Review

Linking omics and gene editing tools for rapid improvement of traditional food plants for diversified foods and sustainable food security

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Abstract: The indigenous communities across the globe especially in the rural areas consume locally available plants known as Traditional Food Plants (TFPs) for their nutritional and health-related needs. Recent research shows that many of the traditional food plants are highly nutritious as they contain health beneficial metabolites, vitamins, mineral elements and other nutrients. Excessive reliance on the mainstream staple crops has its own disadvantages. TFPs are nowadays considered important crops of the future and can act as supplementary foods for the burgeoning global population. They can also act as emergency foods in times of pandemics and other situations like COVID-19. The current situation necessitates locally available alternative nutritious TFPs for sustainable food production. To increase the cultivation or improve the traits in TFPs, it is essential to understand the molecular basis of the genes that regulate some important traits such as nutritional components and resilience to biotic and abiotic stresses. The integrated use of modern omics and gene editing technologies provide great opportunities to better understand the genetic and molecular basis of superior nutrient content, climate-resilient traits and adaptation to local agroclimatic zones. Recently, realising the importance and benefits of TFPs, scientists have shown interest in the prospection and sequencing of traditional food plants for their improvements, further cultivation and mainstreaming. Integrated omics such as genomics, transcriptomics, proteomics, metabolomics and ionomics are successfully used in plants and have provided a comprehensive understanding of gene-protein-metabolite networks. Combined use of omics and editing tools has led to successful editing of beneficial traits in few TFPs. This suggests that there is ample scope of integrated use of modern omics and editing tools/techniques for improvement of TFPs and their use for sustainable food production. In this article, we highlight the importance, scope and progress towards improvement of TFPs for valuable traits by integrated use of omics and gene editing techniques.

Keywords: Traditional food crops, Climate change, Food security, Omics, Translational genomics, Gene editing

1. Introduction

As per FAO estimates, the global population is expected to reach nine billion by 2050 and the world will have to produce 50% more food than we produce today to feed the burgeoning population of the world [1]. However, increasing the food production of the currently available crops on available land is a challenging task [2]. This challenge to produce more food is further limited by several factors such as excessive reliance on a limited

number of industrialized crops, decreasing land for agriculture purposes, and global climate change [2]. Several factors such as desertification, conversion of agricultural lands for nonagricultural activities, and global climate change pose a major threat to the global food-producing systems [3]. State of the world's plants reports 2016 has estimated the existence of more than 3,91,000 species of vascular plants on this planet [4]. This report has further estimated that approximately 30,000 species have at least one documented use and more than 5000 of them provide food to humans [5]. It is evaluated that nearly 2500 species of plants belonging to more than 160 families have undergone domestication throughout the world [6]. Surprisingly, despite having a huge diversity of vascular food plants, the world relies on only a limited number of approximately 15 major crops for 70 percent of food and nutritional requirements that have been domesticated by our ancestors more than 10,000 years before the present [7,8]. Of the 15 major crops, more than 50 percent of the calories come from five cereal crops namely wheat, rice, millet, sorghum, and maize [7,9]. This suggests that a limited number of plants are consumed as mainstream crops for the nutritional requirements. Excessive reliance on a limited number of mainstream domesticated crops has been flagged as an important issue in the global fight against food insecurity and in ensuring global food security to achieve zero hunger by 2030 as envisaged in the Agenda 2030 of Sustainable Development Goals [10]. The current widespread cultivation of uniform domesticated varieties carries huge risks of crop failures as they are more vulnerable to biotic (pathogen and pests) attacks and abiotic stresses caused by global climate change [11]. We have already experienced such crop failures in the past, for example, over-dependence on the potato, and the attack of *Phytophthora infestans* resulted in Irish famine that leads to starvation, widespread deaths, and emigrations to the other parts of the world [12]. Southern leaf blight of corn in the United States is another example of the risks that single or one type of crop carries to the pathogens [13]. There are several other examples of major crop failures from across the world indicating the potential risks inherent to the cultivation of less diversified and uniform types of crops across the world [14,15]. Unsurprisingly, uniform varieties are most likely to be destroyed uniformly and simultaneously with the evolution of resistant pathogens or with climate change unless region-specific strategies and preventive measures are in place [16]. It has been estimated that rise in global mean temperatures may result in a reduction of significant yields of several crops currently in use such as wheat, rice, maize, and soybean [17,18]. However, the effect of global climate change is perceived differently by different varieties/crops, and in different regions of the world [19]. There are regions that are severely affected, whereas some others are not that severely affected [19,20]. It further necessitates the identification of the local species/varieties that are used in different agroclimatic regions of the world [21]. Therefore identification of new crops and varieties with superior nutrition content suitable to the local agro-climatic zones is an important agenda for the plant scientists [21,22].

A number of recent studies have pointed towards the exploration and exploitation of traditionally used food crops (TFPs) for nutritional food security and their mainstreaming [23–25]. The TPFs can act as supplementary diets and also as emergency foods in times of pandemics or when the global supply chains are disrupted due to man made or natural disasters. A traditional food crop is an indigenous crop species that is native to a particular region of the world or those crops which are introduced from other places a long time ago and due to its use for a longer time, generations after generations, it has become a part of the culture of that particular community or region [26,27]. Several local indigenous communities of the world still use and rely on such traditional crops which were in use for centuries but are currently neglected, underutilized, restricted to particular geographical locations, and are not in the mainstream use [28]. Nevertheless, recent years have seen increased preference of the consumers towards these ancient traditional varieties and there is an increased focus on the reintroduction and mainstreaming of such traditionally used ancient food crop varieties [29–31]. Traditional food crops provide nutritional bene-

fits to the communities relying on them and they are very important for them [32]. Experimental evidence suggests that ancient traditional food crops have certain important nutritional and stress-resilient traits that can be exploited to reduce global hunger and malnutrition under increasing global climate change [33]. They are regionally cultivated for years and are adapted to local agroclimatic zones, they also show resilience towards weather changes and are also considerably more resistant to pests and diseases as compared to the mainstream food crops [34,35]. Moreover, if concerted efforts are not taken in the immediate future to revive them and conserve them, they may disappear from the global food menu [30,36,37]. This will contribute to the loss of genetic diversity and resources important for breeding the nutritionally superior and climate-resilient varieties [38–40]. Therefore it becomes necessary to enhance our focus from the model crops, and select domesticated crops to the less consumed, the more ignored traditional crops that hold promising potential in alleviating global hunger and ensuring food security [41]. There is an increasing interest among scientists in the exploitation of TFPs, understanding their genetic basis of important traits and further improvement. However, breeding improved varieties that are nutritionally superior and climate-resilient requires a complete understanding of the genetic and molecular basis of such traits [42]. Recent technological advancements in the high throughput omics approaches provide opportunities to dissect the genetic and molecular basis of nutritional and stress tolerance related traits. Integration of multi-omics tools such as genomics, transcriptomics, metabolomics, proteomics, and ionomics can help us comprehensively investigate the gene-protein-metabolite networks of nutritional, climate resilient and other traits [43]. Considering the nutritional, economic, and agricultural importance of traditional food crops in the future and their use as future climate-resilient crops, it is important to explore the application of the modern omics technologies for dissection of the nutritional and stress-resilient traits [44]. Besides that, the extensive exploitation of genetic diversity is required to address the genetic vulnerability of germplasm-narrowing crops [45]. Modern technologies can be used to characterize the crop germplasm collections for better and sustainable food supply, for example, Milner et al. [46] and Langridge & Waugh [47] presented more than 20,000 wild and domesticated barley genotypes with the aid of genotyping and informatics technologies and demonstrated the scope of exploitation of genetic resources in crop improvement [46,47].

In this background, this review article discusses the use of integrative omics technologies such as genomics, transcriptomics, proteomics, and ionomics for understanding the genetic makeup, proteomes, metabolomes, and nutritional composition of traditional food crops. The review further provides details about the use of available genomics information from model crops and its translation to the traditional food crops. We further provide a detailed futuristic outline of integrated use of omics and gene editing technologies for rapid improvement/domestication of traditional crops using the recent successful example of *Physalis peruviana* (groundcherry).

2. Why should we focus on traditional food plants?

2.1. Wide diversity of traditional food plants exist across the globe

The climate change and pathogen-triggered incidences of crop failures are expected to rise in the future [48]. The uniform cultivation of few crops will be more susceptible to synchronous crop failures leading to widespread hunger, malnutrition, migrations, and may even lead to civil wars [11,49]. Therefore the existence of diversity in food plants is a crucial and desirable factor for the breeding of improved varieties for desirable traits such as stress resistance and nutritional superiority [50]. To feed and ensure the food security of the growing population, the increased genetic diversity in plants is desired for future crop improvement programs under unpredictable regimes of climate change [51]. It is also desirable to ensure healthy sustainable food security [52]. Crop diversity provides opportunities and valuable genetic resources for breeding purposes as well as for the use

of translational genomics approaches for their improvement [53]. Moreover, diversity in traditional food crops is an important asset to reduce the impacts of diseases and climate change. They are important for improving the stability of food production as they are better adapted to fluctuating climatic conditions [54]. The minor traditional food crops have so far largely been ignored and much attention is not given to them for their role in sustainable food security because of certain undesirable characteristics and their restricted geographical availability [55]. However, recent years have seen an increased interest in the revival of the traditional plants and the food systems that are based on the traditional food plants [54–57]. Efforts across the globe are going on to diversify the currently cultivated basket of food crops,   to provide more options to the farmers to grow crops, to provide more options to the consumers for diversifying the food menu of their dining [58]. Large amounts of fragmented ethnobotanical data on traditional food plants are available from various countries [59]. Several studies have performed their nutritional and stress-related analysis and results from these studies suggest the potential roles of traditional food diversity in ensuring global food security [60].

Crop diversification is a solution to fight against the hidden hunger of the world. Diversification of nutritionally rich and stress-resilient traditional, orphan and underutilized crops can help to achieve the goal of a zero hunger world as envisaged in the United Nations   Sustainable Development Goals (SDGs), which specifically propose to end hunger, achieve food security, improved nutrition, and promote sustainable agriculture globally by 2030 [61,62]. However, extensive research is needed on traditional food crops to integrate them into the global food systems [62]. It is necessary to understand consumption barriers as well as production constraints [63]. It is pertinent that traditional food crops are very important for food security [64], but many of them produce relatively lesser yields because of no selection for the improved traits. They are also not cultivated at large scale because of unfavourable policies for their promotion [65]. However, several initiatives are recently taken that are focussed on the promotion of traditional food crops and improvement of their traits with the aid of genetic and genomic tools [65]. For example, African Orphan Crops Consortium (AOCC) is involved in the sequencing of 101 orphan crops and their integration   into African food production-consumption systems [66]. AOCC is a global partnership dedicated to the genome-enabled advancement of 101 African orphan crops that have superior nutrient and adaptive characteristics [63,67]. The consortium is aimed to elucidate reference genomes of 101 species for exploring genetic diversity. AOCC is an important model that can be adopted in other parts of the world especially those areas which have rich diversity of traditional food crops [63]. Similarly, there exists an independent international organization named 'Crops For the Future (CFF) which is aimed to promote and facilitate the use of underutilized, neglected and orphan crops and its integration into human diets. The mission of CFF includes increasing the knowledge base of neglected crops, advocating policies related to promotion of neglected crops, and spreading awareness about the relevance of neglected crops for rural livelihoods [68]. The Food and Agricultural Organization of the United Nations is also taking initiatives for the promotion of neglected crops by collaborating with agencies such as the International Council for Research in Agroforestry (ICRAF) and other partners which aims to better focus research and development, plant breeding and seed delivery systems of underutilized crops [69]. Therefore, for attaining food sustainability, collective efforts are required to advance the research and development of traditional food crops [65].

