frontiers
in Sustainable Food Systems

REVIEW
published: 12 August 2021
doi: 10.3389/fsufs.2021.711820

Improvement of a Traditional Orphan Food Crop, *Portulaca oleracea* L. (Purslane) Using Genomics for Sustainable Food Security and Climate-Resilient Agriculture

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Specialty section:
This article was submitted to
Crop Biology and Sustainability,
a section of the journal
Frontiers in Sustainable Food Systems

Received: 19 May 2021
Accepted: 13 July 2021
Published: 12 August 2021

Citation:
Kumar A, Sreedharan S, Singh P, Achigan-Dako EG and Ramchiary N (2021) Improvement of a Traditional Orphan Food Crop, Portulaca oleracea L. (Purslane) Using Genomics for Sustainable Food Security and Climate-Resilient Agriculture.
Front. Sustain. Food Syst. 5:711820.
doi: 10.3389/fsufs.2021.711820

Purslane (*Portulaca oleracea* L.) is a popular orphan crop used for its nutritional properties in various parts of the world. It is considered one of the richest terrestrial sources of omega-3 and omega-6-fatty acids (ω-3 and 6-FAs) suggesting its importance for human health. This ethnomedicinal plant is also an important part of traditional healing systems among the indigenous people. Many studies have indicated its tolerance against multiple stresses and found that it easily grows in a range of environmental gradients. It has also been considered one of the important biosaline crops for the future. Despite its huge nutritional, economic, and medicinal importance, it remains neglected to date. Most of the studies on purslane were focused on its ethnomedicinal, phytochemical, pharmacological, and stress-tolerance properties. Only a few studies have attempted genetic dissection of the traits governing these traits. Purslane being an important traditional food crop across the globe can be valorized for a sustainable food security in the future. Therefore, this review is an attempt to highlight the distribution, domestication, and cultivation of purslane and its importance as an important stress-tolerant food and a biosaline crop. Furthermore, identification of genes and their functions governing important traits and its potential for improvement using genomics tools for smart and biosaline agriculture has been discussed.

Keywords: purslane, sustainable food systems, traditional foods, food security, climate change, climate smart agriculture, biosaline agriculture, ethnic foods

INTRODUCTION

The *Portulaca* L. is the only genus in the family Portulacaceae as per APG III classification of angiosperms (The Angiosperm Phylogeny Group, 2009; Ocampo and Columbus, 2012) and comprises more than 100 species which are widely distributed and adapted to a range of environmental conditions (Nyffeler and Eggli, 2010). The genus *Portulaca* shows a great phenotypic plasticity in its various traits such as flower, fruit, leaves, stem, and growing habit

(Coelho and Giulietti, 2010). The members of *Portulaca* genus are either herbaceous perennials or annuals usually with tuberous roots, slightly succulent stem, and leaves with alternate or rarely opposite phyllotaxy and cymose terminal inflorescences (Nyffeler and Eggli, 2010; Walters et al., 2011; Ocampo and Columbus, 2012; Dalavi et al., 2018). The flowers are sessile or rarely pedicellate and are easily distinguishable by their inflorescence and fruits which are operculate capsules termed as pyxidia (Nyffeler and Eggli, 2010). The *Portulaca* is characterized by thick and dense homogenous populations in nature (Walters et al., 2011). Due to the presence of facultative C4/CAM photosynthetic pathways in purslane, it has become an important model crop for facultative C4/CAM photosynthesis evolution in plants and its future role for food security (D'Andrea et al., 2014; Ferrari et al., 2020). The species of *Portulaca* are adapted to the shady and moist environments, show extensive branching (Matthews and Levins, 1985), and are generally characterized by tuberous roots (Geesink, 1969; Carolin, 1987). The leaves are succulent in nature, and fruits are round or egg-shaped operculated capsules and produce tiny, oval-shaped reddish-, brown-, or black-colored seeds which are rich in phytochemicals (Matthews and Levins, 1985; Grubben, 2004). The leaves and inflorescences show the presence of trichomes (Matthews and Levins, 1985). It produces many seeds with very high dormancy (Alam et al., 2014e). Most of its species such as *P. oleracea*, *Portulaca grandiflora*, *Portulaca amilis*, *Portulaca molokiniensis*, *Portulaca pilosa*, and *Portulaca umbraticola* show C4 photosynthesis (Koch and Kennedy, 1982; Guralnick et al., 2002; Voznesenskaya et al., 2010). Interestingly, some C4 species such as *P. oleracea*, *P. grandiflora*, *P. australis*, *P. pilosa*, *Portulaca digyna*, and *Portulaca cyclophylla* also show Crassulacean acid metabolism (CAM) pathway, a special type of photosynthesis found in the succulent plants adapted to desert conditions (Sage, 2002). Most of the species except a few such as *Portulaca cryptopetala* show Kranz anatomy (Ocampo et al., 2013). However, the CAM pathway in the C4 *Portulaca* species operates only during drought conditions when water availability is reduced (Lara et al., 2004; D'Andrea et al., 2014). Besides a model plant for C4/CAM photosynthesis, it is also an important crop for understanding the salt-tolerance mechanisms in plants (Borsai et al., 2018, 2020). Of the more than 100 species of *Portulaca*, *P. oleracea* L. (hereafter purslane; **Figures 1a–d**) is the most important and well-studied species. Purslane also shows wide phenotypic plasticity in its flower colors that make it an important ornamental plant (**Figure 2**). Purslane is an important plant rich in important phytochemicals and nutritional components possessing medicinal, nutritional, medicinal, phytoremediation, stress-tolerance, and pharmacological properties (Alam et al., 2014c, 2015b; Uddin et al., 2014; Zhou et al., 2015). Purslane is also traditionally used as an ethnomedicinal plant (Sultana and Raheman, 2013; Iranshahy et al., 2017). Despite its multiple benefits, such as its nutritional and phytochemical richness, purslane still remains a neglected food crop of the indigenous communities, and studies on the genetic regulation of important traits and their improvement strategies is limited. Except for the C4-CAM switch, very limited information on distribution, domestication, and cultivation of purslane is available. Information on application of genetics and genomics for the improvement of nutritional and stress-resilient traits of purslane, and hence to be adopted for the extensive cultivation and industrial applications is not available. Furthermore, since the purslane grows profusely across a range of environmental

