Review article

Grasspea, a critical recruit among neglected and underutilized legumes, for tapping genomic resources

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A B S T R A C T

Environmental perturbations are persistent threats to sustainable agriculture, and thus recruitment of resilient crops, especially legumes, exhibiting agronomically important traits has become a priority for plant biologists. It is of utmost importance that the neglected and underutilized legumes (NULs) are identified and utilized as source of germane genes and gene-products, through concerted research platforms. In the present article, we analyzed the current status of NULs with specific emphasis to the potent utility of grasspea owing to its unique characters including stress adaptation, nutritional superiority and ease of cultivation. We have highlighted the landmarks in the history of grasspea, delineating the rapid progress achieved in grasspea biology during the past decades. Despite possession of a neurotoxic compound, β-N-oxalyl-L-α,β-diaminopropionic acid (β-ODAP), this neglected legume outshines most food crops with its distinct physicochemical attributes, health and agricultural benefits and resilience to environmental constraints. With the availability of genome sequence, grasspea is now established as an appropriate genetic resource for sustainable agriculture and phytoremediation rendering its genes, proteins and metabolites for targeted genetic manipulation. We conclude that grasspea would serve as a resource for plant translational genomics (TG) research, particularly resilience of legumes to environmental challenges.

1. Introduction

In view of the present scenario of global climate altercations, identification and characterization of crop varieties, resilient to stress conditions, are imperative to achieve sustainable food production and agricultural security. The goal of sustainable agriculture is compromised by over-dependency on few staple crops and underutilization of others, besides constant climate change as well as land deterioration. Nonetheless, there is a plethora of derelict crops, and the neglected and underutilized legumes (NULs) constitute a significant fraction. The NULs may be so classified if they exhibit one or more of the typical attributes including absolute remoteness from national and international agricultural policies, besides research and development, local significance in consumption and production, adaptation to marginal areas, indigenous propagation and fewer or none *ex situ* collections [1–3]. Unlike the conventional grain legumes, NULs can withstand indelible alterations in climate and soil conditions, ameliorate micronutrient deficiencies from variable sections of the society and can potentially reduce the carbon footprint for daily protein requirement of humans. In fact, individual or parallel cultivation of NULs significantly replenishes the agricultural fields, as well as boost nutritional and economic security [4]. For the present review, we elaborated the pioneer landmarks and advancements achieved in grasspea biology, canvassing it as a promising crop of the future. We focused on the potential of grasspea as a stress resilient legume, bringing forward intriguing questions regarding the dissipative adaptation mechanism, besides contribution in phytoremediation and medicinal usage. Furthermore, we highlighted the progress and prospects of its own improvement by conventional breeding and genomics transcending to its bright future as a reference crop species, while opening new avenues for improvement of all legumes in general.

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2. Neglected and underutilized legumes

A significant number of genomic sequences, belonging to NULs, are well represented in various databases including Legume Information System (LIS) and International Nucleotide Sequence Database Collaboration (INSDC). The classified NULs have remained far from molecular comprehension with respect to crops such as soybean and maize, and model plant species Arabidopsis, for which the PubMed articles and nucleotide sequences range approximately from 28–78 thousand and 24–52 lakh bp, respectively. We analyzed the overall progress made, thus far, in the domain of NUL research as represented in the NCBI portal (Supplementary Table 1). Of the 43 NULs, maximum research efforts have been deployed in *Cajanus cajan, Canavalia ensiformis, Cyamopsis tetragonoloba, Lathyrus sativus, Lupinus angustifolius, L. albus, Mucuna pruriens, Psophocarpus tetragonolobus, Phaseolus coccineus, P. lunatus, P. aureus, Vigna mungo* and *V. angularis,* (Fig. 1; Supplementary Table 1). The remaining NULs have a long road ahead since the identification of their unique molecular attributes is yet to gain momentum. The lack or minimal representation of even nucleotide and protein sequences is the bitter truth for most NULs (Fig. 2; Supplementary Table 1). The genetic relationships and diversities among NULs have, so far, been established with the aid of random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), inter simple sequence repeats (ISSR), single feature polymorphism (SFP), single-nucleotide polymorphism (SNP), and chloroplast gene RBCL, among others. Recent advancement in omics technologies has enhanced our understanding of the genetic structure of these species and highlighted unique stress-adaptive responses [5–9]. The emergence of clustered regularly interspaced short palindromic repeat (CRISPR/Cas9) technology combined with marker-assisted selection (MAS) and genome-wide association study (GWAS) shall open new avenues for sustainable utilization of NULs. These crops may be genetically improved for traits like poor seed setting, pre- and post-harvest diseases, pod shattering, anti-nutritional factors (ANFs), low yield and late maturity. The lack of a genome is a bottleneck in implementation of MAS- and GWAS-mediated improvement of NULs. However, we have witnessed higher incidences of genome sequencing of NULs during the past few years, the latest addition being grasspea.