2.2. Traditional food plants possess important nutritional traits

Traditional food crops are promising future crops considering their multiple benefits to the farmers, consumers, and the environment as well [33–35,55]. Traditional crops that are used from generation after generation are mostly consumed in a particular region by the local communities for nutritional and therapeutic purposes [70,71]. Several studies have experimentally proved that a number of traditional crops are highly rich in nutritional components, and many of them are resilient to several stresses [24,72]. Some of the

examples are the fruit of *Elaeagnus umbellata* have ten times higher quantity of lycopene in their fruit than tomato [73] and *Chenopodium quinoa* has higher mineral content than maize and barley including, calcium, magnesium, iron, copper, potassium, phosphorus and zinc [74]. Traditional food crops provide important opportunities to improve diet and sustainability of food production because of their adaptability to multiple agroclimatic, low-input conditions and nutritional rich character [24]. But due to the lack of domestication and their cultivation being limited to geographical boundaries hinders the integration of traditional food crops into the large-scale production systems [28]. Although traditional food crops possess several important traits, some are also burdened with certain undesirable traits [55]. Therefore it becomes necessary to remove undesirable traits before they are made available for extensive cultivation [55]. The prior knowledge of the undesirable traits and the genes governing them is also crucial and   we can employ modern gene editing tools to get rid of them. Therefore, rapid domestication of traditional food plants using gene editing tools is an effective solution for this problem [75]. Redomestication of crops for their wild traits that could be lost due to domestication is another important strategy to access the lost gene pools [76].

2.3. Traditional food plants show varying degrees of tolerance to stresses

FAO has emphasized four important dimensions that determine the food security of a country, region, or population viz. enough availability of food, sufficient access to food, food utilization, and stability of the first three dimensions [56,77]. Availability of food means enough production of a particular food and its seamless distribution to the consumers [52,77]. Sufficient food access indicates economic affordability or freedom to sufficient food, sufficient allocation of the food resources [78,79]. The third component indicates bio-assimilation of the food that is eaten [77]. The fourth and the last component indicate seamless and sustainable availability of, access to, and utilization of the food resources [56,78]. The disturbance in the stability of three dimensions would eventually result in the food insecurity of a region, country, or population [80]. Ensuring the food security of a growing population in the future is going to be a challenging task [81]. Various factors affect the components of a healthy and secure food system [56,77]. The production of food is already limited by several factors such as global climate change, biotic and abiotic resources, and loss of genetic resources [82]. The sustainable food supply (first component) is disrupted by various factors such as pandemics, wars, natural disasters, droughts, climate change, excessive rainfall [83,84]. Sufficient access to food (component 2) is limited by factors such as poverty, food price rises, unemployment, low per capita income, and poor market access [85]. If the food is not biologically utilized in the body, it may lead to widespread diseases or malnourishment [86]. Therefore stability of all three components over time is essential for ensuring sustainable global food security [80]. One of the most important factors that contribute towards disruption of the stability of the three dimensions of food security is climate change, its associated negative impacts, .biotic and abiotic stresses. Such disruptions may result in widespread food insecurity across the globe [85]. A number of studies have reported that climate change and stresses pose serious threats to the growth and reproduction of crop plants and reduce their yields by affecting various processes in the cells [84,87]. Excessive threats of failures that the currently cultivated crops face across the globe necessitate identification of the new climate-resilient crops, and the diversification of the crops [19]. Several studies have also indicated the identification and cultivation of climate-resilient food crops with biotic and abiotic stress tolerance traits [84]. Therefore, there is a larger consensus among various stakeholders about urgency to identify and promote climate-resilient crops that possess climate-resilient traits. Interestingly, a large number of traditional plant species are adapted to the region of their origin, they have huge regional importance to the regional local communities [88], show considerable resilience to climate change, and can perform better even under unfavorable environmental conditions [24]. Traditional food plants are more climate-resilient, disease, and pest resistant, and can survive in harsh environmental conditions [89]. Cultivation of traditional food plants is in congruence with the four

important dimensions of food security as defined by FAO [55] (Fig. 1). The promotion of climate-resilient underutilized food crops along with modern crop varieties will be important for stable food production systems especially under fluctuating environmental conditions [90]. A non-exhaustive list of traditional food plants with their nutritional and stress-resilient traits is presented in supplementary table S1.
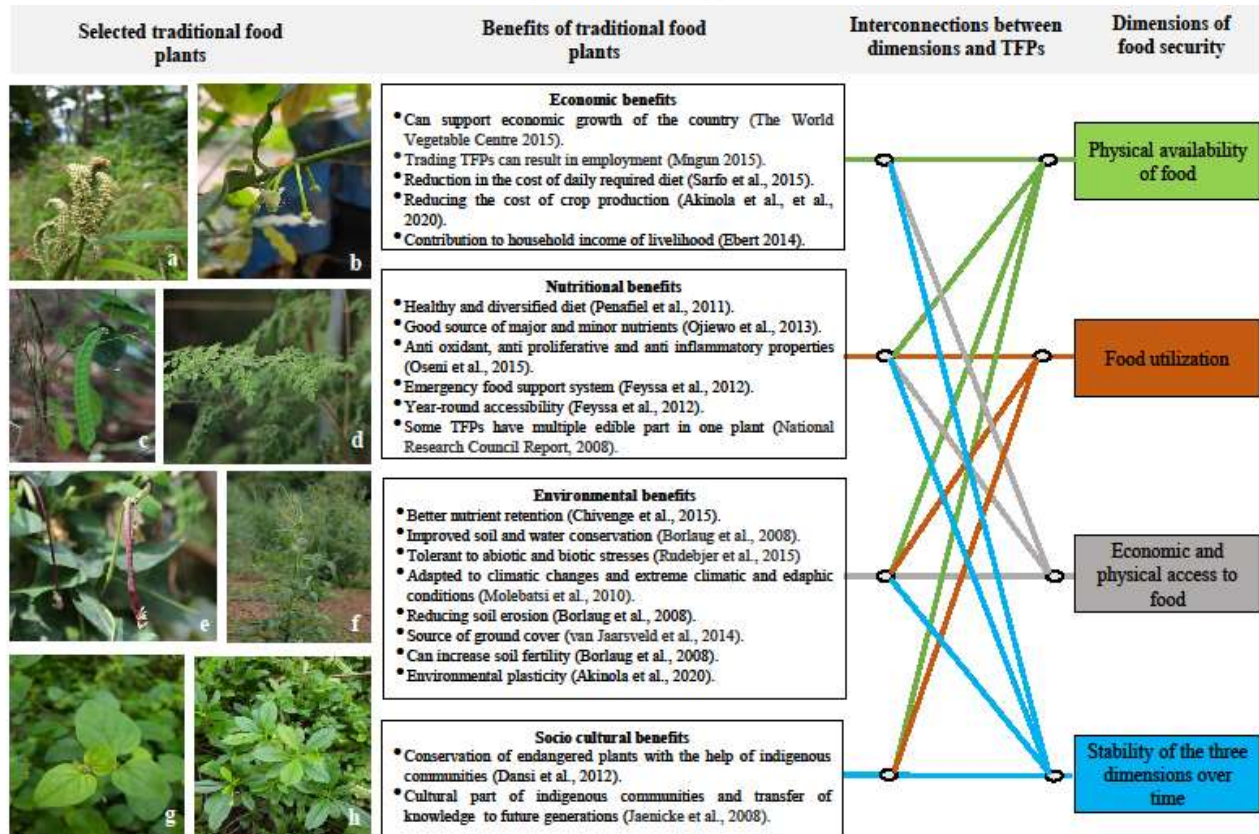

Figure 1. Diagram represents four dimensions of sustainable food security and the congruence of traditional food plants with these four dimensions of food security [55,69]. Some of the traditional food plants are shown from a-h. (a) *Eleusine coracana* (L.) Gaertn., (b) *Garcinia madruno* (Kunth) Hammel., (c) *Canavalia ensiformis* (L.) DC., (d) *Moringa oleifera* Lam., (e) *Vigna unguiculata* L. (Walp), (f) *Amaranthus palmeri* S. Watson, (g) *Boerhavia diffusa* L., and (h) *Talinum triangulare* (Jacq.)

2.4 Traditional food plants are grown and consumed locally and they ensure stable and sustainable food security

Stability of food supply, access to food, and food utilization over the period of time is important for a healthy food system and ensuring food security [52,56,77]. In an interconnected, interdependent, and globalized world, several countries are involved in bilateral and multilateral trades in food and food-related products [91]. Situations like global pandemics, wars, and physical disruptions to logistics can disrupt global food supply chains resulting in a global, regional, or local food insecurity endangering a large population [92]. Currently, COVID-19 has threatened multilateral and bilateral trades between the nations [93]. The supply of foods from one country to another is severely affected [94]. Some countries which are excessively dependent on the import of food grains are the most affected due to COVID-19 [95]. Such pandemic related disruptions in food security can be averted if foods are locally grown and made available for the local populations [96]. Traditional food crops are locally grown and consumed, therefore they are less susceptible to global disruptions due to situations such as pandemics, wars, logistics issues [35]. Locally grown traditional food plants can ensure considerable and sustainable food security during such situations. Additionally, the cultivation of local varieties promotes local agriculture and conserves the biodiversity of the local agroecosystems [97]. It has also been argued that consumption of locally grown foods may

be advantageous over the long-distance foods as locally harvested foods are almost available within a less time to the consumers and their freshness ensures that they are better in nutritional quality [98]. The promotion of traditional food plants will also promote the role of local communities in maintaining and managing local genetic diversity for sustainable food and nutritional security [97].