FIGURE 1 | Natural habitat and parts of purslane plant. **(a)** Purslane plant in natural habitat; **(b)** young stem with leaves; **(c)** harvested plant showing roots; and **(d)** young fruits, known as pyxidia with black-colored seeds.

FIGURE 2 | (a–i) Morphological diversity of flowers observed in purslane (scale bar, 1 cm).

gradients, and shows salinity tolerance, it is not surprising that the species holds a potential as a biosaline crop for urban agriculture. Taken together with this background, this review summarizes current knowledge on various aspects of purslane with an emphasis on its distribution, cultivation, domestication, and its importance as a nutritional, medicinal, and biosaline crop. It further discusses a futuristic approach combining genomics and gene-editing tools for the editing of genes governing important traits for urban and biosaline agriculture.

DISTRIBUTION AND DIVERSITY OF PURSLANE

Purslane is the eighth most commonly distributed plant in the world (Anastácio and Carvalho, 2013). The molecular phylogenetic study of the genus *Portulaca* shows that it is a monophyletic genus with two major clades, namely, opposite leaves (OL) and alternate leaves (AL; Ocampo and Columbus, 2012). The study further showed that OL clade includes species that possess opposite leaves and are distributed in Africa, Asia, and Australia, whereas AL clade represents species that possess alternate to subopposite leaves and are distributed in the New World. There was a debate around its origin in the Old World and its further introduction to the New World countries during the Columbus period. However, the presence of Pre-Columbian archaeological evidence in the New World suggests that purslane is distributed in the Old World as well as New World countries thereby ending the debate whether it was introduced by Columbus (Byrne and McAndrews, 1975). Recovery of the carbonized fossils of purslane from prehistoric human settlement sites suggests its importance as an important food plant for the indigenous communities since prehistoric times (Chapman et al., 1973; Byrne and McAndrews, 1975; Simopoulos et al., 1995). Simopoulos et al. (1995) suggested Mexico as the center of origin of purslane because the maximum number of species including its three ploidy types exists there. Although germplasm collections and their characterization for various important traits such as stress tolerance, superior metabolic and nutritional traits, and biomass accumulation are important for improvement of purslane; however, no such study reports are available in plenty.