3. Grasspea: unique traits and trails

The genus *Lathyrus* (ITIS TSN: 25834) is one of the largest of the family Fabaceae (Leguminosae) [Subfamily Papilionoideae; tribe Fabeae (Adans.) DC., formerly Viceae [10] with 159 species (http://www.theplantlist.org) across the temperate regions of the world [11]. The nomenclature of most *Lathyrus* spp. has witnessed several alterations, but not so in the case of grasspea (*Lathyrus sativus* L.; 2n = 14). *Lathyrus sativus* is the name accepted by International Legume Database and Information Service (ILDIS) for the taxon with a spelling variant *L. sativas* (https://ildis.org). Grasspea is the crucial food and fodder grain of the genus, and also the species to witness maximum molecular advancements (Fig. 3; Supplementary Table 2). It is a survival food for the difficult times of crop failures, as is characteristic of NULs. Since it is a marginalized crop, the exact area under grasspea cultivation as well as annual production, cannot be accurately ascertained. However, the maximum production of grasspea has been witnessed in India, Bangladesh and Ethiopia.

The *Lathyrus* spp. across the genera, display multiple levels of tolerance to abiotic and biotic stress conditions including water-deficit, hypersalinity, mineral deficiency, pests and pathogens thus qualifying as a potential genomic resource [12–15]. While the *Lathyrus* spp. are excellent sources of protein, and can be an important part of human diet,
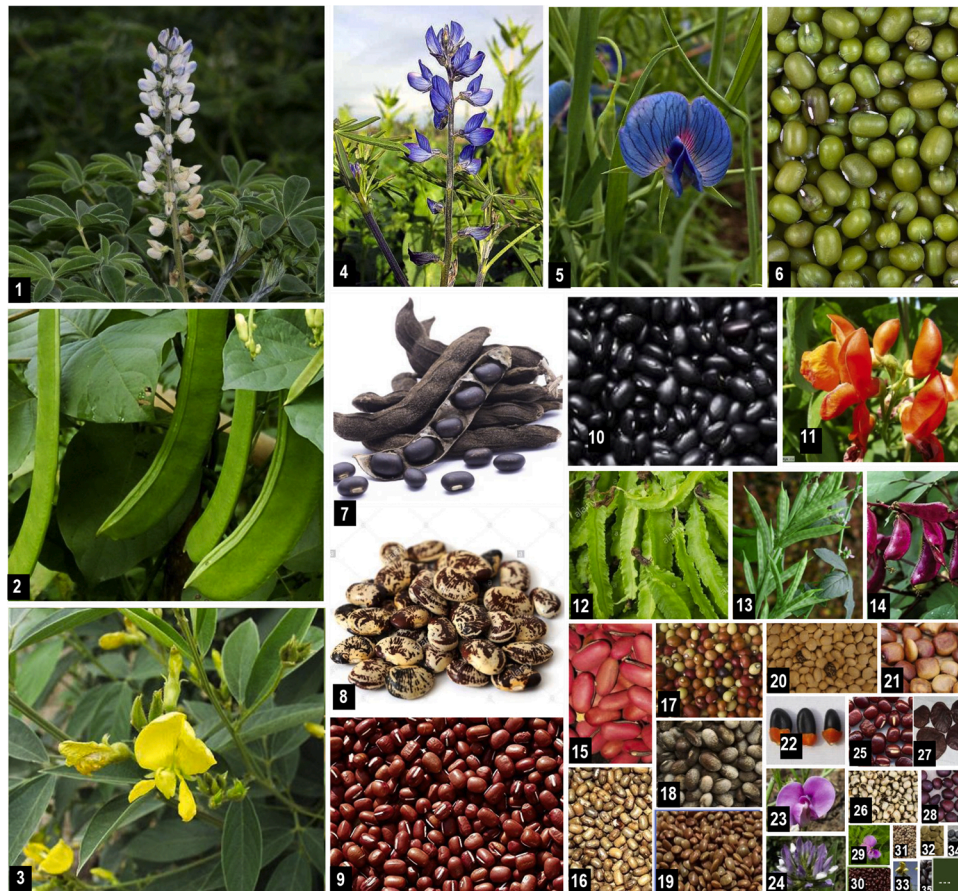