2.5 Traditional food plants provide alternative sources of income to the poor farmers and unorganized workers

In addition to having a key role in subsistence agriculture, as a source of food, medicine, for rural communities especially during situations of shortage of food supply, they provide livelihood opportunities to the people [99,100]. Therefore, traditional food plants simultaneously act as a source of income for local communities. Among vegetables, *Cleome, Amaranthus, Corchorus,* and *Vigna* spp. and fruit trees such as *Azanza garckeana, Adansonia digitata, Sclerocarya birrea, Strychnos spinosa, Vangueria infausta,* and *Grewia* spp. are the major traditional food crops of Botswana communities providing them income [101]. They grow naturally and the local women and children sell such crops or their products in formal and informal markets. This helps them raise their incomes; it may not be significant but at least help them fulfill daily needs [101,102]. Cruz-Garcia & Price [103] reported that in the case of the poorest Northeast region of Thailand, sale of traditional food plants constitute an important household income strategy to deal with situations of stress. Traditional crops such as *Eleusine coracana* (finger millet), *Vigna radiata* (green gram), *Coix lacryma-jobi* (job's tears), *Lens culinaris* (lentils), *Vigna radiata* (mungbean), *Sesamum indicum* (sesame), *Glycine max* (local soybean), *Ipomoea batatas* (sweet potato), *Dioscorea spp* (yam) are the main source of income for the poor and marginal farmers from East and South Asia [104]. In South Africa, traditional food plants are the vital source of income for indigenous communities [105] and in West Africa also the survival of small farmers in the tribal communities is completely dependent on traditional food plants [106] Secondary products of the traditional food crops are also highly marketable. For example, the malt produced from *Panicum sumatrense* (little millet) provides good incomes in India [107]. The processing of little millet led to generation of employment in the villages and increased the income of the rural folks significantly [108]. In India, it was reported that traditional food crops are a good source for increasing the incomes as well as improving the nutritional security of community people through the sale of several items such as ethnic millet papad, chakli, fermented breakfast food paddu and other novel foods prepared using minor millet [109]. Islam et al. [110] reported that the poorest families in Kurigram district of Bangladesh depend heavily on traditional food plants especially in times of famines. Considering these limited studies, it can be stated that traditional food plants act as an alternative source of income for poor farmers, and other poorer communities including tribal communities.

3. Multi-omics tools to dissect nutritional and stress-related traits for ensuring sustainable global food security

Being traditionally and culturally important, traditional food plants are used across the globe for nutritional purposes by a larger proportion of the population [33]. Traditional food plants are regionally important. However due to selective breeding, the yield and quality of traditional food crops are not up to the mark and modern technologies can be used to improve yield and quality traits [111]. Advanced crop improvement tools can be implemented effectively to have a clear understanding of complex molecular machinery governing growth, development, nutrients, other quality traits, and stress responses in traditional food crops [112]. This can be achieved with the help of various omics tools such as genomics, transcriptomics, proteomics, ionomics, and phenomics [31]. The recent advancements and revolutions in omics technologies allow large-scale investigations of organisms at the gene, genome, metabolome, ionome, and proteome levels at a faster rate within a relatively shorter period of time [113]. The chromosomal organization, sequence

polymorphism, and genome structure of the plants can be studied by using structural genomics tools and it is possible to develop genetic and physical maps of genomic regions controlling a particular trait of an organism [114]. While functional genomics technologies enable the understanding of the functions of genes regulating these traits [31,114]. Transcriptomics allows the study of the expression of total mRNA in a cell, tissue or in an an organism under a given condition [115]. Transcriptomics also enables the identification of the transcripts and the study of their correlation with the phenotypic data provides opportunities to decipher gene-trait relationships [115]. With the advancements in next-generation high-throughput sequencing technologies and the availability of advanced bioinformatics tools, it is easier to analyze large datasets including sequence alignment, annotation, and expression profiling of genes. [116]. Establishing a correlation of transcript abundance with the protein and metabolite accumulation is slightly challenging because of the post-translational protein modifications and the regulation of metabolites often by complex enzymatic pathways [117]. The quantitative and quantitative measurement of protein content and metabolites is attained with the help of proteomics and metabolomics approaches [118]. Similarly, the complete mineral and elemental composition of a plant species can be understood with ionomics tools, and the integration of the other omics tools such as genomics, proteomics, and transcriptomics can help establish links between the elemental composition, transport, and storage with the genes regulating various processes [119]. Omics tools are very important for the discovery of the genes controlling a particular trait of interest in a crop plant [120] and it has revolutionized crop improvement programs [121]. The information obtained using omics tools can help in enhancing the quality, taste, nutritional composition, stress resistance of food crops, increasing agricultural production for food, feed, and energy, reducing the time and expense of production [120]. Integrating the multi-omics technologies can help understand the structural organisation of the genes, their functions, biological and metabolic pathways and regulatory networks governing growth, development, nutrients, other quality traits, and stress responses of plants more efficiently, thereby helping in crop improvement programs [31].

Omics tools are increasingly employed in diverse fields including crop breeding and improvement programs. In the past two decades, we have seen an increased number of plants being sequenced [122]. Arabidopsis was the first model plant to be sequenced and it has provided significant insights about the various processes in the plants. Completion of its sequencing took several years [123]. However, innovations and improvements in the sequencing technologies have made it possible to sequence large and complex genomes in a shorter period of time at lower costs [124]. Therefore, many of the genomes of major crops have been recently sequenced within a relatively shorter span of time [125]. Many studies have focussed on the genome sequences of the model crop plants, however recently we have seen the application of omics technologies to the non-model crops also [126,127]. To date, whole genomes of more than 328 vascular plant species (comprising 323 angiosperms, 5 gymnosperms, and 3 lycophytes), three non-vascular land plant species (2 mosses and 2 liverworts), and 60 green algae have been sequenced [128]. Genome sequencing technologies provide a holistic overview of the various genetic components of an organism [129]. Whole-genome sequencing studies of plants have led to the identification of thousands of genes and other regulatory elements controlling the traits [130]. The integration of the low cost sequencing technologies with the computational bioinformatics tools and high throughput phenotyping technologies can enhance the identification of genes that govern important agronomic traits relevant to the production of food and its quality [131]. Recently, transcriptomes, proteomes, ionomes, and metabolomes of many models and nonmodel crop plants have been analyzed using high throughput omics tools coupled with high-performance computational bioinformatics tools [132]. The results of multi-omics studies provide a holistic overview of the various genes, proteins, metabolomes, and ionomes of the organisms. Therefore convergence of multi-omics technologies provide an important opportunity to accelerate the task of identification of genes that control agronomically relevant traits in plants including traditional food crops and speed up

the improvement programs using both conventional breeding as well as modern revolutionary CRISPR/Cas9 mediated and other gene editing technologies [44].

Several studies have shown that many traditional food plants are nutritionally rich and show varying degrees of stress tolerance, therefore the extension of integrative omics tools to decipher the genetic and molecular basis of nutritional and stress-related traits in traditional food plants is not only crucial but also urgent [37]. Extension of whole-genome sequencing to traditional food plants can help us understand the important genes that are responsible for nutritional and stress tolerance traits[31,133,134]. Recently, genomic sequencing technologies have been applied to some traditional plants and the results obtained are impressive and crucial for further improvement programs [31,63,135,136]. The extension of information obtained using omics tools to the nonmodel traditional food crops may be crucial and provide unique opportunities to improve crops in a relatively shorter period of time [126,137,138]. Table 1 presents some important traditional food plants where omics tools have been applied successfully for the comprehensive dissection of valuable traits such as nutritional composition and stress resilience. The following subsections explain some important plants where omics tools have helped understand the genomic basis of important traits in wonder traditional food crops.
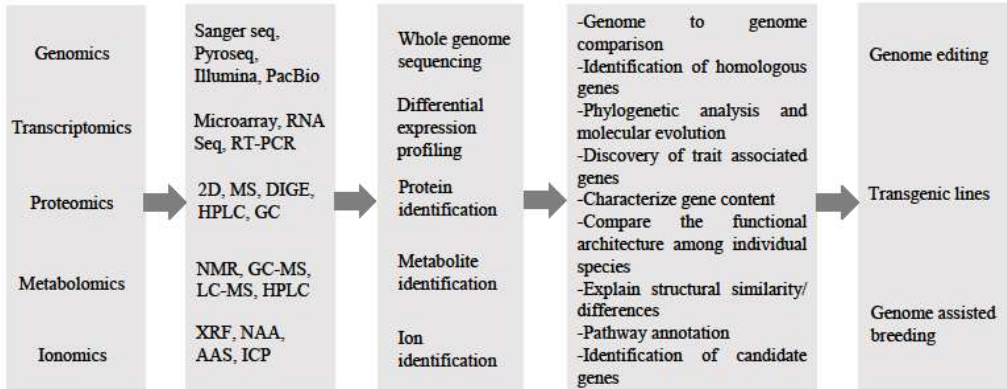

Figure 2. Improving traditional food crops with the aid of multi-omics approaches: Candidate genes for the improved varieties can be selected by combining the data from genomics, transcriptomics, proteomics, metabolomics, and ionomics. Manipulation of candidate genes by using techniques such as genome editing to generate improved varieties. Modified from [37].

4. Examples of application of multi-omics tools to selected TFPs

4.1. Lysine biosynthesis in Amaranthus (Amaranth)

One of the most important traditional plants, also known as pseudocereal is *Amaranthus* which belongs to the family Amaranthaceae. The genus *Amaranthus* comprises nearly 70 species [139,140]. *A. caudatus, A. cruentus*, and *A. hypochondriacus* are three important species of *Amaranthus* that are traditionally consumed worldwide because of their nutritional and stress-resilient traits [141]. It is estimated that species of *Amaranthus* were domesticated nearly 8000 years before the present in Central and South America and they have sustained the Inca and the Aztec civilizations for several thousand years [142]. Unfortunately, consumption of the Amaranth was reduced in modern times and it is only recently, there is an increased consumption of this species [143]. The growing interest in the consumption of Amaranth has risen due to its unique nutritional composition [144]. *Amaranthus* is unique in its lysine content (5.19 g/16g N) which has been found to be even more than milk [145]. This unique nutritional composition and resilience to a wide range of environmental conditions have led to its categorization as an important future, alternative wonder crop [146,147]. The Amaranths are very important for another reason that they are C4 crops rather than most of the protein-yielding legume crops which are C3

plants [148]. Being C4, *Amaranthus* can perform better even at elevated temperatures when compared with the C3 species [148]. These nutritional and stress-related traits make Amaranth a wonderful future crop. As the global temperature is rising, it is expected that such crops will provide nutritional security to the growing population under elevated temperatures. Therefore, understanding the genetic basis of the nutrition and stress-resilient traits of *Amaranthus* is necessary. Genome and transcriptome sequencing of *A. hypochondriacus* have shown nearly 24,829 protein-coding genes [148]. Lysine biosynthesis genes have also been annotated using comparative genomics and expression analysis that provided lysine rich phenotypes. *A. hypochondriacus* C4 is also an edible grain which is rich in lysine, the most limiting essential amino acid in cereals. Sunil et al. [148] sequenced the genome and transcriptome of Amaranth *A. hypochondriacus*. The draft genome is useful in understanding the various traits such as its exceptional nutritional profile, its growth rate, resistance to drought, and other environmental stresses. This study also provided important details about the genes involved in the biosynthesis of betalains of Amaranth. Draft genomes of *Amaranthus tuberculatus*, *Amaranthus hybridus*, and *Amaranthus palmeri* species were also reported recently by Montgomery et al. [149]. This will further enhance our genomic understanding of the amaranths.

