pea is essentially suitable for the marginal soils (saline, sodic and alkaline), waterlogging conditions, drought stress and salinity stress (Butsayawarapat et al. 2019; Dachapak et al. 2019; Yoshida et al. 2020). Thus, wild zombi pea can be used as a genetic resource for breeding of cultivated *Vigna* species. Genomics and genome editing advancements can be successfully exploited to decipher the genetic basis of resistance traits, identification of genes/QTLs, candidate gene mapping for trait of interest and identifying target genes for genome editing based crop inmprovement in zombi pea (Fig. 5).

Insights into abiotic stress tolerance

The environmental stresses like water stress, drought, heat, salinity, marginal soils and nutrients availability significantly influences the crop growth and development. Soil salinity is one of the devastating abiotic stresses which have negative effects on crop yield and quality. When the electrical conductivity of the saturation extract in the root zone surpasses 4 dS m^{-1} (about 40 mM NaCl) at 25 ^{0}C and the exchangeable sodium percentage is higher than 15%, the soil is deemed saline (Shrivastava and Kumar 2015). Globally about 424 million hectares of top soil and 833 million hectares of sub soil are salinity affected (FAO 2021). Currently, India has 6.73 million hectares of salt-affected areas which could be doubled by 2050 and will induce serious threat to sustainable food security (Mohanavelu et al. 2021). The situation may further aggravate with the projected area under salinity might be 16.2 million hectares by 2050. The salinity stress induces significant crop losses annually of value more than ₹23,000 crore. In this context, revitalization of saline soils and search for alternative crops carrying genes to fight with salinity could be a sustainable solution. The multiple studies have proved that zombi pea has gained the adaptive traits to various environmental stresses during the process of domestication (Panzeri et al. 2022). Zombi pea, which holds the potential of a future climate smart crop, exists in two types (seed types and tuber types) (Priyadarsini et al. 2024). It is noteworthy that the wild forms of zombi pea commonly found growing on marginal soils like alkaline, saline or acidic soils (Karuniawan et al. 2006). Unravelling the genetic basis of stress resistance and mapping underlying genes or QTLs is fundamental in genetic improvement of crop plants. In line with this, some efforts