Fig. 1. Pictorial representation of the progress achieved in research of NULs. The picture area reflects the extent of research progress in the specific NUL, decreasing from the top right corner to bottom left corner. The blocks correspond to *Lupinus albus* (1), *Canavalia ensiformis* (2), *Cajanus cajan* (3), *Lupinus angustifolius* (4), *Lathyrus sativus* (5), *Phaseolus aureus* (6), *Mucuna pruriens* (7), *P. lunatus* (8), *Vigna angularis* (9), *V. mungo* (10), *P. coccineus* (11), *Psophocarpus tetragonolobus* (12), *Cyamopsis tetragonoloba* (13), *Lablab purpureus* (14), *Canavalia gladiate* (15), *V. aconitifolia* (16), *V. subterranean* (17), *P. acutifolius* (18), *Macrotyloma uniflorum* (19), *L. mutabilis* (20), *Pachyrhizus erosus* (21), *Afzelia africana* (22), *Sphenostylis stenocarpa* (23), *Bituminaria bituminosa* (24), *P. angularis* (25), *Detarium microcarpum* (26), *V. racemose* (27), *Tylosema esculentum* (28), *V. vexillata* (29), *P. calcaratus* (30), *Brachystegia eurycoma* (31), *V. luteola* (32), *M. geocarpum* (33), *M. flagellipes* (34) and *Parkia timoriana* (35), respectively. The data corresponds to the number of publications, retrieved from the NCBI platform.
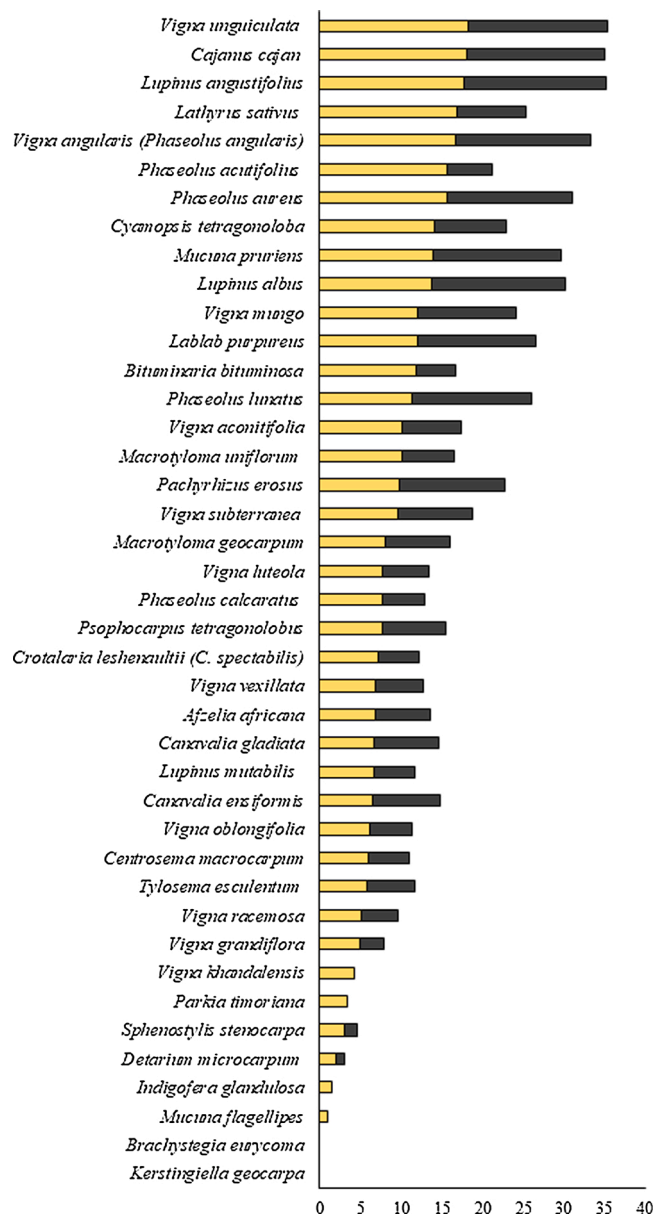
Fig. 2. Graphical representation of the number of gene and protein sequences for NUL species available in NCBI. The X-axis represents the number of sequences in logarithmic scale and the Y-axis represents the NULs. The white bars represent nucleotide sequences and black bars the proteins (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

the genus experiences a stigma for discrimination. This is because almost all *Lathyrus* spp. suffer from serious impediment of being toxic, as its overconsumption may cause neurolathyrism, a neurodegenerative disease. The crippling effect of prolonged dependence on grasspea led to its ban as food during '60 s to '90 s in several countries across the world due to the presence of the neurotoxin β-N-oxalyl-L-α, β-diaminopropionic acid (β-ODAP). The sale of seeds was banned imparting it the status of "orphan crop" in terms of negligible utilization as a food crop and exploitation as a research plant system. Nevertheless, the ban on feeding of grasspea could not conceal its potential as a model crop in the domain of stress resilience. The versatility of grasspea is reflected in its research history and unmet challenges.