4.2. Transcriptional regulation of anti-nutritional saponins in Chenopodium quinoa (Quinoa)

Quinoa (*Chenopodium quinoa*) is a n excellent nutritious grain that is designated as an important alternative future crop to improve global food security. Many genetic resources are not available for its improvement [150]. Jarvis et al. [151] have reported the assembly of the reference genome sequence of quinoa and its two diploid ancestral gene pools. The genome sequencing has led to the identification of the transcription factor which may regulate the production of saponins which are anti-nutritional triterpenoid compounds synthesised in quinoa seeds. This is an important step towards establishing genetic resources for quinoa improvement [151]. Recently, Golicz et al. [152] performed genome-wide identification and analysis of orthologous genes of the *Arabidopsis thaliana* flowering genes in quinoa and provided important information about genes that controls vernalization, photoperiod, flowering and gibberellin pathway. The study further provided insights about the orphan genes that are unique to quinoa. This information is valuable as it will to facilitate further programs aimed at quinoa improvement.

4.3. Genetic mechanism of stress tolerance in Manihot esculenta (Cassava)

Cassava (*Manihot esculenta*) is a crop that is adapted to marginal soil conditions and erratic rainfall and is rich in carbohydrates and protein content [153]. Rabbi et al. [154] identified markers associated with the nutritional traits and have performed a genome-wide association mapping and identified candidate genes for carotenoid (*phytoene synthase*) and starch biosynthesis (*UDP-glucose pyrophosphorylase* and *sucrose synthase*) through this study. The transcriptomics study performed by Siirwat et al. [155] resulted in the identification and expression profiling of genes responsible for starch biosynthesis and also revealed the mechanism behind the stress responses of Cassava. Several transcriptomic studies on Cassava have helped in unraveling the mechanisms of tolerance to various stresses. Utsumi et al., [156] have reported upregulation of nearly 1300 genes during drought stress. The expression of Cu/Zn-superoxide dismutase and catalase together during cold and drought stress improved drought and cold stress tolerance in Cassava [157]. Lokko et al. [158] have characterized heat stress transcription factors such as *A3* (*heat-shock transcription factor 21*) and *ATHB12* (a *homeobox-leucine zipper protein*) drought stress. In the same study, they reported expression of dehydration tolerance related transcription factors such as *Early response to dehydration* (*ERD1*), *Responsive to dehydration 19* (*RD19*), *Responsive to dehydration 22 precursor* (*RD22*) at the time of drought stress [158]. An et al. [159] reported drought-induced protein Di19-like during drought stress with the

aid of proteomic tools [159]. Wang et al. [160] presented draft genome sequences of a Cassava wild ancestor and a domesticated variety of cassava. This study led to the identification of gene models specific to the wild and domesticated varieties respectively.

4.4. Genetic dissection of pathogen resistance and the early fruit developmental evolution in Physalis (groundcherry)

The genus *Physalis* belongs to the Solanaceae family. Several members of the Solanaceae family are important sources of food, spice, and medicine. *Physalis ixocarpa*, *P. peruviana*, *P. pubescens* are underutilized berries that have many essential minerals and vitamins notably potassium and the immune system supporting Vitamin C [161]. They are also well known for the phenolic compounds which provide excellent antioxidant activity [162]. Much information on *Physalis* is not available and it is necessary to broaden the information about its nutritional content and other properties [163]. Garzón-Martínez et al. [164] demonstrated leaf transcriptome of *Physalis peruviana* and identified genes responsible for major biological processes and molecular functions. This study provided candidate genes   responsible for resistance against diseases caused by viruses, fungi and bacteria. Even though tomato and ground cherry are in the same family, *Physalis* possess modified calyx which is absent in *Solanum*. Gao et al. [165] presented floral transcriptomic resources of *Physalis* for the first time and identified some candidate genetic variations accounting for the early fruit developmental evolution in *Physalis* in comparison to *Solanum*. They analyzed transcriptome sequence variation and gene expression at the transcriptomes of *Physalis floridana* and *Solanum pimpinellifolium* and reported 14,536 strict single-copy orthologous gene pairs between *P. floridana* and *S. pimpinellifolium*. It was revealed that the distinction between *Solanum* and *Physalis* is because of nine types of gene variations that were differentially expressed in either trend or dosage at the flower–fruit transition between the two.

4.5. Detection of genes regulating uptake and storage of micronutrients in traditional food crops

Plants are an important source of a large number of mineral ions. Minerals and trace elements in optimal levels are very important for the growth and development of a plant and such minerals are a very important part of the human diet [166]. Uptake of micronutrients from the soil and further transport within the plants is facilitated by several transporter proteins [167]. There are several metals that are toxic to plants as well as humans when consumed in higher concentrations. For example, excessive accumulation of aluminium, lead, zinc, cadmium results in metal toxicity which can harm the plants, and at times may result in the death of the plants as well [168,169]. Their entry into the food web is also problematic as it may lead to serious health issues for humans. Therefore quantitative determination of the total composition of such minerals and metals in edible plants is important for ensuring the safety of humans [170]. The total mineral and element composition of an organism has been termed as an "ionome" [119,171]. Ionome profiling of the plants belonging to different species, collected from various habitats, and cultivated in different soils can inform us about the fundamental differences in the total ionome composition [172]. Minerals such as sulphur, nitrogen, and phosphorus are essential components of several metabolites, whereas trace metals such as zinc, copper, iron, and manganese are essential components of several proteins [173]. Therefore minerals and trace metals also regulate the composition of metabolites and proteins within the plants and perform important biological functions [173]. High-throughput techniques such as inductively coupled plasma mass spectroscopy (ICP-MS), Inductively coupled optical emission spectrometry, X-ray fluorescence, Neutron activation, and atomic absorption spectroscopy analysis are nowadays employed to profile complete ionomes of the plants [171]. Genomic technologies have enabled the identification of a large number of transporter genes and even gene families from model plants that facilitate mineral and metal uptake

and transport in the plants [174]. A large number of tribal communities still rely on tradi-tional food crops, and the mineral and metal composition of traditional food crops greatly influences their health and well-being [175]. For example, analysis of mineral and heavy metal contents of traditionally important aquatic plants of Tripura, India was studied by [176] using atomic absorption spectroscopy. Several other new studies have recently tried to investigate the nutritional composition of traditional food crops which will have huge implications on future crop improvement and breeding strategies. For example nutrient and antinutrient composition analyses *Launaea cornuta, Vigna vexillata, Momordica foetida, Basella alba* performed by Chacha et al. [177] showed that they are rich in vitamin A, B1, B2, B3, and C and minerals such as Ca, Fe, Mg, and Zn.   The rich sources of micronutrients in the underutilized crops promise their capacity to abolish hidden hunger in future. Com-bining results of ionomics with genomics can help in the detection of genes responsible for accumulation of elements in plants [178]. For example, Pasha et al. [179] uncovered the molecular mechanism behind the nutritional quality of moringa plant parts. They re-ported genes responsible for mineral content including, vacuolar iron transporters (VIT), calreticulin for calcium storage, zinc transporters, and magnesium transporters inside dif-ferent tissues. Similarly, several calcium transporters such as calcium ATPase, calcium exchanger (CaX), calcium-dependent protein kinase (CDPKs) and calcium-binding pro-teins (CBPs) of *Eleusine coracana* (L.) were identified by Nirgude et al. [180] and Kumar et al. [181] with the aid of high throughput genomics tools. The identification of the plants with higher amounts of essential minerals and their genes would further enhance our un-derstanding of the traditional food crops.

4.6. Unraveling the mechanism behind high amount of α-linolenic acid and salinity tolerance in Portulaca oleracea (Purslane)

Purslane (*Portulaca oleracea*) belongs to the Portulacaceae family. It is a highly nutri-tious vegetable with several medicinal properties [182]. They have been recognized as the richest source of a-linolenic acid, essential omega-3 and 6 fatty acids, ascorbic acid, gluta-thione, alpha-tocopherol, and beta-carotene [183]. Because of exceptional quantities of omega-3 fatty acids in purslane, there is a growing interest to introduce this as an im-portant vegetable crop [183]. Levey [184] showed that purslane is a future powerful food that can grow and establish in numerous geographical locations globally and it is highly adaptable to various environmental stresses such as salinity, nutrient deficiency, heat and drought. Liu et al. [185] quantified the fatty acid and β-carotene content of purslane with the aid of HPLC and GC. They reported a 1.5 to 2.5 mg/g amount of fatty acid from leaves and   0.6 to 0.9 mg/g, 80 to 170 mg/g from stems and seeds respectively. Its leaves contain about 60% of α-linolenic acid (C18:3ω3) of total fatty acids. The β-carotene content ranged from 22 to 30 mg/g fresh mass in leaves. The first metabolite profile of *P. oleracea* was performed by Farag & Shakour [186] by using ultra-performance liquid chromatog-raphy-mass spectrometry on three taxa and recognized hundreds of metabolites including amino acids, phenolic compounds, alkaloids, and fatty acids which indicate their nutritive and health benefits. Besides having an extraordinary nutrient profile, *Portulaca* shows ex-cellent tolerance towards salinity stress and drought stress. The transcriptome sequencing and metabolome analysis of *P. oleracea* regarding salinity tolerance were done by Xing et al. [187]. They reported that genes of photosynthesis and aquaporins were depressed dur-ing salinity treatment which indicates the inhibition of photosynthesis and water uptake during salinity stress. But the expression of L-3-cyanoalanine synthase/cysteine synthase and cyanoalanine synthase were elevated, suggesting the increase in ethylene production which acts as a key regulator of salinity tolerance. Higher content of pyrophosphate, D-galacturonic acid, and elaidic acid was detected in salinity tolerant plants that positively regulate glycolysis, energy supply, and integrity of cell membrane. These studies regard-ing nutritional profiling and genes that regulate the tolerance to salinity are important for further programs related to its improvements.

4.7. Higher accumulation of lycopene in   Elaeagnus (silverberry)

 Silverberry (*Elaeagnus*) belongs to Elaeagnaceae family which is recognized as an important fruit crop widely because of the presence of high lycopene content in the berries which is ten times higher than tomatoes especially in the species *E. umbellata*. [73]. The berries are well known for their high ascorbic acid, protein, and magnesium content as well as drought tolerance, adaptation to a variety of moisture, and edaphic conditions also [188]. The proteomic study of *E. umbellata* with special emphasis on fruit quality traits was performed and the quantity of soluble sugar, organic acids, lycopene, and total protein analyzed by [189]. The expression of   *phytoene synthase* (*EutPSY*) gene was found to be correlated with the higher accumulation of lycopene in *E. umbellata* suggesting its importance [190]. The results suggest that the *EutPSY* gene can be considered as a target for increasing the lycopene content in other fruits and thereby increasing their quality.