DOMESTICATION AND CULTIVATION OF PURSLANE AND MEASURES TO UPSCALE ITS PRODUCTION AND CONSUMPTION

A very few studies have focused on the cultivation and domestication of purslane. Cros et al. (2007) carried out comparative study of its cultivation using peat, vermiculite, coir, perlite, and mixtures of peat and perlite and found that plants grown on peat showed the highest total fatty acid, alpha-linolenic acid, and linoleic acid. Application of *Rhizophagus irregularis*, an arbuscular mycorrhizal fungi (AMF) increased the phosphorus uptake, grain yield, biomass weight, total antioxidant activity, and unsaturated fatty acid, leaf essential oil, and leaf ω3 and improved the soil cation exchange capacity (CEC) of plants (Hosseinzadeh et al., 2020, 2021). Application of nitrogen fertilizers also improved phosphorus and nitrogen uptake, biomass weight, flavonoid content, total antioxidant capacity, and fatty acid content (Hosseinzadeh et al., 2020). The best season for its sowing is spring of fall, and it completes its life cycle in 60–75 days (Alam et al., 2014e). In Malaysia, nearly seven cultivars are cultivated for ornamental purposes and are propagated through cuttings (Alam et al., 2014e). However, the wild purslane can germinate through the seeds (Alam et al., 2014e). Although it is nutritionally and medicinally important across different cultures, it is considered a weed in several parts of the world (Banerjee and Mukherjee, 2002; Rapoport and Drausal, 2013; CABI, 2021).

Safdari and Kazemitabar (2009) have attempted tissue culture in wild and cultivated races of purslane using different explants and hormone concentrations, and the results show that 10 μM IBA combined with 5 or 10 μM BAP sufficiently induce callus formation in the wild race whereas 2.5 μM IBA was enough for root generation in both the races. A study on the development of *in vitro* plant regeneration and *in vitro* flowering using various concentrations of PGRS showed that 0.5 mg L^{-1} of kinetin is optimum for maximum shooting and 0.2 mg L^{-1} of GA_3 induced bud formation in purslane (Sharma et al., 2011). Shekhawat et al. (2015) observed maximum shooting when MS medium was supplemented with 2.0 mg L^{-1} BAP. These studies provide a basis for the cultivation of purslane. However, to better understand the best performance conditions, further field trial experiments are needed. Moreover, the standardization of tissue culture protocols in purslane would be helpful for future breeding programs aimed at upscaling cultivation of purslane. The future studies should be aimed at the methods for improved productivity, phytochemical composition, and its suitability for urban agriculture. Dewanti et al. (2021) found the highest amount (9.73 mg kg^{-1}) of vitamin C in purslane obtained from lowland areas.

IMPORTANCE OF PURSLANE

The purslane is cultivated in various parts of the world mostly for ornamental purposes because of its phenotypic diversity in its flower color and for nutritional and medicinal purposes because of its richness in important phytochemicals (Simopoulos et al., 1992; Coelho and Giulietti, 2010; Melilli et al., 2020). **Figure 3** provides an overview of the importance of purslane for sustainable food security and human benefits.

Nutritional Value

A number of studies have shown that purslane is very rich in important nutritional components such as vitamins, proteins, carbohydrates, ω-3-FAs, carotenoids, and minerals (Simopoulos et al., 1995, 2005; Aberoumand, 2009; Uddin et al., 2014; Petropoulos et al., 2016; Alam et al., 2021). It shows a very high amount of ω-3-fatty acids which is not generally found in vegetarian diets suggesting its important role as a functional food (Palaniswamy et al., 2001; Alam et al., 2014e; Petropoulos et al., 2016). Several studies have done analysis of its various nutritional constituents. The purslane contain high quantity of protein, ash, fiber content, and minerals (Aberoumand, 2009; Almasoud and Salem, 2014; Uddin et al., 2014; Chugh et al., 2019). It is also a very good source of various types of vitamins including vitamins A and C (Guil-Guerrero and Rodríguez-García, 1999; Chugh et al., 2019). The high nutritional composition of purslane indicates its potential as an important nutraceutical food for the future.

Medicinal Potential

Purslane is an important traditional ethnomedicinal plant as its leaves, roots, and stems contains rich medicinally important phytochemicals such as alkaloids, flavonoids, phenolic acids, homoisoflavonoids, lignans, polysaccharides, and catecholamines (Banerjee and Mukherjee, 2002; Xiang et al., 2005; Lim and Quah, 2007; Alam et al., 2014b; Zhou et al., 2015). Several authors have reviewed the phytochemical composition of purslane. It has been a part of indigenous healthcare systems across the continents (Xiang et al., 2005; Bosi et al., 2009; Sultana and Raheman, 2013; Hwess et al., 2018; Sdouga et al., 2020; Zaman et al., 2020). Many ethnobotanical studies have reported its use against multiple diseases and ailments (Ahmad and Beg, 2001; Bosi et al., 2009; Nedelcheva, 2013; Sultana and Raheman, 2013; Hwess et al., 2018; Chaachouay et al., 2019; Manzanero-Medina et al., 2020; Nanagulyan et al., 2020). Recent pharmacological studies also suggest its important medicinal benefits against a number of diseases such as cancer, diabetes, and viral, bacterial, and fungal infections (Dong et al., 2010; Ye et al., 2015; Jin et al., 2017; Park and Han, 2018; Zhao et al., 2018; da Silva et al., 2019; Li et al., 2019; El-Desouky, 2021; Park et al., 2021; Tleubayeva et al., 2021). These results of pharmacological studies provided important evidence toward the potential of purslane in drug development against diseases.