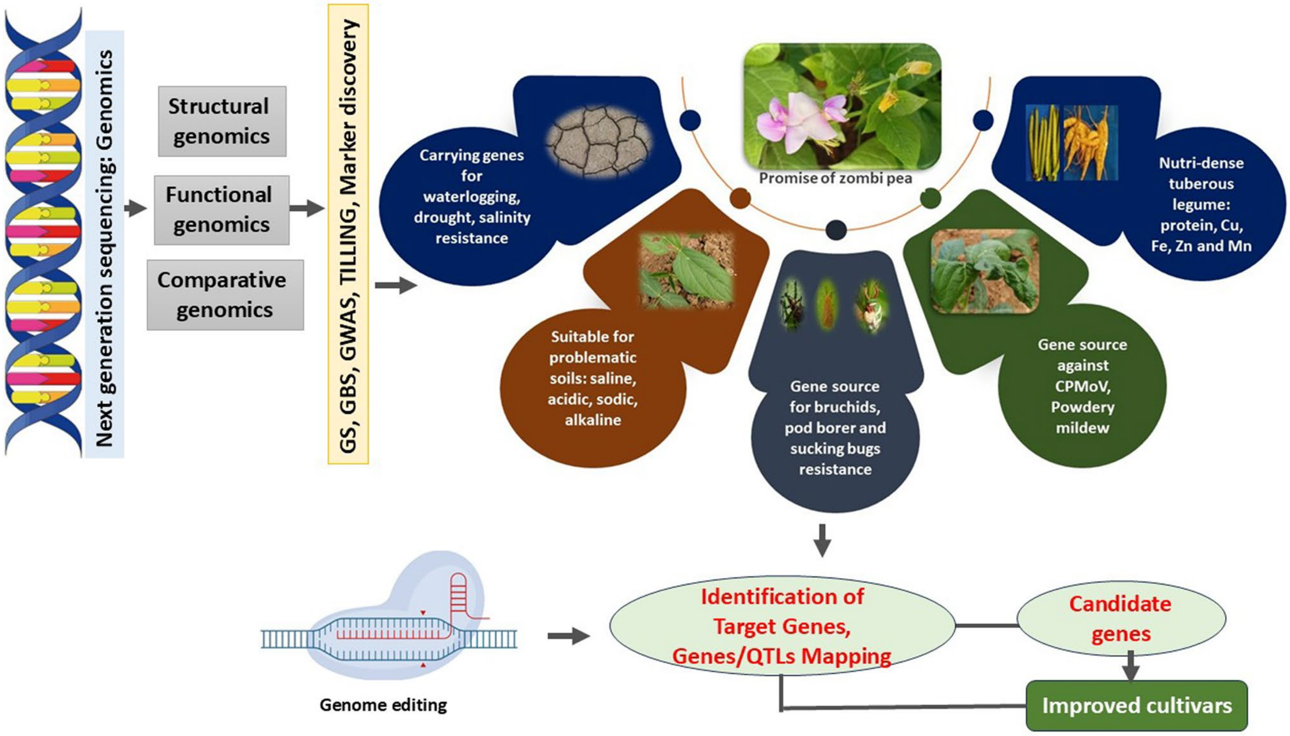

Fig. 5 Illustration of genomics and genome editing in zombi pea improvement

have been made in exploring the mechanisms of stress tolerance in zombi pea which is a carrier of genes to deal with unpleasant future. The QTLs governing salt tolerance in zombi pea have been identified using the wild accession (JP235908) of *Vigna vexillata* var. *ovata* (Dachapak et al. 2019) (Table 1, Fig. 6). The biparental F_2 mapping population derived from the cross of JP235908 (*Vigna vexillata* var. *ovata*) × TVNu240 (*Vigna vexillata* var. *macrosperma*) was used in detection of target QTLs. A total of 1881 SSR markers and RAD-seq markers were employed to detect the polymorphism and genotyping of population (Dachapak et al. 2018; 2019). The three QTL loci governing salt tolerance, *qSaltol1.1* mapped on LG1, *qSaltol2.1* mapped on LG2, and *qSaltol6.1* mapped on LG6, were identified (Fig. 6.). The major QTL exhibiting salt resistance is *qSaltol1.1,* which might be utilized for fine mapping and cloning of salinity tolerance genes in zombi pea. The three respective candidate genes identified were, *Vigan.01G480200.01*,

Table 1 Genes/QTLs underlying biotic and abiotic stress tolerance in zombi pea

Trait	Genes/QTLs	Population	Linkage group	Reference (s)
Salinity stress	*qSaltol1.1* *qSaltol2.1* *qSaltol6.1*	F_2	1 2 6	Dachapak et al. 2019
Salinity stress	*qSaltol_3.1 qSaltol_7.1*	BC_1F_2	3 7	Laosatit et al. 2024
Bruchid resistance (*C. chinensis) (QTLs for percentage of damaged seeds: PDS)*	*qCc_PDS6.1* *qCc_PDS3.1* *qCc_PDS11.1*	F_2	6 3 11	Amkul et al. 2019
Bruchid resistance (*C. chinensis*) (QTLs for area under the disease progress stair: AUDPS)	*qCc_AUDPS6.1* *Three minor QTLs, qCc_AUDPS2.1, qCc_AUDPS3.1 and qCc_AUDPS11.1*	F_2	6 2 3 11	Amkul et al. 2019
Bruchid resistance (*C. maculatus*) (QTLs for percentage of damaged seeds: PDS)	*One major QTL: qCm_PDS6.1* *One minor QTL: qCm_PDS11.1*	F_2	6 11	Amkul et al. 2019
Bruchid resistance (*C. chinensis* and *C. maculatus*)	*qBr6.1-A and qBr6.1-B*	F2 and F2:3	6	Amkul et al. 2023