4.8. Nutritional composition of Dioscorea (Yam), a neglected staple tuber crop of the tribal communities

 Yam (*Dioscorea*) is one of the oldest tuber crops harvested from the wild in the tropical regions throughout the world and acts as a chief food item for a number of tribal groups [191]. Yam is the main source of diosgenin-steroid which is effective against neurodegenerative diseases [192]. It is also an effective nutritional supplement with a high amount of proteins. There are about 600   *Dioscorea species*, but only seven contribute to the human diet in the tropics [193]. Despite its wide utility, this tuber crop remains orphaned and its genomic and proteomic information is not available in detail [194]. Recently, we have seen little progress on advanced molecular studies of *Dioscorea*. Nakayasu et al. [195] have performed comparative transcriptome analysis of high saponin containing yams i.e. *D. esculenta* and *D. cayenensis*, and a low saponin containing, *D. alata*, for understanding biosynthesis of steroidal saponins   and identified the *β-glucosidase* (*DeF26G1*) gene to be responsible for higher accumulation of saponins in *D. esculenta*. The first report of genome-wide characterization of *Dioscorea* taxon was reported in *D. zingiberensis* by Zhou et al. [196] and identified 4935 genes, 81 tRNAs, 661 miRNAs, and 69 rRNAs from them. Transcriptome profiling of *D. alata* led to the identification of several thousand unigenes, some of them code for enzymes involved in the flavonoid biosynthesis pathway. The study further found the upregulation of several genes such as flavanone 3-hydroxylase (F3H), chalcone isomerase (CHS), dihydroflavonol 4-reductase (DFR), leucoanthocyanidin dioxygenase (LDOX), flavonoid 3'-monooxygenase (F3'H), and flavonol 3-O-glucosyltransferase (UF3GT) in the tubers of purple flesh cultivar than white flesh cultivar [162]. Price et al. [191]   performed whole metabolite profiling of yam and identified 152 metabolites. They developed biochemical phenotyping accessions of the yam varieties through metabolomics and integration with other omics studies that can be used for yam breeding programs.

4.9. Transcriptional basis of lipid biosynthesis in chia, a wonder seed for the 21st century

 Some species of the genus *Salvia* such as *S. columbariae*, *S. hispanica*, and *S. polystachya* are commonly known as Chia and consumed for their seeds which have multiple nutritional and medicinal benefits [197,198]. Chia seeds are rich in insoluble fiber, high omega-3 and omega-6 fatty acids, *α*-linolenic acid, linoleic acid, proteins, amino acids, antioxidants, and minerals [199,200]. Because of their high nutritive value, chia is known as the "seed for the first 21st century" [199]. The seeds of chia also contain metabolites that show anti-cancer, anti-inflammatory, antioxidant, anti-blood clotting, and antidiabetic activities. The seeds have also been found to show action against cardiovascular diseases and hypertension [200–203]. The transcriptomic study of wild and cultivated accessions of *S. hispanica* suggests the genetic basis of oil and protein content accumulation in chia seeds [204]. The study has also identified several transcription factors such as AP2/EREBP202

and simple sequence repeat (SSRs) markers that are helpful for breeding or translational genomics programs. The transcription factor AP2/EREBP is known to regulate the expression of genes related to fatty acid biosynthesis [204]. Transcriptome analysis of chia seeds from its different developmental stages has further identified important candidate genes such as *monoacylglycerol acyltransferase* (*MGAT*), Acyl-CoA desaturase 1 (*OLE1*), *diacylglycerol acyltransferase* (*DGAT1, 2* and *3*), *phospholipid:diacylglycerol acyltransferase* (*PDAT*), *Thiolase* and *Desaturase* responsible for lipid biosynthesis and oil accumulation [205].

4.10. The genetic diversity of a wonder tree, Baobab (Adansonia digitata) that contains more vitamin C than oranges

The *Adansonia digitata* L. is commonly known as african baobab and belongs to the family, Malvaceae. It is a very important tree with multiple benefits including a source of traditional food in the Saharan countries [206]. Additionally, it is also a source of medicine, fibre and incomes for the rural communities [207,208]. Almost all its parts can be consumed and it contains high vitamin C content as compared to oranges [207]. Using microsatellite loci, Chládová et al. [208] have suggested a huge genetic diversity among its populations. However, further research is needed to understand the genetic basis of the higher accumulation of the vitamin C and other important compounds that make it a wonder tree.

Table 2. This is a table. Tables should be placed in the main text near to the first time they are cited.

Sl. No.	Crop plant	Distribution	Important nutritional and stress resilient traits	Exceptionally notable	Applications of different omics technologies
1.	*Eleusine coracana* (L.) Gaertn. (Finger millets, Poaceae)	Majorly produced in Mali, Niger, India, Burkina Faso and China [209].	Tolerant to pathogens and pests. Drought resistant. Rich in minerals such as calcium and iron, vitamins, protein, dietary fiber and phenolics [209,210].	Minerals and micronutrients are superior to rice and wheat [211].	1. Using genomics tools, Nirgude et al. [180] reported higher expression of opaque2 (regulate seed storage proteins), calcium transporters and calmodulin gene (calcium storage) and Kumar et al. [212] reported *PiKh* and *Pi21* genes that show resistance against *Pyricularia oryzae* blast disease. 2. Using transcriptomics, expression of several genes such as calcium transporters (*CaX*, *CDPKs*, *CBPs*) are reported [181]. Several transcription factors such as MYB, MYC, WRKY, ZFD were detected during drought stress [210]. 3. Proteomics study led to the identification of calcium binding protein, calreticulin [213]. Anatala et al. [214] reported heat shock proteins (HSPs), storage proteins and late embryogenesis abundant

(LEA) during drought stress.

2	*Setaria italica* (L.) P.Beauv. (Foxtail millet, Poaceae)	Majorly cultivated in Asian countries such as India and China [215].	Great drought tolerant potential and grows well in barren and arid land [215].	Rich in essential amino acids, vitamin B, protein and micro elements [216].	1. Lata et al. [217] and Shi et al. [218] reported *POD* precursors, late embryogenesis abundant (*LEAs*) and aquaporins for drought tolerance by using transcriptomics. Phospholipid hydroperoxide glutathione peroxidase (*PHGPX*), ascorbate peroxidase (*APX*) and catalase 1 (*CAT1*) during salinity tolerance were reported using transcriptomics by Sreenivasulu et al. [219].
3.	*Moringa oleifera* Lam. (Drumstick, Moringaceae)	Distributed mainly in Middle East, African and Asian countries [220].	It has high micronutrient and vitamin content. It also shows antioxidant and medicinal activities. They can withstand occasional waterlogged conditions and adapt to hot and semi-arid conditions [221]. They are tolerant to heat, cold, salinity, nutrient starvation, variable light conditions and water deficiency [222].	Rich in micronutrients and vitamin A [221].	1. *WRKY* transcription factors for various abiotic stress tolerance and copies of Cys$_2$His$_2$ zinc finger motifs (C2H2), *APETALA2*/ethylene-responsive element binding protein (*AP2-EREBP*), *C3H* transcription factors for drought and cold resistance were reported [222]. High BRI1-associated receptor kinase 1 (*BAK1*) gene expression for abiotic stress tolerance [223]. Nutritional component related genes such as Vacuolar iron transporters (*VIT*), calreticulin for calcium storage, Zinc transporters, magnesium transporter, and genes for vitamin C biosynthesis recognised [179]. 2. Flavonoid compounds and

				rutinoside sugar compounds were detected using metabolomics by Makita, [224].
4.	*Chenopodium quinoa* Willd. (Quinoa, Amaranthaceae)	Cultivated as an important crop since ancient times in various parts of North-Altiplano, South and Central Chile [225].	Rich source of minerals such as magnesium, iron, calcium, copper, potassium, zinc, and phosphorus [74]. They have antioxidant activity (eg. polyphenols) and rich in vitamins such as Vit. A, B1, B2, B9, C, and E, lipids, proteins rich in essential amino acids particularly methionine and lysine, dietary fiber, and carbohydrates [226]. They have extreme agro-ecological adaptability [227].	Higher mineral content than maize and barley including calcium, magnesium, iron, copper, potassium, phosphorus and zinc [74].	1. Salt overly sensitive 1 gene (*CqSOS1A* and *CqSOS1B*) were gene identified [228]. 2. Xyloglucan endotransglucosylase genes, an expansion A7-like gene and Ethylene Responsive Factor (*ERF*) genes were found to be downregulated in salt tolerant plants [229]. 3. Sobota et al. [230] reported albumin and globulins through proteomics. 4. Root cell membrane's potential, net H+, Na+ and K+ fluxes during salinity adaptation through Ionomics study [231].
5.	*Vigna unguiculata* (L.) Walp. (Cow pea, Fabaceae)	Cultivated across Africa, Southeast Asia, Latin Southern and the United States of America. It is not widely cultivated in Europe but used in some Mediterranean countries [232].	Rich in proteins and carbohydrates [233]. Proteins are rich in lysine and tryptophan amino acids [234]. Shows considerable adaptation to the warm climate with adequate rainfall [233].	High quantity of folic acid and low quantity of antinutrients [235].	1. Up regulated expression of chalcone isomerase and chalcone synthase in the salt tolerant plants were reported [236]. 2. Sugars, proline, galactinol, and quercetin were identified as osmolytes during osmotic stress using metabolomics [237]. 3. Identified amino acids which are related to glycolysis, and tricarboxylic acid cycle [238].

				4. Lutein and beta carotene were reported using metabolomics [239].
6.	*Vigna radiata* (L.) R.Wilczek (Mungbean; Leguminosae)	African regions, South and Southeast Asia [240].	Drought resistant. Higher iron and folate content [240].	Rich in digestible protein quantity than other pulses [241].	1. Eight flavonoids (vitexin, isovitexin, rutin, kaempferol 3-O-rutinoside, isoquercitrin, genistein, daidzein and isorhamnetin) and two phenolics were reported using metabolomics [240].
7.	*Sorghum bicolor* (L.) Moench (Sorghum, Poaceae)	Major food in semi arid tropical temperatures of African and Aisan regions [242].	Suitable for cultivation in dry areas and poor soil conditions [243]. Gluten free cereal that is rich in antioxidants and phenolic compounds [244].	grains have igh digestive levels [245].	1. Quantitative trait loci for sorghum polyphenols were recognised [243]. 2. Increased expression of Late Embryogenesis Abundant (*LEA*), delta 1-pyrroline-5-carboxylate synthase 2 (*P5CS2*) and high-affinity K+ transporter 1 (*HKT1*) for drought tolerance [246]. Expression of 42 genes related to osmotic stress [224]. Salinity and osmotic stress tolerance genes reported [247]. 3. Presence of Fructose, galactose, lactose, cellobiose and sedoheptulose as an osmotic protectant were detected using metabolomics [248]. 4. Glutathione-S transferases and l-ascorbate peroxidase during salinity stress identified [249].