Potential for Biosaline Agriculture

Salinity is also an important stressor that limits crop productivity. There is plenty of saline water, and if salinity-tolerant crops are

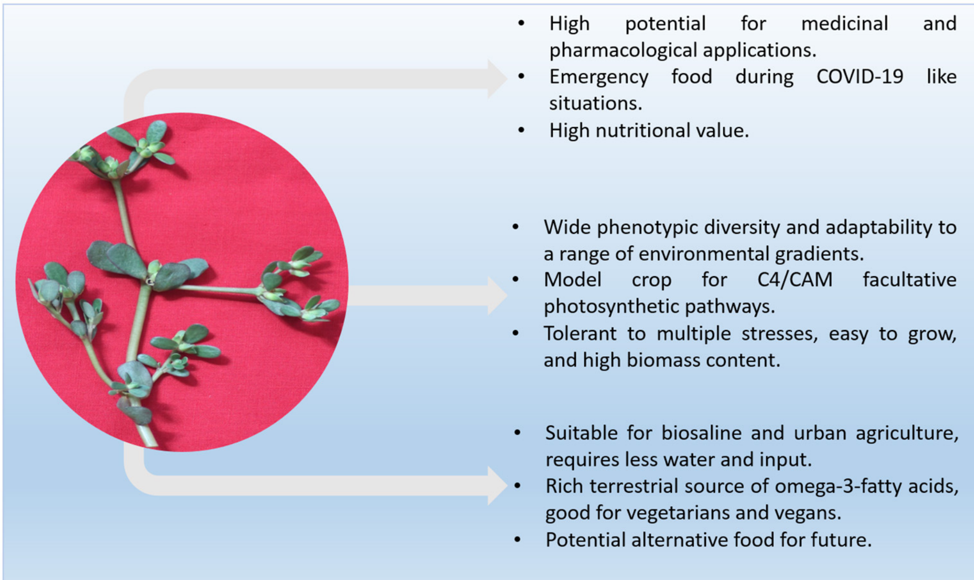

FIGURE 3 | Potential of purslane for sustainable food security and health benefits.

available, we can use the saline water for agriculture and can reduce the usage of freshwater in agriculture (Flowers, 2004; Yamaguchi and Blumwald, 2005; Roy et al., 2014; Fita et al., 2015). Moreover, the current agricultural practices which involve the use of chemicals have increased the salinity of agricultural soils (Shrivastava and Kumar, 2015). Therefore, soils have become less fertile and the normal varieties cannot survive in the saline environments. Plants respond to salinity stresses in a variety of ways including expression of important genes related to salinity tolerance (Chandna et al., 2014; Borsai et al., 2018). Therefore, looking for crop plants which can withstand salinity condition should be one strategy so that saline environment can be utilized for agriculture.

Purslane is considered salinity tolerant and can perform even under high salinity conditions (Yazici et al., 2007; Kafi and Rahimi, 2011; Alam et al., 2014b,e; Hniličková et al., 2019). Experimental evidences by several studies showed that purslane could grow in saline soils, therefore, it could be popularized as an important biosaline crop (Hasanuzzaman et al., 2014; Panta et al., 2014; Dagar, 2018; Elouafi et al., 2020). The plant responds to salinity stress by the production of proline which is an important osmolyte and helps in salt tolerance (Yazici et al., 2007; Rahdari et al., 2012). Similar response is observed in another species, *P. grandiflora* suggesting its adaptability to stresses (Kichenaradjou et al., 2018). Studies have shown reduced accumulation of proteins and lipids following salinity stress and increased accumulation of carbohydrates (Morgan, 1992; Dhanapackiam and Ilyas, 2010). Unlike salt-sensitive crops, purslane is known to keep its photosynthetic activity on even under higher salinity conditions through increased chloroplast biosynthesis and chlorophyll accumulation (Rahdari et al., 2012), although, the application of salinity decreases its germination potential. Another study found that intermediate levels of salinity are not detrimental to purslane as they continue to perform well under moderate salinities (Teixeira and Carvalho, 2009). Several metabolites in response to salinity have been identified in *P. oleracea* (Zaman et al., 2020). Increased accumulation of proline in the salt-tolerant purslane genotypes correlated with higher expression of *pyrroline-5-carboxylate synthetase* (*PC5S*) gene which is a key enzyme for the biosynthesis of proline (Sdouga et al., 2019). Increased accumulation of proline and its correlation with *PC5S* show important transcriptional control of salt tolerance in purslane. Due to its salt-tolerance potential, it is suggested to be an appropriate crop, with greater pharmacological and nutritional potential that can be grown in areas where the irrigation water is saline and solar radiation levels are high (Franco et al., 2011).