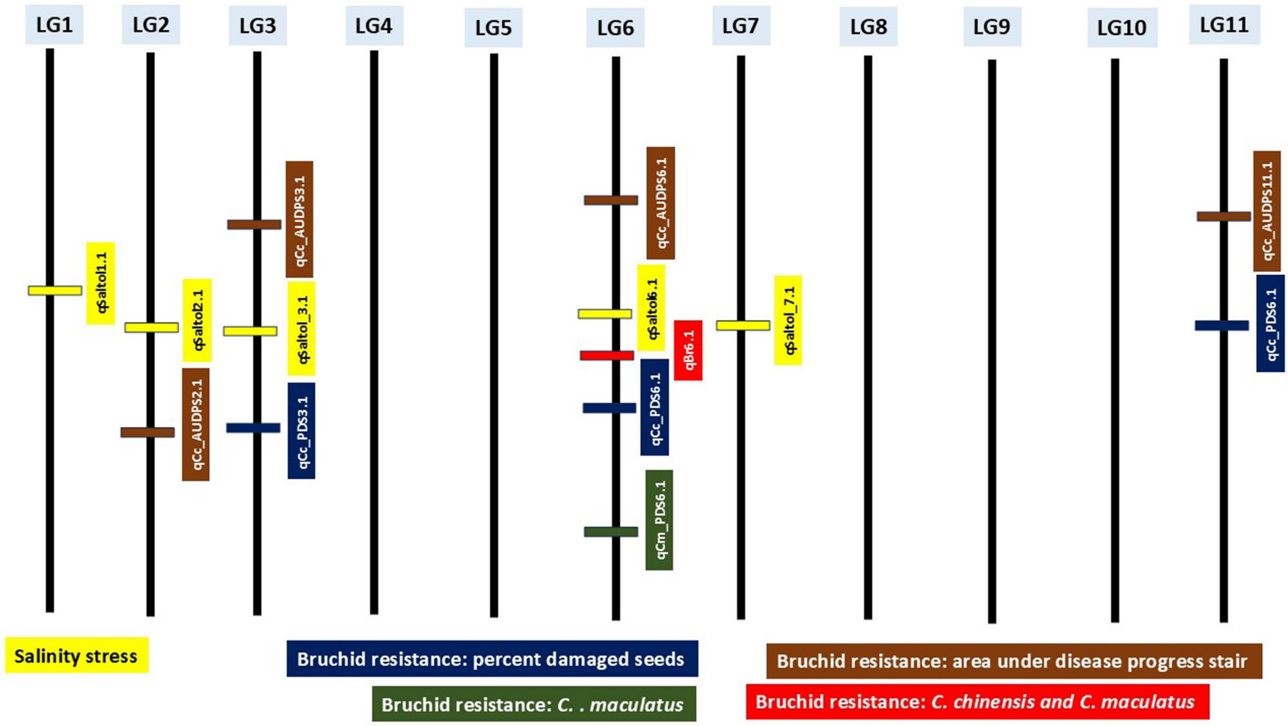

Fig. 6 Pictographical representation of major QTLs/genes for biotic and abiotic stress resistance traits in zombi pea (Dachapak et al. 2019; Amkul et al. 2019; 2023)