8.	*Manihot esculenta* Crantz. (Cassava, Euphorbiaceae)	Used by different communities all over the world mainly tropical and subtropical areas [250].	Adapted to marginal soil conditions and erratic rain. Carbohydrate and protein rich [155].	Rich source of energy [251].	1. Using genomics, carotenoid markers on chromosome 1 and candidate genes for carotenoid (*phytoene synthase*) and starch biosynthesis were reported [154]. 2. Identification of starch biosynthesis genes [155]. Genes responsible for proline, soluble sugars and soluble proteins during dehydration stress [252]. Upregulation of 1300 genes during drought stress [156]. Transcription factors related to heat stress (A3, heat-shock transcription factor 21, and a homeobox-leucine zipper protein ATHB12) and dehydration tolerance (*ERD1*, *RD19*, *RD22* precursor, drought-induced protein Di19-like) were reported [158]. *WRKY* genes related to abiotic stress tolerance [153]. 3. Proteomics- ATP synthase subunit beta, Rubisco activase (RCA), Rubisco, phosphoglycerate, chaperone peroxiredoxin, heat shock protein, glutathione transferase profiling during cold stress [159].
9.	*Amaranthus hypochondriacus* L., *Amaranthus viridis* L.(Amaranth, Amaranthaceae)	Consumed in China since ancient times. Central America, South America. It is also used in in Africa and Caribbean [253].	Leaves and seeds are rich in quality proteins and its quantity is higher than maize. Proteins contain higher amounts of amino acid lysine and sulfur containing amino acids [145]. Amaranth oil contains unsaturated linolenic fatty acid which is good for human health [254].	High quality protein with rich lysine content in leaves and seed [145].	1. Gene annotation of lysine biosynthetic pathway and expression analysis was analysed [148]. 2. Chloroplast chaperones, Rubisco large subunit, cytochrome b6f, oxygen evolving complexes, and ascorbate peroxidase expression variation during drought stress were studied [255]. 3. Lutein and beta carotene detection [239].

10.	*Sesuvium portulacastrum* (L.) L. (Shoreline purslane, Aizoaceae)	Locally consumed in various regions of India, South East Asia, Philippines [256].	Salt, drought and oxidative stress tolerance. Salty taste and fleshy nature of leaves [257].	Rich source of sodium [256].	1. Identified Late embryogenesis abundant 2 as the gene for salt and drought tolerance [257]. Fructose-1,6-bisphosphate aldolase gene (*FBA*) for abiotic stress tolerance was isolated [258]. 2. Copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn) accumulation during salinity tolerance was reported [259].
11.	*Ipomoea batatas* (L.) Lam. (Sweet potato, Convolvulaceae)	Consumed throughout the world. Asia and Pacific islands produce 92 % of the world's sweet potato supply [260].	It is pest and disease tolerant and adapted to high moisture conditions. Rich in complex carbohydrates, vitamin A, vitamin C, Fe and K. Orange-fleshed sweet potatoes are one of the storehouses of beta-carotene. It is a highly resistant crop [260].	Rich source of beta carotene [260].	1. *APX*, manganese-dependent superoxide dismutase (*MnSOD*), *LEA*, early responsive to dehydration (*ERD*), sodium/hydrogen antiporter (*NHX*), aquaporin (*AQP*), vacuolar calcium ion transporter (*CAX*), metallothionein (*MT*), betaine aldehyde dehydrogenase (*BADH*), pyrophosphatase (*PPase*), catalase (*CAT*), polyphenol oxidases (*PPO*), ABRE binding protein (*AREB*) during abiotic stress tolerance reported [261]. 2. Amino acids, carbohydrates and flavonoids were detected using metabolomics [262]. Beta-carotene content [263].
12.	*Ipomoea imperati* (Vahl) Griseb. (Beach morning glory, Convolvulaceae)	Distributed in coastline all over the world [264]. Consumed by local communities for the underground tuber.	Salinity tolerant and grows well in poor nutrient soil [264].	Rich in sodium [264].	1. Expression profiling of *AP2/EREBP*, *bHLH*, *HD-ZIP* and *MYB* transcription factors during salinity tolerance reported [264].
13.	*Dioscorea spp*, (Yam, Dioscoreaceae)	Tropical and subtropical Countries. Major food in Africa [250].	Great source of fiber, potassium, manganese, copper, and antioxidants. They also exhibit abiotic stress	Vitamin C and Potassium rich [265].	1. Metabolite profiling revealed amino acid content, malic acid content, fatty acids & phosphate content [191]. 2. Genome sequencing revealed

				tolerance [191].		the hybrid origin of *Dioscorea rotundata* from *D. prehensilis* (wild rainforest plant) and *Dioscorea abyssinica* (Savannah adapted plant [266].
14.	*Portulaca oleracea* L. (Common purslane, Portulacaceae)	Distributed all around the world such as New Zealand, Canada, America, temperate countries of Europe, Australia and is highly abundant in India [267].	It contains high amounts of α-linolenic acid and oxalic acid in their leaves which are highly health beneficial [268]. It is also rich in carbohydrates, protein, minerals (calcium, magnesium, sodium, potassium), vitamin C, carotene, riboflavin, thiamine and nicotinic acid. It is well adapted to dry and salinity conditions, therefore ideal for arid areas [269].	High amount of alpha-linolenic acid and oxalic acid in the leaves [268].	Metabolomics study reported 6 amino acids, 22 phenolic compounds, 16 alkaloids, and 11 fatty acids [186]. α-Linolenic acid accounted for about 40 % to 60 % of total fatty acid [185].
15.	*Physalis peruviana* L. (Wild tomatillos, Solanaceae)	A cultural staple of Mexico, Central America, South Africa, North America and Europe [163].	They have carotenoids, minerals and vitamin rich fruits and seeds and show adaptability towards various environmental conditions [270,271].	Carotenoid and vitamin rich fruits and seeds [270].	Metabolomic profiling reported lutein as the most abundant carotenoid (64.61 µg/g at the half-ripe stage) and presence of gamma carotenoid (rare in fruits) [272].
16.	*Rumex vesicarius* L. (Ruby dock, Polygonaceae)	Cultivated in North Indian states as a vegetable [273].	Rich in phenols, ascorbic acid, α-tocopherol and β-carotene [274].	Vitamin rich [274].	Metabolomic study reported 13 Phenolic compounds, ascorbic acid, α-tocopherol, and β-carotene content and 6-C-glucosyl-naringenin identified as the key phenolic compound which have high antioxidant capacity [274].
17.	*Corylus avellana* L (Hazelnuts; Betulaceae)	Consumed by human civilizations from Mesolithic time onwards	Rich source of starch, protein, lipids, vitamin E and C, potassium, phosphorus,	Rich in malic acid and unsaturated fatty acids [278].	Reported higher concentration of palmitic acid which prevents metabolic syndromes such as diabetes [279].

	and cultivated worldwide especially in Spain, Turkey and Italy, United States and Canada [275,276].	magnesium, and calcium [277].			
18.	*Avena sativa* L. (Oats, Poaceae)	Consumed in developing as well as developed countries [280].	Nutritionally rich, traditionally used cereal crops as a major protein diet in cold climate countries including Northern Europe [281]. Better adapted to acid soils and variable soil types than other grain cereal crops [280].	High dietary fiber content and 78–81.5% unsaturated fatty acids out of 5-9 % lipids [282].	1. Barley yellow dwarf virus tolerance QTL on chromosome 3C using genome wide association study was reported [283]. 2. Presence of polyamines detected during osmotic stress detected [284].
19.	*Bacopa monnieri* (L.) Pennell. (Brahmi, Plantaginaceae)	Sri Lanka, India, Nepal, China, Taiwan, Viet Nam and Pakistan. Traditionally used as a medicinal plant from ancient times onwards [285].	Rich in Fe, Mg and Zn. Studies have proven the ability of Brahmi to enhance memory. They grow well in Marshy areas [285].	Rich source of microelements [285].	1. *De novo* assembly of transcriptome and draft chloroplast genome from RNAseq data [286]. 2. Proline content elevation during osmotic stress [287].
20	*Elaeagnus umbellata* Thunb. (Autumn olive, Elaeagnaceae)	Berries consumed in tropical and temperate Asia. Nowadays it is available in European countries also [73].	The berries are a rich source of lycopene and possess 10 times higher quantity of lycopene in their fruits than tomatoes [288]. They are rich in β-cryptoxanthin, α-cryptoxanthin, lutein, β-carotene, phytofluene and phytoene and vitamins. Exhibit drought tolerance, temperature	Ten times higher quantity of lycopene in their fruit than tomato [73].	1. Phytoene Synthase (*EutPSY*) gene expression correlation with lycopene [190]. 2. Sugar metabolism related enzymes (R-amylase, UGPase, phosphoglucomutase, acid invertase and triose-phosphate isomerase) and carotenoid biosynthesis related proteins (Acetyl-CoA C-acetyltransferase, IPP isomerase and dimethylallyl diphosphate) reported [189].

			tolerance, and highly tolerant to pruning. Can grow in high saline soils [73].		
21.	*Porteresia coarctata* (Roxb.) Tateoka (Wild rice, Poaceae)	India, Sri Lanka, Bangladesh, and Myanmar [289].	Grows in Saline estuaries and adapted to salinity [289].	With increase in salinity stress, carbohydrate and ash content increases [290].	Elevation of proteins related to photosynthesis such as Rubisco Large subunit, Rubisco small subunit and Light harvesting complex-chlorophyll a, b reported during salinity [289].
22.	*Atriplex lentiformis* (Torr.) S.Watson (Quail Bush, Chenopodiaceae)	South western United States and northern Mexico [231].	Good salinity adaptation capacity [231].	Rich source of sodium [291]	1. Studied the H+-ATPase activity of plasma membrane during salinity stress, which leads the plant for K+ retention and Na+ exclusion for better salt tolerance [231].
23	*Fagopyrum esculentum* Moench (Buckwheat, Polygonaceae)	Worldwide distribution [292].	Grows in hilly areas and marginal ecosystems [292]. Rich in sulfur containing amino acids such as cysteine and methionine than any cereal. Fatless, gluten-free grains that are rich in starch and minerals such as Ca, Mo, S and vitamins [281,293].	Excellent quality of protein with a high amount of essential amino acid lysine [294].	1. Draft genome of buckwheat was developed and the same study identified expression of three granule bound starch synthase (*GBSS*) genes [228]. 2. Differential expression of sugar biosynthesis and metabolism related genes in *F. esculentum* and *F. tataricum* [295].
24	*Panicum miliaceum* L. (Proso millet, Poaceae)	It is cultivated widely in Asian countries, some African countries and the Middle East [296].	More efficient in water usage, because it shows C4 pathway, hence suitable for cultivation in dry areas. High productivity in low input soil and marginal lands [134]. Rich in both major nutrients and minor nutrients such as phenolics,	Richer in essential amino acids than wheat [297].	1. Genes related to C4 mechanisms such as carbonic anhydrase (*CA*), NAD dependent malic enzyme (*NAD-ME*) and *NADP- malic enzyme* (NADP-ME) [298]. 2. Protein related to metabolisms such as polysaccharide and starch [299]. 3. Nearly 48 metabolites including several primary metabolites and five phenolic acids were detected