Potential for Urban Agriculture

Another issue that we face today is the nonavailability of land resources in urban areas (Fischel, 1982; Fazal, 2000; Satterthwaite et al., 2010; Kapil, 2019). The urban populations are dependent on market foods that are not fresh and sometimes, it takes many days to reach the kitchens of urban areas (Satterthwaite et al., 2010). However, if crops are devised that takes very less space and gives high biomass, it can be adopted in the future especially by urban people/consumers to have quick chemical-free fresh vegetables and foods. As purslane takes very less space and produces huge biomass rich in very important nutrients and health-promoting phytochemicals, this crop has tremendous potential for urban agriculture (Ren and White, 2019).

Rich Terrestrial Source of Omega-3-Fatty Acids

Several quantitative studies from various parts of the world have reported very high amounts of ω-3-fatty acids in its various plant parts of purslane (Davis and Kris-Etherton, 2003; Simopoulos et al., 2005; Uddin et al., 2014). It is considered one of the richest sources of ω-3-fatty acids. Marine algae are also rich in ω-3-fatty acids; however, they are not available beyond the coastal areas. Moreover, cultivation of algae needs skill and expertise. In contrast, cultivation of purslane is very easy and does not require special care or expertise. Vegetarian and vegan diets are relatively low in alpha-linolenic acid (ALA), an important ω-3-fatty acid (Davis and Kris-Etherton, 2003). ALA is further broken down to eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) and the latter are essential for cardiovascular health. However, plasma, tissue, and blood of vegetarians and vegans are also low EPA as well as DHA as these (Davis and Kris-Etherton, 2003; Rosell et al., 2005; Saunders et al., 2013). Lower EPA and DHA in vegetarians and vegans may lead to cardiovascular-related health issues. Dieticians and health experts suggest increased intake of ALA to vegetarians and vegan people since their diets are deficient in ALA (Davis and Kris-Etherton, 2003). The presence of a high amount of ALA in purslane suggests its suitability for vegetarians and vegans as an important source of ALA (Uddin et al., 2014). Therefore, the promotion of consumption of purslane among vegetarians and vegans is an important step toward enriching their diets with ALA, EPA, and DHA.