Vigan.01G464900.01 and *Vigan.01G501900.01*. Further, the comparative genome analysis revealed that salt tolerance in halophytic *Vigna* species, the beach cowpea [*Vigna marina* (Burm.) Merr.] is due to QTL *Saltol1.1* which corresponds to QTL *qSaltol1.1* in zombi pea (Dachapak et al. 2019). These results provide foundation for breeding salt resistance cultivars of zombi pea. Recently, novel QTLs were reported for salt tolerance in wild zombi pea using the BC_1F_2 mapping population derived from cross of TVNu240 × AusTRCF 322105 (Laosatit et al. 2024). The QTL analysis identified two novel QTLs, *qSaltol_3.1* and *qSaltol_7.1,* preventing leaf wilting and leads to plant survival under salinity conditions. The comparative candidate gene analysis revealed that, *Vigve.0024s001200.01* encoding MSR (methionine sulfoxide reductase) and *Vigve.0024s002000.01* encoding PIMT (protein-L-isoaspartate O-methyltransferase), could be the candidate genes for salt tolerant QTL '*qSaltol_3.1*' (Laosatit et al. 2024). The MSR enzymes have been reported to convert methionine sulfoxide to methionine, that plays a role in stress tolerance mechanisms (Lee et al. 2014; Roy and Nandi 2016). For instance, a recent study reported that MSRB5 (methionine sulfoxide reductase B5) enzyme from *Arabidopsis* protects the Arabidopsis and rice from salinity stress through regulation of Na + /K + homeostasis (Cai et al. 2023). On the other hand, PIMT is an enzyme critical in protein structure repairing and functioning. It has been suggested that PIMT helps in proper growth and development of crop plants under salinity stress through enhancing the efficacy of ROS-scavenging enzymes and repairing of damaged repairing isoaspartyl coupled with bolstering oxidative and heat stress tolerance (Ghosh et al. 2020). In addition, about 46 genes were identified in the genomic region of QTL, '*qSaltol_7.1'*, e.g. candidate genes (*Vigve.0049s001800.01*) encoding KCS (3-ketoacyl-CoA synthase) (Laosatit et al. 2024). KCS induced long-chain fatty acids are the key players in plant survival under stress conditions. For instance, in *Arabidopsis* the upregulation of KCS gene from *Vitis vinifera* enhanced tolerance to salt stress during germination and seedling stage (Yang et al. 2020). Although, further investigations are needed to validate the associated candidate genes with these salt tolerant QTLs.

Flooding or waterlogging stress, which induces numerous physical and chemical alterations in soil properties, is another major factor which impedes the sustainable food security (Renziehausen et al. 2024). Because of erratic rainfall patterns, waterlogging can occur in any developmental stage of plants in rainfed or irrigated farming systems. Consequently, a stressful environment arises when plants are subjected to waterlogged or soggy conditions that exhibits anoxia (absence of oxygen) or hypoxia (deficiency of oxygen) and cause a range of responses that hinder the rate at which net CO_2 is assimilated by the plants as well as stomata conductance and hydraulic conductivity of the roots (Wiraguna et al. 2021; Sharmin et al. 2024). This soggy condition cause suppression of oxidative phosphorylation, which results in an ATP shortage, reduction in photosynthetic rate, reduced water and nutrient uptake (Juntawong et al. 2014). Unravelling of molecular mechanisms governing waterlogging tolerance and identification of genetic resources in wild and cultivated germplasm is imperative in breeding crop varieties tolerant to soggy conditions. In the Fabaceae family limited studies have been reported on waterlogging tolerance mechanisms and most of the work on this aspect is mainly concentrated on soybean crop (Sakazono et al. 2014; Kim et al. 2015). Recently, in soybean a major QTL '*qWT_Gm_03'* was identified regulating root plasticity under waterlogged or soggy situations (Ye et al. 2018). In the legume family, the genus *Vigna* comprises numerous nutri-dense crops and many of them are sensitive to waterlogging at different development stages. Interestingly, zombi pea (*Vigna vexillata*), a neglected member of *Vigna* genus, is reported to be a potential genetic resource to fight with abiotic stresses like waterlogging (Miller and Williams 1981; Butsayawarapat et al. 2019). Transcriptomics analysis can be utilized to offer a fundamental comprehension of the molecular response governing the waterlogging adaptation in non-model '*Vigna* crops. Plants' ability to adjust to waterlogging stress is greatly influenced by the architecture and plasticity of their roots (Fukao et al. 2019). Hence, to unravel the molecular response of zombi pea towards waterlogging tolerance, Butsayawarapat et al. (2019) performed the comparative transcriptome study using RNA-seq analysis of waterlogged roots and waterlogging tolerant phenotypes. The waterlogging tolerant varieties of zombi pea develop lateral roots and aerenchyma in the hypocotyl and taproots (Butsayawarapat et al. 2019). While the sensitive varieties to waterlogging stress exhibits decrease in leaf photosynthesis and leaf chlorophyll content, damaging of root system and root growth suppression in contrast to stress tolerant cultivars. The waterlogging stress tolerant cultivars of zombi pea have numerous starch grains in the parenchyma and stress conditions further leads to development of aerenchyma in the taproots and hypocotyls (Butsayawarapat et al. 2019). The aerenchyma development in the tolerant cultivars is associated with enhancement of oxygen diffusion from aerial parts to underground roots in waterlogged conditions permitting aerobic respiration. The comparative transcriptome analysis revealed that in the waterlogging sensitive varieties, the gene regulating glycolysis (e.g. *aldolase, enolase, glucose 6 phosphate, phosphofrucktokinases, phosphoglycerate mutase, pyruvate kinases*) and fermentative enzymes significantly upregulated. On the other hand, only the tolerant variety exhibited expression of the genes linked to auxin-regulated lateral root initiation and development. Furthermore, during waterlogging, the tolerant variety exhibited enhanced expression of genes for cell wall modification, aquaporin, and peroxidase (Butsayawarapat et al. 2019). The comparative transcriptome analysis of waterlogging tolerant, susceptible cultivars of zombi pea with *Arabidopsis*, identified 31 core hypoxia genes. The results indicated that only tolerant cultivar depicted the induction of *non-symbiotic hemoglobin* 1 cluster.