3.1. Germplasm diversity of Lathyrus

Global germplasm collections have exemplified humungous genetic diversity among *Lathyrus* accessions endemic to defined geographical areas. Due to its importance as a survival food for the poor, grasspea is a part of the multilateral system of access and benefit sharing under the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA). Significant collections of cultivated and wild *Lathyrus* spp. have been assembled and maintained in situ as well as *ex situ* globally [16]. Conservative Botanique National des Pyrenees et de Midi-Pyrenees (CBNPMP), France, has as many as 4477 germplasm accessions for merely two *Lathyrus* spp., *L. sativus* and *L. cicero*. Co-ordinated international efforts towards conservation of *Lathyrus* spp. have been initiated by *Lathyrus* Genetic Resources Network [17] and the Global Crop Diversity Trust [18]. A model-based population structure analysis previously divided the relative wild accessions into three sub-groups, those from Asia and those from Europe and Africa [19]. So far, markers identified for specificity of diverse populations have been morphological [20], biochemical [21] as well as molecular [22,23]. The divergence of Asian species was quite distinct from other geographical regions, discordant with Vavilov's predictions of Central Asia and Abyssinia as the primary centers of origin [24]. The natural distribution of grasspea is yet to be conclusively identified, making it difficult to precisely locate the center of origin [25].

A number of genetic markers have been described for grasspea, and a detailed genomic map is now available which reveals an approximate size of 6.3 Gb [26]. The paired end (PE) sequencing of LS007 genomic DNA was carried out using PCR-free libraries, followed by sequencing of the Long Mate Pair libraries (LMP) on the HiSeq Illumina platform. A phylogeny of grasspea (LS007), determined in the context of 17 other plant species, revealed close homology with field pea, barrel medic and chickpea. Legume genomes, particularly species in the tribe Fabeae including the genus *Lathyrus*, are highly variable in size owing to repeat elements [27]. The implementation of SSR markers in grasspea has remarkably improved our understanding of the inter-specific associations among *Lathyrus* spp. and inter-varietal kinds among grasspea members. Twenty-three grasspea accessions could be statistically associated by utilizing 50,000 SSRs that were specified to distinct loci in species from Africa, Europe, Asia and International Center for Agricultural Research in Dry Areas (ICARDA) [28]. Moreover, a grasspea linkage map was developed to identify QTLs associated with resistance to *Ascochyta* blight [29]. This linkage map was unsaturated, thus disenabling comparative genomics with other legumes. Extensive genome conservation is exhibited by members of the legume Papilionoideae subfamily (such as *Pisum, Lens, Vicia or Cicer*) [30]. The incorporation of co-dominant markers of the likes of microsatellites, shall aid accurate determination of genetic distances among markers in repulsion phase [31]. Recently, 42 single nucleotide polymorphisms (SNPs) have been validated from a differential pool of approximately 1.5 lac transcripts and classified as kompetitive allele specific PCR (KASP) markers for 43 grasspea accessions [32]. Plausible genetic variation leading to differential water use efficiency shall allow identification of QTLs of significance in grasspea subjected to dehydration conditions [33]. There is a pressing need to develop a comprehensive genetic map with highlights of QTLs of agronomic value, and with the availability of genome sequence, saturated linkage maps are not distant.

Additionally, numerous large and small-scale expedients including hybridization-based improvement of varieties have been observed for the genetic improvement of grasspea. The interspecific hybridization in *Lathyrus* spp. recognized and facilitated the transfer of desirable traits from exotic and wild germplasm and offers many opportunities for improvement, especially for readily crossable species. Since grasspea is utilized as the food crop, significant efforts have been made for reducing β-ODAP content and increasing nutrient values [34]. In recent past, a number of grasspea varieties have been developed with very lesser β-ODAP, ranging from 0.074 to 0.109 %, including cv. Ratan, Prateek,
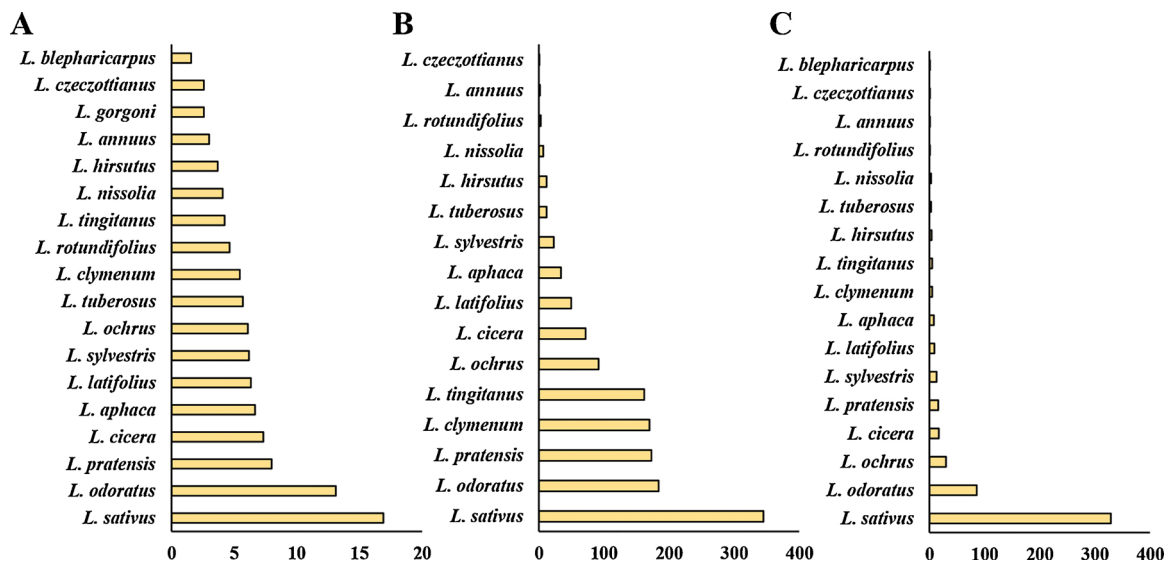
Fig. 3. A comparative account of the molecular comprehension of *Lathyrus* biology. The number of nucleotides (logarithmic scale, base 2) **(A)**, proteins **(B)** and publications **(C)** in representative *Lathyrus* spp. generated using NCBI platform. The X-axis represents the number of nucleotides, proteins and publications in the respective figures, and the Y-axis represents the *Lathyrus* spp.