Wide Phenotypic Diversity and Adaptability to a Range of Environmental Gradients

The *P. oleracea* is a cosmopolitan species, and huge phenotypic plasticity is observed for various traits such as flower color, phytochemical constitution, leaf size and number, growth habit, and overall plant size (Danin et al., 1978; Ezekwe et al., 1999; Ren et al., 2011; Alam et al., 2014d). Ren et al. (2011) reported genetic variation study in purslane using amplified fragment length polymorphic markers in 10 drought-tolerant accessions from different geographical locations, namely, POS, PO, and Turkey (Turkey), Keren and Tokombiya (Eritrea), Golden E (UK), Golden G and T (Netherlands),Wild Greece (Greece), and Egyptium (Egypt). They reported Tokombiya and Egyptium as the most tolerant accessions to drought stress at the adult stage (Ren et al., 2011). Commercial cultivars, Glystrida 0425 and Purslane Dark Green, and local populations, Sari, Gorgan, and Aliabad originating from Iran had relatively higher biomass yield (Karkanis and Petropoulos, 2017). Ezekwe et al. (1999) have characterized eight accessions namely *P. oleracea*, *P. sativa*, Golden Gerber (GG Dutch), Garden (Gn Dutch), Golden (G England), and wild (W) accessions (Beltsville, Egyptian, and Greece) of purslane from different geographical regions for chemical composition, crude protein, total lipids, and carbohydrate content. They reported the highest crude protein content (27.1%) in Wild Greek accession and the highest omega fatty acid content in Dutch Garden accession (Ezekwe et al., 1999). Alam et al. (2014d) studied 45 accessions of purslane from the Western Peninsula of Malaysia and grouped them into seven types based on their characters such as leaf type and color, stem color, and flower type and color. Molecular analysis of these 45 accessions of purslane using expressed sequence tag (EST)-derived simple sequence repeat markers (ES-SSR) showed high genetic diversity among the accessions (Alam et al., 2015a). Evaluation of antioxidant compounds, antioxidant activities, and mineral composition of 13 collected purslane accessions showed wide phenotypic diversity (Alam et al., 2014c). Several accessions of purslane were screened for high salt tolerance (Alam et al., 2014b), and it was found that salinity affects phenolic compounds and antioxidant activities of 13 collected purslane germplasms (Alam et al., 2015b). Characterization of 45 accessions of West Peninsular, Malaysia for various morphological and physiological parameters and mineral composition identified potential accessions that can be used for supplementing the nutritional and mineral requirements (Alam et al., 2014a,e). Liu et al. (2000) have evaluated 12 varieties of purslane (nine Australian wild, two North American origins and one local), and the results of the study showed a wide variation in fatty acids and β-carotene composition. Lim and Quah (2007) characterized six cultivars (PO1–PO6) of purslane for total phenol content (TPC) and found that the ornamental cultivars have higher total phenolic (TPC) content and antioxidant activities than the common variety (PO1). Among the six varieties, PO6 showed the highest TPC and antioxidant activity. Tiwari et al. (2008) found that two species of *Portulaca*, i.e., *P. tuberosa* and *P. oleracea* are good heavy metal accumulators. Zhu et al. (2010) used 11 *Portulaca* accessions from five provinces of China and obtained consistent GC-MS and IR spectral fingerprints that are important for quality assurance. A comparative study of two subspecies of *Portulaca*, i.e., *P. oleracea* subs. *granulatostellulata* and *P. oleracea* subs. *edulis* for their growth and nutritional quality showed that both the subspecies were rich in minerals. However, K content was higher in *P. oleracea* subs. *edulis*, whereas the Ca content was higher in *P. oleracea* subs. *granulatostellulata* (Yun et al., 2016). Analysis of physicochemical properties of oil from seed, leaf, and stem of purslane from the Dire Dawa region of Ethiopia showed the highest oil content in seeds (11.25%) compared with leaf and stem (Desta and Cherie, 2018). Furthermore, the analysis of 13 common Malaysian-cultivated accessions of purslane showed differential morphological responses to salinity stress (Alam et al., 2016). The results showed that except plant height in Ac 1 (accession 1), all morphological parameters showed negative correlation with salinity and Ac 13 was the most affected accession among all. Egea-Gilabert et al. (2014) characterized 12 accessions of purslane using morphological, molecular, agronomical, and biochemical analyses and identified CM 13-00809 as an important accession with superior traits such as yield, dry matter, and potassium content. Kaşkar et al. (2009) analyzed agronomic parameters of several accessions of purslane such as Golden purslane, "C," one local Turkish accession, and three Spanish accessions and found variation in various parameters such as nitrate and oxalate content, plant height, number of leaves, leaf area, and yield component. They further found that accession "C" which was obtained from Pasa Seeds company showed better agronomic traits which includes plant height, number of leaves, leaf area, and yield component. The Turkish accession showed minimum amounts of oxalate and nitrates (undesirable/antinutrients) suggesting their suitability for human consumption. Analysis of 19 characters in four populations of purslane showed wide interpopulation heterogeneity in Tunisia (Salah and Chemli, 2004). Sdouga et al. (2020) found wide diversity in morphological and biochemical characters between wild populations and cultivated varieties. Karkanis and Petropoulos (2017) studied comparative physiological responses under Mediterranean semiarid conditions between two commercial cultivars, three local populations of Iran, and one local population of Greece and found that the Aliabad, a local population of Iran showed the highest yields. Balabanova et al. (2020) analyzed 33 Bulgarian and five Greek accessions of purslane and reported 50 metabolite markers. Metabolic profiling of leaves and roots of two purslane genotypes, Tall Green (TG) and Shandong Wild (SD), under the control and saline exposures was performed by Zaman et al. (2020) who found a huge variation in the concentration of 132 metabolites under control and treated conditions. Furthermore, salinity-induced reduction in the number of leaves and roots, diameter of the stem, and length of roots was reported.