Historically, plant breeders have given priority to above ground plant architecture and yield traits. While, the underground root system plays multiple roles such as water and nutrient uptake, interactions with soil microbes, and stress response mechanism (Hodge et al. 2009). After realizing the potential of root system architecture (RSA) as important breeding target, plant breeders have focused on RSA as important breeding objective specifically for adaptation to abiotic stresses. The root traits are polygenic in nature and are significantly influenced by environmental factors (Meister et al. 2014). The efforts have been made across the crop plants including legume vegetables for determining QTLs for root traits that exhibits significant relationship with flooding and drought stress conditions (Wang et al. 2024). In common bean, the QTLs related to RSA have been identified which governs drought stress tolerance (Asfaw and Blair 2012). Recently, based on GWAS, the genetic basis of drought resistance in common bean were dissected by analysis root related traits (Wu et al. 2021). In garden pea three QTLs related to drought tolerance viz. *rwclF-2, rwcsF-2*, and *audpc_rwcs-2,* were identified (Iglesias-García et al. 2015). Thus, by altering the RSA, plant adaptation to stress conditions can be improved. Some of the zombi pea accessions have natural adaptation to drought stress conditions. The results on close realtives like pea, French bean and soybean, suggests that modern molecular breeding approaches like GWAS, GBS and QTL-seq analysis can be effectively utilized to dissect the genetic basis of drought tolerance in zombi pea. Plant growth and development is substantially affected by nutrient stress or soil fertility status. It is reported that, the blossom retention in tuberous zombi pea leads to higher accumulation of K, Mg, Zn, Fe and Mn in tubers, pericarp and pods of zombi pea (Priyadarsini et al. 2024). Likewise, the protein content in tubers of zombi pea is found maximum under wider spacings. It is suggested that blossom retention significantly affects the partitioning and allocation of nutrients to various plant parts. In the near future, development of closely linked molecular markers to different abiotic stresses and its application in marker assisted selection (MAS) could be useful in breeding waterlogging stress tolerant varieties in orphan crops. Furthermore, GWAS in conjunction with omics, including transcriptomics (eQTLs), proteomics (pQTLs), and metabolomics (mQTLs), may make it possible to identify new genes and functional pathways in the underutilized legumes such as zombi pea against abiotic stresses. Rare information is available regarding molecular mechanisms and genetic basis of drought and heat stress resistance in zombi pea accessions. There is a huge scope in exploring the potential of zombi pea in a fight with climate change to improve the food and nutritional security. Further identification of genes/QTLs governing abiotic stress resistance, closely linked molecular markers, transcriptome analysis, genome editing applications would be rewarding in strengthening the potential of zombi pea and other orphan legumes to tackle the ghastly future.