Mahateora and Nirmal [34–36]. Among the improved varieties, Prateek was found to yield highest under rice-utera conditions [37].

3.2. Lathyrus research has come a long way

The oldest publication on *Lathyrus*, dating back to 1931, described the chromosomes of *L. tuberosus* [38]. Until 1950, there were few articles (as estimated from PubMed records) related to *Lathyrus* research, mainly dealing with either chromosomal biology or the toxin β-ODAP. Interestingly, during the next decade, there was a boom in this research field with more than 40 publications. The research was categorically focused

on the effects of neurotoxin in vertebrates, derived either from grasspea or sweetpea [39–41] (Fig. 4). The only exception was the analysis of flavonoid pigments in sweetpea [42]. For the first instance, the non-toxic nutritional value of grasspea was analyzed by Sastry et al. [43]. Besides β-ODAP, non-protein amino acids including L-homo-arginine and O-oxalylhomoserine are also abundant in the seeds of grasspea [44,45] and redpea [46]. Notably, few novel amino acids such as derivatives of isoxazolinone and pyrimidinyl amino acid were identified in sweetpea [47,48] and tangierpea [49]. The decades of 1970–1980 were dominated by research efforts focused on detection of unique amino acids in *Lathyrus* spp. and the effect of neurotoxin on
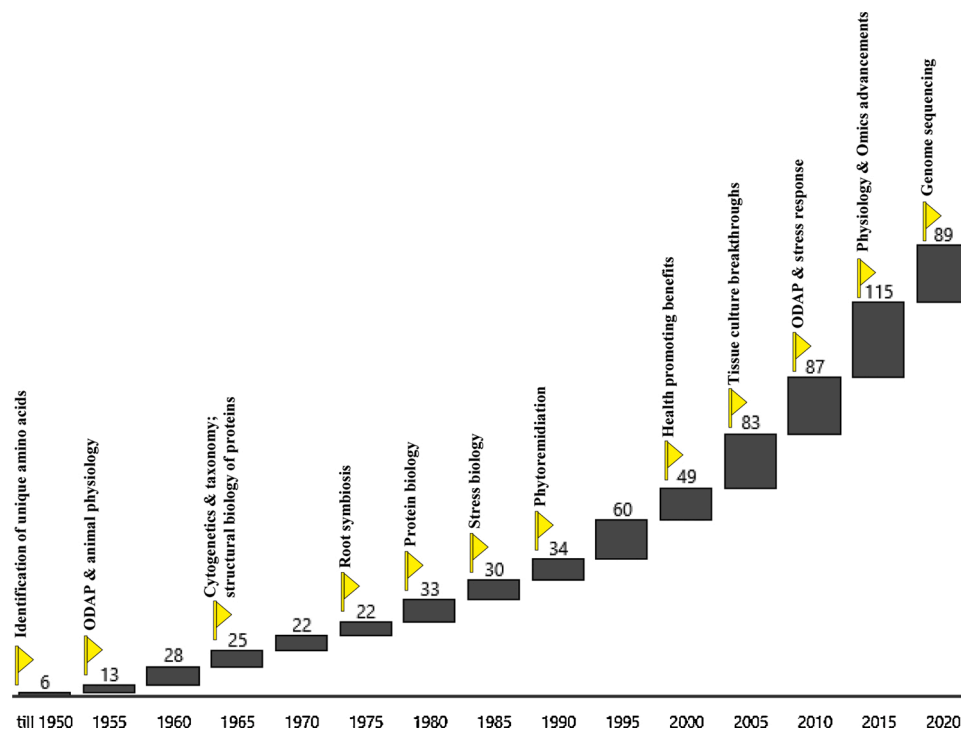