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			minerals and vitamins. Gluten free grain [297].	[300].
25	*Sclerocarya birrea* (A.Rich.) Hochst. (Marula, Anacardiaceae)	Popular African tree [301].	Ascorbic acid, arginine and glutamine rich fruits [301,302].	Highest level of Arginine and ascorbic acid [302].	1. Draft genome reported and identified genes involved in starch biosynthesis pathway [136].
26	*Ziziphus jujuba* Mill. (Chinese jujube, Rhamnace	Mainly cultivated in Asian countries [303].	Salt tolerant and drought tolerant [304]. Good source of phenolics, vitamin C, triterpenic acids, flavonoids, and polysaccharides [305].	Rich in unsaturated fatty acid, specially omega-6 fatty acid [306].	1. Expression of 5269 differentially expressed genes during salinity were recognized and among them, 2540 were downregulated and 2729 were upregulated [304]. Expression profiling of genes during heat stress led to identification of heat responsive factors [305]. Expression profiling of three UDP-glucose flavonoid 3-O-glucosyltransferase (*UFGT*), responsible for anthocyanin accumulation in fruit peel [307].
27	*Dacryodes edulis* (G.Don.) H.J.Lam	Cultivated in tropical countries of Africa [308].	Rich source of protein, vitamin and lipid [308].	Selenium content is high compared to other crops reported with selenium. Beta-carotene is higher than Papaya, Avocado and Amaranth. They are rich in Potassium too [309].	NA
28	*Basella alba* L.	Tropical Asian countries [310].	Heat and drought tolerant plants, high quantities of vitamin A, C, iron and calcium are present [310].	Leaves are rich in calcium [310].	NA
29	*Solanum quitoense* Lam.	Suuth American countries and nowadays found in European countries also [311].	Adapted to shady areas and rich in vitamins [311].	Rich in carotenoids [312].	NA

30	*Chenopodium pallidicaule* Aellen	Mainly cultivated in Bolivia and Peru [313].	Disease and pest resistant. Adapted to salinity, heat and drought tolerance. Rich in protein [313].	Exceptional protein content and quality, equivalent to that of milk proteins. Balanced amino acid composition [314].	NA
31	*Adansonia digitata* LL.	Tropical African countries [315].	Adapted to arid and semi-arid conditions and rich source of vitamin A and C [315].	Fruit pulp vitamin C is almost ten times that of oranges [316].	LC-MSMS analysis of fruit pulp identified 91 metabolites [252].
32	*Strychnos cocculoides* Baker	America, African and South tropic Asian regions [317].	Adapted to warm climate conditions [317]. Rich in iron, zinc and vitamin C [318].	Essential source of Iron [318].	NA
33	*Panicum sumatrense* Roth	Tropical region of Asia and Africa [296].	Grow with minimal requirements and adapted to harsh environmental conditions and rich in micronutrients [296].	Grains are a good source of iron and calcium [108].	1. Whole genome sequence was performed by Zou et al. [298] and identified 339 genes for microRNA and 55930 genes that code for protein 2. Illumina transcriptome sequencing was done by Yue et al. [319]. Identified 292 DGEs, 32000 SSR markers and 4,00,000 SNP markers. 3. Drought tolerance mechanism was studied by Zhang et al. [320] in leaf transcriptome. 4. RNa sequences were performed and differential gene expression at the time of drought and salinity stress also studied. At the time of drought stress 241 DGEs were upregulated and 134 DGEs were downregulated [321].

5. Linking omics and gene editing tools for rapid improvement/domestication of the traditional food crops

A lot of information is available on the genetic regulation of yield, nutritional quality, and stress-related traits of several model domesticated crops [322–324]. The genetic and genomic analysis of many domesticated crops such as maize, tomato, rice, sorghum, wheat has led to the identification of several genes/QTLs that regulate domestication traits [322,323,325,326]. Some of the important domesticated crops, their relative traditional crops and the genes regulating domestication traits are shown in supplementary table S2.

The results of genomics and other omics research have provided fundamental clues about the genetic regulation of important traits [327]. The knowledge obtained using omics approaches can be used for crop improvement programs such as the development of nutritionally superior, disease-resistant, and stress-tolerant crops with high yields [112]. The linking of genomics with the gene-editing tools is now possible and allows   editing of important genes with greater precision, accuracy and rapid pace [328]. Gene editing using CRISPR/Cas9 has become a method of choice because of its versatile nature, simplicity to design and implement, and less expensive than other genome editing technologies [329]. Finding plants with desirable traits and having superior traits is an important step [330]. The plants with one or more of the desirable traits such as superior nutritional composition, high yields, and biotic and abiotic stress tolerance should be given priority [331]. With the development of both genomics tools and bioinformatics pipelines, it is now easier to identify the genetic variation in wild species, which can be utilized for the transfer of traits to accelerate adaptive introgression in crops, as well as de novo domestication of wild relatives and landraces [90]. Since much genomic information is available on domesticated crops and other model plants, it is now possible to directly translate this information to the non-model traditional food crops for their rapid improvement by with various gene-editing tools such as meganucleases, Zinc Finger Nucleases (ZFNs), Transcriptional activator-like Effector Nucleases (TALENs), and Clustered Regularly Interspaced Short Palindromic Repeat-Associated Protein 9 (CRISPR-Cas9) [38,332–334]. Among the several gene-editing tools, CRISPR-Cas9 has been one of the most important and popular gene-editing tools and has attracted the considerable attention of crop scientists [25,330,333,335–337]. Omics combined with gene-editing tools such as CRISPR/Cas9 has revolutionized precise gene editing and holds a huge potential for rapid improvement of the crops for valuable traits, and for engineering genes for important metabolites [338,339]. The CRISPR-Cas9 editing has increased possibilities for genome modification and enables metabolite engineering, biofortification, and crop improvement [330,331,336]. Several attempts for improving various traits such as yield and stress tolerance in several crops have been done using CRISPR/Cas [330].

The CRISPR-Cas9 mediated gene editing is based on the guidance of short RNA sequences termed as guide RNAs which are designed to complement target DNA [340]. The target DNA is cleaved by a Cas endonuclease that results in a single or double-strand breaks in the DNA [340], followed by ligation of the DNA by the endogenous repair mechanisms [341–343]. In case of gene editing of less studied plants, for the identification of particular traits and related genes, homologous genes from extensively studied plants such as model plants are used. The supplementary table S2 provides a list of several domesticated crops, domestication genes and some of the traditional food plants related to the domesticated crops. The genetic information from the domesticated species can   be translated to the traditional food plants (See next section for the example of translation of genetic information from *Solanum lycopersicum* and *S. pimpinellifolium* to *Physalis pruinosa*.). With the help of databases such as the National Center for Biotechnology Information (NCBI), identification of target genes for their construction of sgRNA by comparing with a homologous sequence is possible [344]. Softwares are used for the construction of plasmid that carries Cas9, gRNA, and reporter gene along with their promoter. Cas-Designer is a good software for this purpose. For delivering the construct Cas9-gRNA-Reporter several methods such as agroinfiltration and electroporation can be used [345]. After delivery, induction of precise breaks at target sequences takes place in the target site. Endogenous machinery of cells repairs the breaks by non-homologous end joining (NHEJ) in the absence of a homologous repair template that results in insertions/deletions (indels) that disrupt/change/edit the target sequence or homology directed recombination (HDR) by providing a homologous repair template thereby inducing genomic mutations at the target locations [333,346]. For the validation of CRISPR/Cas9 editing the construct pCas9-gRNA-reporter is introduced into nodal-explants after tissue culture using the *Agrobacterium*-mediated transformation method. After the regeneration of successful transformed

plants, phenotypic and genotyping (using RT-PCR) and screening help to check the mutation effect [344]. A generalized work-flow involving various steps in genome editing for improved varieties is presented in Fig. 3.
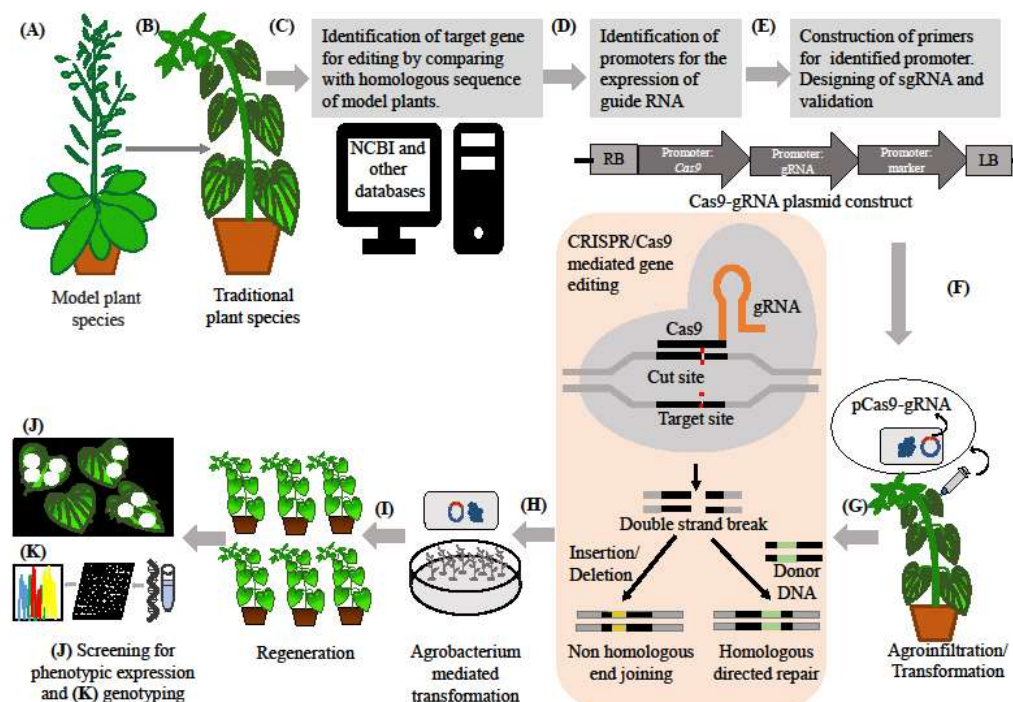

Figure 3. General work-flow of CRISPR/Cas9 based gene editing in neglected crops for their improvement. (A) Extensively studied model plant species chosen for the ease of investigating homologous genes for particular traits (B) Underutilized/ orphan/ neglected traditional plants that carry undesirable traits that can be edited for crop improvement, biotic and abiotic stress tolerance. (C) Identification of target genes for their construction of sgRNA by comparing with a homologous sequence of model plants with the help of databases such as NCBI and their validation using sanger sequencing. (D) Identification of promoters for the expression of guide RNA. (E) Construction of plasmid that carries Cas9, gRNA, and reporter gene along their promoter with software Cas-Designer. (F) Agroinfiltration on young leaves with *Agrobacterium* harboring the construct Cas9-gRNA-Reporter. (G) Induction of precise breaks at target sequences. Endogenous machinery of cells repairs the breaks by non-homologous end joining (NHEJ) in the absence of a homologous repair template that results in insertions/deletions (indels) that disrupt/change/edit the target sequence or homology directed recombination by providing a homologous repair template thereby inducing genomic mutations at the target locations. Other than CRISPR/Cas9 Zinc finger nucleases (ZNF), Mega nucleases and Transcription activator-like effector nucleases (TALEN) are also used in the field of gene editing. But the feasibility of CRISPR/Cas9 is more when compared with other methods. (H) Validation of the efficiency of CRISPR/Cas9 for targeted mutagenesis in stable transgenic plants. The construct pCas9-gRNA-reporter introduced into nodal-explants after tissue culture using the *Agrobacterium*-mediated transformation method. (I) Regeneration of stable transgenic plants. (J) Screening of the regenerated plants for the mutated effect by checking their phenotypes. (K) Genotyping or putative transgenic plants contained Cas9 as confirmed by PCR analysis [333,344,346].