Besides its tolerance to a range of environmental conditions (Miller et al., 1984; Simopoulos, 2011), it produces a very high number of seeds with very good germination rate even under stress conditions (Fernández et al., 2008; Chauhan and Johnson, 2009; Alam et al., 2014e; Ren and White, 2019). Purslane grows profusely even on the less fertile and waste lands (Nyffeler and Eggli, 2010; Subramanyan, 2017). Its adaptability to various climatic conditions makes it a suitable crop for extensive agriculture. Various varieties are regionally important, and people collect it from the natural habitats (Turner et al., 2011; Uddin et al., 2014; Borelli et al., 2020). In some cases, people also cultivate it at a small scale especially for ornamental purposes (Osma et al., 2014). Efforts must be taken to exploit its genetic diversity for regional agricultural programs based on the availability and suitability of *Portulaca* species/cultivar. Moreover, except for *P. oleracea*, only a few other species of *Portulaca* are studied to date. This suggests that further studies on other species of *Portulaca* will help us to identify potential genotypes including higher content of ω-3-fatty acids and other nutritional and phytochemical components.

Important Model Crop for C4/CAM Facultative Photosynthetic Pathways

Portulaca oleracea is an important plant that uses both C4 and CAM photosynthetic pathways depending upon the prevailing situations (Lara et al., 2004; D'Andrea et al., 2014). The C4-CAM switching depending upon the prevailing environmental conditions makes it an important and desirable crop for the twenty-first century. The scientists are working toward development of climate-smart crops using the gene and genome engineering/editing tools (DeLisi et al., 2020; Zaidi et al., 2020). However, purslane is a naturally occurring smart crop that operates its machinery smartly (D'Andrea et al., 2014). Due to the presence of C4 and CAM enzymes in purslane, it has become an important model crop for C4-CAM facultative photosynthesis studies. It behaves as a C4 plant when grown under normal conditions whereas it switches to CAM pathway under drought conditions. Since CAM pathway is a highly water-efficient system of photosynthesis, switching into CAM by purslane surely helps it to survive under drought conditions (D'Andrea et al., 2014). Further investigation on the mechanisms governing C4-CAM switching in purslane and the identification of the genes would provide important insights into this important facility used by purslane (Winter and Holtum, 2014). The enzymes that are activated during these situations have been studied (Lara et al., 2003, 2004; D'Andrea et al., 2014, 2015).

Emergency Food During COVID-19-Like Situations

Various indigenous communities rely on traditional food plants including purslane for their nutritional requirements (Kuhnlein and Receveur, 1996; Pieroni et al., 2005; Muthoni and Nyamongo, 2010; Uddin et al., 2014; Pawera et al., 2020). Traditional plants are also used for medicinal purposes in various parts of the world (Mahomoodally et al., 2012; Shikov et al., 2017; Kumar et al., 2019). As discussed, purslane is also one of the most important ethnomedicinal plants among various countries (Ross, 2003; Bosi et al., 2009; Iranshahy et al., 2017). The traditional food plants are regionally very important and local communities rely on them for their nutritional needs. During the coronavirus disease 2019 (COVID-19)-like situations, purslane can be one of the important emergency foods for far-flung areas where food aid is disrupted due to COVID-19-like situations in the future. It is not surprising that COVID-19 has disturbed the global supply chains of the foods, and in the future, such crops can be important for sustaining the communities that lack basic food distribution.

Stress Tolerance in Purslane

The depletion of water resources is one of the biggest challenges to modern agriculture in the world (FAO, 2011). It directly translates to reduced productivity and yields, and if arising in a large-scale agricultural land, would lead to global food insecurity (Falkenmark, 2013; Misra, 2014). Scientists across the globe are putting efforts to devise and innovate strategies to engineer new varieties of crops that can perform well even under extreme conditions such as drought condition (Zhang et al., 2000, 2018; Jewell et al., 2010; Vandenbroucke and Metzlaff, 2013; Jaganathan et al., 2018; Zaidi et al., 2020). Considering the global water shortages, and the susceptibility of the modern crop cultivars to drought conditions, it is highly desirable to discover new crops/varieties that are naturally drought tolerant.