Fig. 4. Schematic representation of the landmarks achieved in *Lathyrus* biology. The X-axis demarcates the time line since 1950 till date and the successive blocks along the Y-axis depict the publications score, proportional to size of each block. Present compilation clearly reflects the major advancements accomplished in the past decade.

animal physiology. However, there was a growing interest in lectins of *Lathyrus* spp. during this time, which continued till the mid of next decade [50,51]. There were also attempts on elucidating specific cytogenetic events, including meiotic abnormalities [52–54] and phylogenetic analysis of organellar DNA [55]. Interestingly, during 1990s, taxonomic relationships among various *Lathyrus* spp. [55,56], and those with other genera [57] were sequentially established. From 1950 till 2000, the progress was majorly observed in nutritional aspects of *Lathyrus* with limited advancements in the molecular biology prospects, the only exception being the exploration of gibberellic acids (GAs) [58, 59].

Although few studies examined the resistance of *Lathyrus* spp. to nematodes [60,61], the mechanisms underlying stress resilience were far from comprehension before 21st century. During 1995–2000, pioneer studies were conducted to dissect the key aspects of stress response in young seedlings of grasspea [62–64]. The other aspects of *Lathyrus* research which had progressed were protein biology [65,66] and symbiotic nitrogen fixation [67,68]. The onset of the 21st century observed a major boom in *Lathyrus* research with inspection of diverse areas. The molecular biologists moved beyond β-ODAP and utilized the non-neurotoxic potential of *Lathyrus* spp. While the primary focus was on stress biology, few unique aspects including phytoremediation also came to the limelight. The developing seedlings of grasspea were observed to significantly sequester europium ions [69,70]. Further, increasing evidence over the years established grasspea as capable of sequestering toxic heavy metals such as cadmium [71,72], lead [73–77] and nickel [78], also. Additionally, health promoting benefits of several unique amino acids of *Lathyrus* spp. were also recognized [79–81]. There were also a few reports describing tissue culture methodologies for regeneration and genetic transformation of grasspea [82–85], *albeit* with limited success.

The maximum advancement in dissection of stress adaptation of *Lathyrus* has been achieved in the last decade, the primary subject being grasspea (Fig. 4), discussed elaborately in forthcoming sections. Fikre et al. [86], for the first time, suggested the role of β-ODAP in imparting resilience to multivariate stress conditions through reduction of cytosolic reactive oxygen species (ROS) [87,88] and alteration of mitochondrial calcium [89]. This decade also witnessed systematic analyses on spatial and temporal variation in physicochemical [7], transcriptomic [90,91,8] proteomic [92,7] and metabolomic facets [8] of grasspea challenged with multivariate abiotic and biotic stress conditions. Further, there were attempts to ascertain antimicrobial [93,94], antioxidant [95] and antixenotic [96] attributes of grasspea. Recently, draft genome sequence of a European accession (LS007) of grasspea has been published, which revealed an estimated size of 6.3 Gb [26].

3.3. Nutritional or antinutritional?

The major focus worldwide has been on grasspea in context of agricultural and nutritional relevance, among *Lathyrus* spp. The protein content of grasspea comprises of 17 amino acids especially lysine, higher than that in any other legume crops. The seeds of cv. Prateek and LP-24 showed 39.24 and 33.26 % protein [97,7] content, which is comparable to lentil (33.4 %) and soybean (37 %). The protein content of grasspea is much higher than that in other legumes such as chickpea (~19 %), pea (~20 %) and kidney beans (~21 %). In a recent study, 173 accessions of grasspea were subjected to quantification of free amino acids, and glutamic acid was found to be the most abundant [98]. The sugar content in grasspea is higher than that in lupin, red beans, pea and faba beans, *albeit* lesser than chickpea. The antioxidant potential of grasspea is well established with higher content of phenols and flavonoids and lower abundance of parabanic acid. The health-promoting phytochemicals, myo-inositol and its derivatives, β-amyrin and glucitol, are found in high abundance in cv. LP-24, when compared with other cultivars [7]. More significantly, the mineral content differentiated grasspea from common bean, peas, chickpea, lentil and soybean in terms of lower Ca, P, Mg and

Mn and higher amounts of Cu, Fe and Zn.

On the contrary, the notorious reputation of grasspea cannot be neglected and is attributable to the anti-nutritional factor, β-ODAP, high dosage of which can lead to health-endangering conditions [88]. Besides the toxic non-protein amino acid, grasspea being a legume family member, also possesses protease inhibitors, lectins, cyanogens, phenolics, tannins, phytic acid, saponins, antivitamins, oxalate and complex sugars [99]. These compounds either reduce protein digestibility and/or nutrient availability, and appropriately termed 'antinutritional factors'. However, few non-nutritive secondary metabolites in grasspea have been reported to have health benefits (discussed in the forthcoming section), and may be rationalised as 'functional food and nutraceutical ingredients'.