Insights into genetics and genomics of biotic stress tolerance

The wild *Vigna vexillata* is well adapted to various biotic stresses like cowpea mottle carmovirus, powdery mildew and insect pests like cowpea bruchid, cowpea weevil or cowpea seed beetle, Mexican bean weevil, sucking bugs and pod borer (James and Lawn 1991; Ogundiwin et al. 2002; Vincenzo et al. 2005; Dachapak et al. 2017; Amkul et al. 2023). Cowpea, which is a prominent crop of African and Asian continents, is affected by numerous pathogens. The cowpea mottle virus (CPMoV) is one of these devastating pathogens of cowpea causing huge yield losses of up to 75% (Kim and Bozarth 1992). There is a lack of resistant sources in cowpea, but *Vigna vexillata* carries potential genes for resistance to CPMoV (Ogundiwin et al. 2002). The inheritance studies were carried out based on F_2 and backcross (BC) populations derived from crosses of three susceptible lines TVnu 1344, TVnu 1443, and TVnu 1554 belonging to *Vigna vexillata* var. *angustifolia* with resistant lines TVnu72 and TVnu73 of *Vigna vexillata* var. *macrosperma* and *Vigna vexillata* var. *vexillata,* respectively (Ogundiwin et al. 2002). The resistance to CPMoV in zombi pea reported to be controlled by a single dominant gene. Further mapping of genes/QTLs or determination of genomic regions governing resistance to CPMoV in zombi pea is the need of hour to tackle such enemies in face of climate change. The successful interspecific hybridization between *Vigna vexillata* and *Vigna unguiculata* has been documented by employing embryo culture technique which is instrumental in transfer of stress tolerant genes (Gomathinayagam et al. 1998).

Bruchids or seed weevils are important members of biotic stresses inducing huge seed yield loss in legume crops. Initially under the field conditions the eggs are laid on the young pods and eventually larvae bore to pods and seeds (Srinives et al. 2007). In principle, the cultivated *Vigna* species are highly sensitive to bruchids like cowpea weevil (*Callosobruchus maculatus* L.) and azuki bean weevil (*Callosobruchus chinensis* F.) (Srinives et al. 2007; Considine et al. 2017). These weevils have wide geographic distribution owing to international seed trading and are a major threat to food security globally. Identification of potential reservoir of resistant genes, breeding of resistant cultivars and inclusion of natural tolerant crop species in the food systems are effective measures to prevent the loss of food and nutritional security through these widely occurring pests. Interestingly, the cultivated and wild forms of zombi pea are potential carrier of genes resistant to cowpea weevil and Mexican bean weevils. In zombi pea the presence of PAPA (para-aminophenylalanine) amino acids provide resistance to bruchids (*Callosobruchus maculatus* and *Zabrotes subfasciatus*) (Birch et al. 1986). But, zombi pea accessions exhibits differential behaviour towards resistance to *Callosobruchus maculatus* without any significant difference in the PAPA amino acids level in mature seeds of zombi pea (Bressan 1990). Thus, PAPA is not the major defensive compound against bruchids in zombi pea. On the other hand, it is documented that in the seeds of zombi pea having resistance to *Callosobruchus maculatus,* high content of α-amylase inhibitor is present (Lattanzio et al. 2005). The resistance to bruchids in zombi pea is quantitative in nature. The development of genomic tools to accelerate the exploitation of genetic potential of zombi pea as a future crop is essentially possible in the post-genomics era. Amkul et al. (2019) developed the high-density genetic linkage map of zombi pea based on SLAF-seq and SNP genotyping and documented the QTLs controlling seed resistance to bruchid species, *Callosobruchus chinensis* and *Callosobruchus maculatus*. To unravel the genetic basis of bruchid resistance in zombi pea, a F_2 mapping population derived from the cross of TVNu 240' (*Vigna vexillata* var. *macrosperma*) × 'TVNu 1623 (wild type susceptible to bruchids) was used for construction of linkage map and QTL analtysis. The Central African line of zombi pea 'TTVNu240' is highly resistant to both the species of bruchids, *Callosobruchus maculatus* and *Callosobruchus chinensis* (Amkul et al. 2029). For *Callosobruchus chinensis* resistance, one major and three minor QTLs were found, while for *Callosobruchus maculatus* resistance, one major and one minor QTL reported (Table 1, Fig. 6). Further, comparative genome analysis revealed that that common bean chromosome 6 included Markers 197,124 and 1,966,422, which flanked major QTL '*qBr6.1*' governing resistance to *Callosobruchus chinensis* and *Callosobruchus maculatus* in zombi pea (Amkul et al. 2019). The 'Phvul.006G087700' gene located on chromosome 6 of common bean can be considered as a candidate gene controlling resistance to bruchids in zombi pea. The fine mapping of '*qBr6.1*' QTL revealed that genomic region of this major QTL comprises two tightly linked QTLs, *qBr6.1-A* and *qBr6.1-B* governing resistance to bruchids in zombi pea (Amkul et al. 2023). The genome sequence analysis demonstrated that the gene '*VvTaXI*' encoding xylanase inhibitor is a candidate gene of '*qBr6.1*' conferring resistance to bruchids in zombi pea. This candidate gene will be exploited for molecular breeding of zombi pea against