6. Recent examples of translational genomics in successfully editing traditional food crops

Traditional food plants are regionally important, especially in developing countries [28]. In addition to the availability of germplasm diversity across the continents, they possess several beneficial traits [55]. However, unfortunately, they are also burdened with undesirable traits that resemble wild relatives and are not suitable for extensive agriculture [55,331]. *Physalis pruinosa* (groundcherry) is a traditionally important plant consumed in

various parts of the world for its important nutritional properties [163,347]. Huge inter and intraspecific diversity of *Physalis* is available in the world but it is not cultivated or consumed on a larger scale because of its certain undesirable traits such as extensive growth habit, smaller fruits, and fruit dropping because of an abscission [332]. It is a relative of tomato as both of them belong to the family Solanaceae and they share common genetic architecture with the same chromosome number of 12. Since both are from the family Solanaceae, and we know a lot about the genetic regulation of various traits in tomato, it is easy to translate genetic information from the model tomato to the non-model traditionally important crop, groundcherry for its improvement using gene-editing tools [327,332]. Gene editing tools can be used to rid of undesirable traits from ground cherries. On these lines, a study was carried out by Lemmon et al. [332] and they obtained very successful gene-edited crops with improved characters in groundcherry. The undesirable characteristics of *Physalis* are similar to the wild ancestor of the tomato, *S. pimpinellifolium* which underwent domestication in its traits leading to modern day *S. lycopersicum*. Using gene editing, Lemmon et al. [332] targeted repressors of the florigen pathway to increase flower numbers and delimit flowering time, both on primary and axillary shoots. They performed a knockout of classical *SELF PRUNING* (*SP*) genes that control determinate and indeterminate growth habits of the plant. The results lead to extreme compactness in *P. pruinosa.* Another knockout of the florigen repressor, *SELF PRUNING 5G* (SP5G), resulted in increased axillary flowering and fruit density. Targeting of the shoot apical meristem size regulating gene *CLAVATA* resulted in increased flower meristem size, additional flower organs, and conversion of small two loculer fruit to a larger three loculer fruit as illustrated in Fig. 4 [332]. This study has opened up new hopes and possibilities for the rapid improvement and fast domestication of traditional orphan and wild crops. Many other groups in the globe are now focussing on editing the genes in non-model crops based on genetic and genomic information obtained from model crops [75,327]. The gene-editing tools are particularly employed with an aim to increase quality, enhance yields, improve biotic, abiotic stress resistance and expand geographical ranges of cultivation of traditional orphan crops [332]. But traditional food crops have not undergone intensive selection for domestication [348]. Thus, traditional orphan crops are less productive, unsuitable for cultivation at larger agricultural scales [63]. Similar studies can be undertaken and the information from omics studies can be combined with gene-editing tools to other traditional food crops. A similar approach can be extended to wild edible species for *de novo* domestication [75]. The *de novo* domestication of wild plants is a viable solution for designing custom crops for the future [75]. By unleashing the multiplexing ability of CRISPR/Cas9 technology, multiple targets can be modified simultaneously in an efficient way by pyramiding multiple beneficial traits [341]. Taken together, the results of these studies suggest that the gene editing tools are a valuable tool to target homologs of domestication genes in traditional food plants quickly [25].
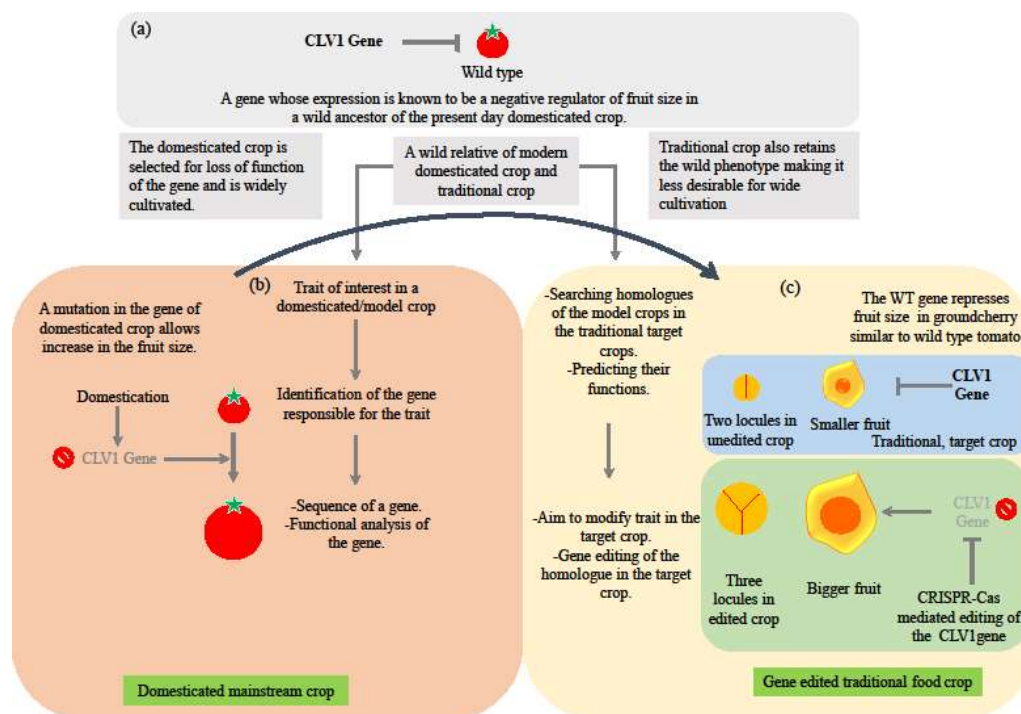
Figure 4. An example of translational genomics approach for rapid improvement of a traditional orphan food crop for larger fruits. The genomics information obtained from the tomato (a domesticated crop) genome sequencing and the functional analysis of the genes is directly translated to the traditional crop, groundcherry (a traditional food crop) [332].

Gene editing has lead to several revolutions in the field of crop improvement and it has been done in several major crops and other plants such as tomato, maize, tobacco, grapevine, apple, opium poppy, cucumber, and cotton for important traits and results obtained are impressive [38,335,336,349–353]. Zsögön et al. [38] engineered *S. pimpinellifolium* (wild) using CRISPR/Cas9 and their several traits were altered that resulted in superior gene edited *S. pimpinellifolium* than the *S. lycopersicum*. In 2014, CRISPR/Cas9 gene editing was successfully applied to tomato and citrus. Some successful cases of CRISPR/Cas9 fruit trait improvement are cucumber, apple, grape (2016), watermelon (2017) and kiwifruit, banana, cacao, strawberry, papaya, and groundcherry [336]. Other examples of the successful gene editing using CRISPR/Cas9 include trait improvement of grain number, grain size, panicle architecture of rice [354,355], grain length, and weight of wheat [356], seed oil composition (high oleic and low polyunsaturated fatty acids) of flax [357], late-flowering in soybean [358], reduced zein protein; salinity tolerance in maize [342,359]. But most of the success works are reported in the case of major crops, efforts are needed to improve and mainstream traditional food crops with the aid of genome editing tools and integrative genomics approaches. Varshney et al. [360] explained the success story of translational genomics of grain legume crops chickpea (*Cicer arietinum*), common bean (*Phaseolus vulgaris*), groundnut (*Arachis hypogaea*), pigeon pea (*Cajanus cajan*), and soybean (*Glycine max*) for their drought tolerance and pathogen resistance by multiple QTLs or genes from model legume *Medicago truncatula*. Ji et al. [361] have attempted gene editing using CRISPR/Cas9 in Cowpea (*Vigna unguiculata*) which is also an important traditional food crop because of its symbiotic nitrogen fixation capability. Recently Syombua et al. [344] introduced a CRISPR/Cas9-based genome editing system for underutilized yam *Dioscorea alata* with improved genetic transformation, which can lead to trait improvement in yam. By the establishment of an efficient CRISPR/Cas9 editing protocol, Syombua et al. [344] suggested that it is possible to remove undesirable traits of *Dioscorea alata* such as poor seed set, and non-synchronous flowering. Considering the importance of gene editing

technology and its application in successfully editing genes of several crops for improved varieties and a beginning of editing traditional orphan crops, the future studies aiming at extension of this technology to traditional crops will lead to the mainstreaming of many traditional crops. It will lead to diversification of the food basket of the people across the globe reducing excessive reliance on a selected number of crops.

8. Challenges to translational genomics using gene editing

Considerable progress has been made in the field of translational genomics particularly with the aid of gene-editing tool CRISPR/Cas9 [362]. However, there are a number of important challenges to gene editing of plants. Several traits are quantitatively controlled and require multiple genes. Therefore, to produce desired phenotypes in the edited crops, we need to edit multiple genes [337]. Further, genomic information of many traditional food crops is not available. Another important challenge is that it is not easy to create precise modifications in DNA sequences. However, several gene editing strategies such as replicons, base editors and targeted nonhomologous insertions provide efficient precise gene editing in plants [345]. Unavailability of efficient delivery methods for gene editing reagents (DNA plasmid, mRNA (Cas9 + sgRNA), Ribonucleoprotein (RNP)) is another challenge [345]. Several other challenges such as ethical issues and technical bottlenecks are discussed elsewhere (See [337,362–364]).

9. Conclusion and future perspectives

Many of the traditional food plants have been a part of human civilizations since ancient times. Different parts of the plants are consumed by humans from generation to generation in the different geographical areas of the world. They are unique as they possess various nutritional components and abiotic stress tolerance related traits. Several studies have shown some traditional food crops such as quinoa, millet, cassava, and amaranth show tolerance to multiple abiotic stresses. The nutritional composition of many traditional food plants is also incredible with a variety of health beneficial and pharmacological values. Multiple omics tools have been applied to several traditional food plants for unraveling the basis of important traits. Genomic information of relatives of many traditional food plants is also available which can be directly translated to the traditional food plants using several tools such as CRISPR/Cas mediated gene editing. Many traditional food plants are grown regionally and have regional importance. Therefore they have undergone some level of domestication and if they have to be domesticated and cultivated at a large scale, it is essential to get rid of undesirable traits that burden these crops. Since they are subjected to a certain level of domestication, tweaking a few genes using gene-editing technologies will make them cultivable at a large scale as evidenced by studies on groundcherry by Lemmon et al. [332]. The reintroduction of improved traditional crops into the current food systems will help diversify the food basket of the public giving them more options. Identification and mainstreaming of traditional food plants having higher nutritional and micro nutritional values will help eradicate hidden hunger prevalent due to the deficiency of the micronutrients in the diets [62].

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1, Table S1: Diversity of some important traditional food crops grown across the globe and their nutritional and stress-resilient traits desirable for sustainable food security under climate change, Table S2: Major domestication traits and the genes governing them in important crop plants (Modified from Meyer and Purugganan, 2013).

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