3.4. Grasspea as a congruous element of sustainable agriculture

Grasspea is advantageous for intercropping with cereals such as barley, corn and panicum grass, and as an *utera* crop with rice [100]. It is an integral part of agricultural ecosystem which adds up to 125 kg/ha nitrogen to the soil by nodulation with *Rhizobium leguminosarum*, thereby benefiting non-nitrogen fixing crops [101,102]. Its unmatched stress resilience has been highlighted multiple times in several reports [103]. Notably, grasspea is utilized as a useful crop for the recovery of marginal lands [104]. Moreover, it has a hardy and penetrating root system suited to a wide range of soil types including very poor soil and heavy clays. Over the past several decades, urbanization particularly in the developing world, has led to eutrophication and soil degradation resulting in accumulation of toxic compounds in soils. Legume species, in general, are known for sequestration of toxic elements owing to the rich population of soil microbiota supported by them. Combined with the fact that lead is tightly retained by the root tissues, it is evidently clear that grasspea has profound potential as a principal phytoextracting species in rhizofiltration setups [73].

3.5. Grasspea defies all environmental odds

In this era of concerted agriculture, major crops are vulnerable to persistent biotic and abiotic stresses posing threat to global food security. Grasspea has an amazing capacity to withstand environmental perturbations and emerged as a successful research translation for stress resilience. Understanding stress adaptation in grasspea would provide a new perspective to countering impending global food crisis. Grasspea seedlings exhibit several morphological characteristics including an extensive root system, narrow leaves and stems with winged margins. A comparative study on effect of water-deficit stress in grasspea and field pea revealed greater resilience of grasspea to withstand such conditions [105]. Additionally, metabolic adjustments such as ABA-responsive stomatal closure have been observed, along with activation of antioxidant defense by both non-enzymatic and enzymatic constituents and osmoprotectants [105]. Notably, increase in polyamines has been hypothesized as one of the mechanisms for scavenging hydroxyl radicals [106]. At the amino acid level, valine, isoleucine, leucine, phenylalanine and methionine contents have been found to be more abundant than proline in grasspea, contrary to the known abundance of proline in most crop species under stress conditions [9].

While β-ODAP is recognized as a neurotoxic component, variation in β-ODAP content has been linked to environmental perturbations and developmental stages. The leaves of grasspea harboring high level of β-ODAP exhibit low level of ROS as against enhanced ROS post-inoculation of rhizobium in young seedlings [87]. Therefore, there is a possibility that β-ODAP may serve as a defense compound against shoot herbivores, as supported by the pattern of β-ODAP concentrations observed in seedlings and tissues of juvenile and mature plants [107]. The toxin has also been proposed to be important to the crop's extended potential of photosynthetic activity [48,108,109]. Additionally, purified β-ODAP has been shown to reduce the growth of insect larvae of the rice

moth [110]. Converging evidence from the above studies suggests the concomitant existence of polyamines, β-ODAP and ABA. Moreover, β-ODAP acts as a chelator of divalent metal cations such as Zn^{2+}, Cu^{2+}, Fe^{2+} and Mn^{2+}. This hypothesis is seconded by an increment in the levels of β-ODAP in grasspea in response to the availability of specific metal ions in the soil [111–113].

There has been growing evidence about the inherent resilience of grasspea, particularly against water-deficit or dehydration, the most severe environmental stress [7–9]. Transcriptomic data was previously limited for sequence utilization. One of the pioneer attempts to decipher water-deficit response in grasspea identified 5200 differentially expressed transcripts. Notably, cross-species comparison revealed 51, 47, 37 and 1 % homology, when compared with those of chickpea, soybean, common bean and horsegram, respectively [8]. Further, screening of the grasspea proteome landscape recognized 120 dehydration-responsive proteins (DRPs), most of which were associated with carbohydrate metabolism, amino acid synthesis, antioxidant reactions and cell defense [7]. These results revealed a major fluctuation in biosynthetic enzymes of sulphur containing amino acids. Furthermore, insights into metabolic changes in suspension cultured cells (SCCs) of grasspea, highlighted 330 dehydration-responsive metabolites (DRMs) belonging to 28 varied functional classes including carboxylic acids, amino acids, flavonoids and plant growth regulators [9]. Species-specific comparison of DRMs in relation with trefoil, soybean and rice revealed 185 unique metabolites of grasspea. A marked similarity was found between the profile of resurrection plant and grasspea, hinting towards its stress resilience. Interestingly, exogenous application of novel DRMs, arbutin and acetylcholine, displayed improved physiological status of stress-resilient grasspea as well as hypersensitive pea [9]. Choi [114] has appropriately described how and why translational genomics (TG) approach plays a central role in omics-based breeding approaches and discovery of trait-associated genes and marker development in not only sequenced crops, but also their orphan counterparts. The stress adaptation traits from grasspea may, therefore, be implied to improvement of other closely related legumes, particularly field pea.