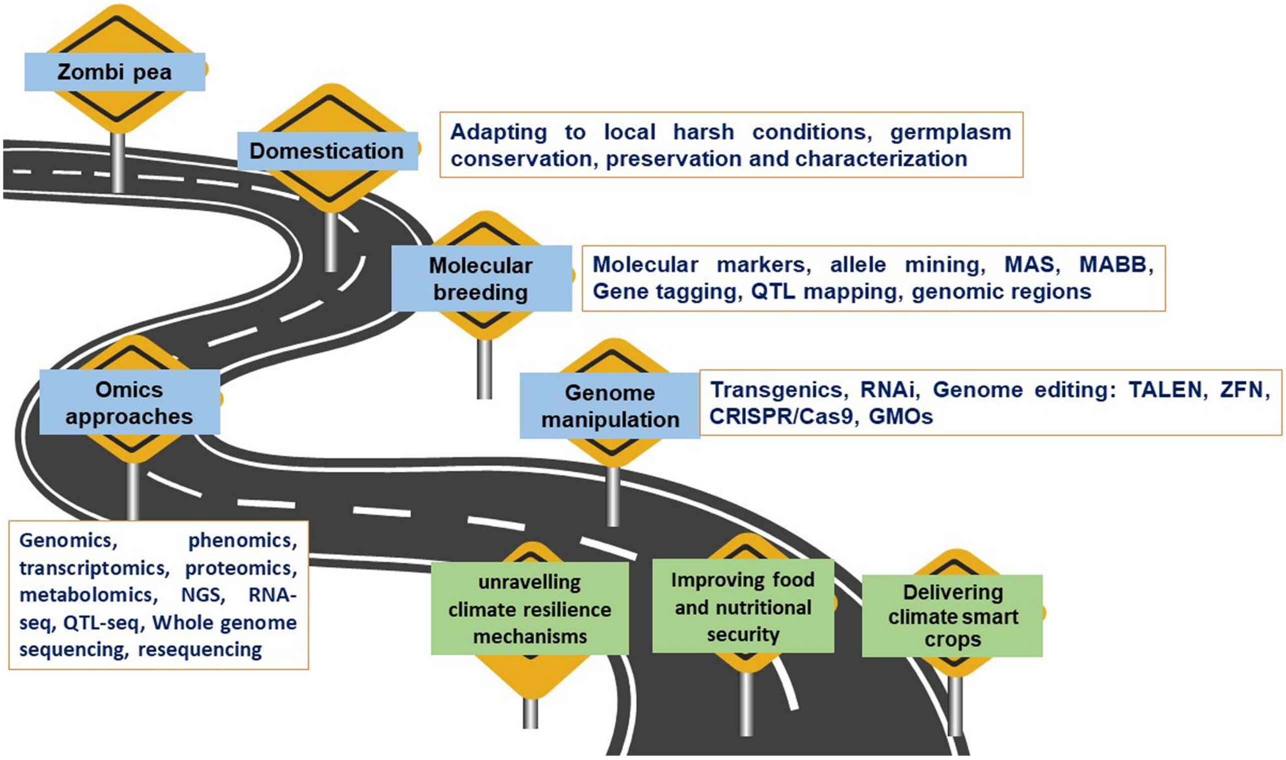

Fig. 7 Future strategies to explore the genetic potential of zombi pea

bruchid resistance. Thus, zombi pea is a potential genetic resource against major biotic and abiotic stresses of legume crops to combat the challenges of food security in the era of climate change.

A long way to go

The comprehensive information regarding potential of zombi pea as a future climate smart crop to feed billions and improving food and nutritional security is presented in this article. The orphan crops like zombi pea are gaining much attention among the scientific fraternity owing to their enormous potential to tackle the ghastly future. Zombi pea is a carrier of genes to win the battle against extreme weathers and major biotic and abiotic stresses in face of climate change. In the post-genomics era, efforts have been made to elucidate the genetic basis of biotic and abiotic stress resistance in zombi pea and some of the major QTLs like '*qBr6.1*' governing bruchids resistance and '*qSaltol1.1*' controlling salinity tolerance in zombi pea have been identified. Likewise, the progress has been made in unravelling the genetic basis of domestication syndrome in zombi pea and major QTLs for domestication related traits have been identified. the genomes of zombi pea and cowpea are highly conserved, but further completion of full genome sequence of zombi pea would be instrumental in harnessing genomics in exploration of genetic potential of this unexplored gem among orphans. Despite having enormous potential, zombi pea lacks in genetic and genomic resources which could accelerate the genetic improvement and role of zombi pea in combating hunger and malnutrition. The bulk of genomics assisted tools can be helpful in hunting stress resistance genes in zombi pea to ensure global food and nutritional security. Zombi pea is a treasure trove of genes to tackle the ghastly future and modern genetic engineering tools like RNAi mediated gene silencing and CRISPR/Cas9 enabled genome editing has a lot of promise to explore the potential of zombi pea. The genetic engineering involving transgenics, RNAi, and CRISPR/Cas systems holds a great promise in enhancing tuber yield in tuberous legumes coupled with development of biotic and abiotic stress resistant cultivars by manipulating target genes involved in tuber formation and stress responses. This can be approached via modification of genes governing tuber related traits like tuber size, shape, and number, and via targeting genes regulating cell division, starch metabolism and intricated hormonal signalling. Zombi pea accessions have adaptive nature to various environmental and biotic stresses. The modern biotechnological tools such as GWAS, GBS, QTL-seq, RNA-seq etc. can be effectively used to identify the functional genes (QTLs and candidate genes) involved in stress response in zombi pea and other underutilized crops. The genomics has also facilitated the isolation and identification of molecular markers with linked traits, and further exploitation using MAS or MABB approaches. The advances in NGS platforms can help in strengthening the genomic resources in zombi pea like sequence-based markers, reference genome assemblies and genomics databases. The genomics and genome editing applications could speed up the domestication of orphan crops and generating resources for diversifying food systems in the era of climate change. In-depth investigations are needed to explore the full genetic potential of orphan crops like zombi pea as they are reservoir of genes for creating a sustainable future for all the lives. We personally feel that the knowledge obtained about the potential of orphan crops like zombi pea is likely the tip of the iceberg, hence more systematic efforts are the need of hour to enhance our knowledge about domestication and genetic potential of orphan crops like zombi pea to feed billions a nutritious diet (Fig. 7).

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Data availability No data was utilized in this article analysis.

Declarations

Conflicts of interest Authors declare that they have no conflict of interest.

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