3.6. Potential pharmacological merits of grasspea

Food is not only a source of nutrients, but also functional non-nutritive components with health promoting properties. The β-ODAP has been shown to participate in various metabolic events like activation of specific protein kinase C (PKC) [81]. This has been linked to reduced expression of phosphatidylethanolamine-binding protein 1 and subsequent activation of mitogen-activated protein kinase (MAPK) cascade and nuclear translocation of hypoxia inducible factor-1α (HIF-1α) [115]. The β-ODAP has also been implicated in mitochondrial thiol oxidation [116,117], neurodegeneration through free-radical generation [118], and inhibition of tyrosine amino transferase (EC 2.6.1.5) leading to elevated levels of catecholamines [119], and a reduced cellular uptake of cysteine [120]. Therefore, β-ODAP has utility as a therapeutic agent which can be employed in a variety of physiological conditions in a dose-dependent manner. It also finds applications in the stabilization of hypoxia inducible factor-1 (HIF-1) [121]. Using a RNA-seq approach, Tan et al. [122] reported increment in cytosolic Ca, post-β-ODAP treatment, which was followed by cytoskeletal modulations caused due to enhanced expression of β1 integrin, focal adhesion kinase and paxillin. The use of β-ODAP, also referred to as dencichine, was tagged as a hemostatic agent [123–125]. This has additionally been shown to be efficacious in the treatment of oral ulcers. The non-protein amino acid, L-homoarginine, first recognized from grasspea, was shown to aid in embryo development [126]. It is an alternative substrate for nitric oxide (NO) biosynthesis, which is an important signaling molecule in cardiovascular system and cerebral metabolism [88]. L-homoarginine, being a poor substrate for arginase, has certain advantages over arginine, that it can linger in blood vessels and is more efficient as a vasodilator. Another potential therapeutic application of grasspea seeds includes possible reduction of glucose as they possess insulin-mimicking glycosylphosphatidyl inositol [8].

4. Conclusions: grasspea, a crop for future?

We acknowledge the toxic nature of grasspea and therefore the impending challenges for it to be introduced as a mainstream crop species. However, the loopholes, which were holding the crop's potential till now, have been resolved well in time. The neurotoxin in the improved varieties has been reduced to less than 0.1 %, which is well within the safe limits of human consumption. It is imperative that only the low-neurotoxin varieties are released worldwide. This can be achieved only if the social stigma associated with grasspea is overcome. Complete blockage of production of neurotoxin is a two-way sword since the same has attributed physiological advantages to this orphan legume. A second perspective for extensive utilization of grasspea is TG approach. We have humungous data for species-specific useful traits in legumes, which remain untapped for crop improvement in terms of abiotic and biotic stress tolerance, yield enhancement and seasonal plasticity. Recent advances in integrated omics have further opened unexplored avenues for sustainable agricultural intensification. TG tool is appropriate to select the most suitable agronomically important traits within plant families and employ them for improvement of target crops. In the present review, we have highlighted the superior grasspea traits, which can be utilized for improvement of other legumes. For instance, dehydration-susceptible garden pea may be improved for better yield under challenging conditions of water-deficit by alterations in its metabolic composition. Molecular dissection of grasspea biology and translation to other legumes, would thus lead to overall increased grain productivity and better food quality.

Food security and nutritional demand of the increasing human population is arguably the greatest challenge today. To fulfill the demands, major focus should be given to mitigate key constraints in existing crop varieties and the production of new varieties that would offer increased yields under precarious climate conditions. The NULs may serve as the major targets for both these accounts. However, the improvement of NULs, including grasspea, not only depends on the availability of a genome, but also global awareness regarding utilization of these abandoned legumes. Grasspea is well-qualified with recommendable resilience towards environmental stress, which would open its potential avenues as a model system. It holds tremendous potential for development of functional foods to improve health conditions. Many unexplored aspects were inaccessible in unsequenced genome, which is no more a hurdle with the availability of a draft sequence. The genome sequence shall pave way for a bright future of grasspea. The prospect of integrating omics data with genome information would open new visions to achieve long-term goals. The impending challenges can be broadly categorized in two categories: (1) detailed comprehension of stress resilience and (2) genetic improvement through MAS and GWAS. The binary information would have the potential to provide biotechnologists with better gene candidates and targeting approaches that will be beneficial not only to the crop *per se*, but also utilization in molecular breeding program for other legumes.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.cpb.2021.100200.

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