Researchers are putting efforts to use genetic engineering tools to modify currently available crops for increased stress tolerance. Some studies have shown encouraging results, although, not up to the mark. Therefore, the alternative option is to discover naturally occurring stress-tolerant plants that can perform well under stressful conditions. Among all, drought, salinity, heat, and temperature stresses are some of the important abiotic stresses concerning agriculture (Yang et al., 2012; Jin et al., 2015). Drought is also an important environmental stress which limits plant growth and development and affects yields (Ren et al., 2011). Several studies have indicated that purslane is drought tolerant and can easily grow in extreme drought conditions (Ren et al., 2011; Rahdari et al., 2012). Jin et al. (2015) studied drought and heat stress tolerance of purslane and observed significant increase in the malondialdehyde (MDA), proline, electrolyte leakage, reactive oxygen species (ROS), and antioxidant activities and decrease in leaf water content (LWC) and chlorophyll content during the progressive drought treatment. The rehydration following drought stress reversed the negative parameters such as LWC and chlorophyll content. Activation and regulation of various physiological mechanisms makes purslane more efficient to cope up with stress conditions and recover during rehydration (Jin et al., 2015). Earlier study has also shown rapid recovery of purslane plants following dehydration (D'Andrea et al., 2014). Purslane responds to stresses at multiple levels using various mechanisms. One study suggests that switching of CAM pathways enhances the water use efficiency and drought tolerance in purslane (Liu et al., 2018). Differences in the metabolites and the enzymes required during their synthesis in the well-irrigated and drought conditions are also observed, suggesting a biochemical basis of salt tolerance in purslane (Lara et al., 2003, 2004). It also improves its tolerance by enhancing the production of antioxidants, proline content, and heat-shock proteins which are all important for survival under high stress conditions (Yang et al., 2012).

TRADITIONAL FOOD SYSTEMS THAT ARE BASED ON PURSLANE

Traditional food plants are an important part of indigenous diets, and they are produced within the restricted local areas (FAO, 1988). Culturally accepted food patterns evolved from available local resources are referred to as traditional food systems (Kuhnlein and Receveur, 1996). Traditional food systems reflect the culture indigenous communities and their dietary patterns (Trichopoulou et al., 2007). Traditional food plants are healthy, nutritious, and serve as the sustainable food resources for indigenous rural communities (Legwaila et al., 2011). A wide variety of food plants form a part of traditional food systems across the world (Turner et al., 2011). Various studies have reported the use of purslane as an important part of traditional food systems (Welcome and Van Wyk, 2019). It is consumed as a vegetable in a variety of ways across the globe, and the mode of preparation and consumption of purslane varies from region to region. It is used as a raw salad in Turkey, Kufla ka saag in India, and as traditionally processed papads in India (Kapoor et al., 2010; Renu and Waghray, 2016; Borelli et al., 2020). It is also consumed in many other countries and forms a basis for novel traditional foods. **Table 1** presents a summary of traditional food systems that are based on purslane across 18 countries. This table provides information related to its local names, mode of preparation, and consumption.

GENETICS OF PHYTOCHEMICAL, NUTRITIONAL, AND STRESS-RESILIENT TRAITS

Since purslane is known for its medicinal and nutritional properties due to the synthesis of important nutrients and phytochemicals such as alkaloids, flavonoids, catecholamines, lignans, terpenoids, betalains, carotenoids, vitamins, and ω-3-fatty acids (Oliveira et al., 2009; Mulla and Swamy, 2010; Singh et al., 2011; Patil et al., 2012; Petropoulos et al., 2016; Verma et al., 2016; Fernández-Poyatos et al., 2021) and tolerance toward several stresses such as drought, temperature, salinity, moisture, and heat (Ichimura and Suto, 1998; Yazici et al., 2007; Alam et al., 2014b; Jin et al., 2016; Borsai et al., 2020; Xing et al., 2020), it is attaining greater attention (Sultana and Raheman, 2013; Uddin et al., 2014). Many plant-derived secondary metabolites have been used as drugs in modern times as these compounds have specific biological activities (Kumar et al., 2019). It is important to isolate and identify the genes that govern stress-resilient traits and biosynthesis of metabolites. Identification of genes involved in biosynthetic pathways of important metabolites and stress-resilient traits is useful for the trait improvement programs and for the development of superior varieties. Only a few studies have reported the genes regulating important traits in purslane. Among the various phytochemicals synthesized in purslane, dopamine is an important catecholamine with a neuroprotective potential (Chen et al., 2003; Chugh et al., 2019). It is important to identify and characterize the genes that synthesize dopamine. Recently, genes for two enzymes tyrosine decarboxylase and tyrosinase have been identified from hair roots using *A. rhizogenes* (Babashpour et al., 2018). Two genes encoding ω-3 fatty acid desaturases *viz. FAD7* and *FAD8* which are involved in the conversion of linoleic to ω-3-linolenic acid have been identified from purslane (Teixeira et al., 2010). In addition to synthesizing ω-3 fatty acids, purslane also produces ω-6-fatty acids. Du et al. (2021) identified 94 genes involved in the biosynthetic pathway of unsaturated fatty acids. Three genes encoding ω-6 fatty acid desaturases *viz. FAD2-1*, *FAD2-2*, and *FAD-6* have been isolated (Teixeira et al., 2009). *FAD2* genes are plasticidal whereas FAD6 is microsomal. Differential expressions of several genes in response to drought stress and after rewatering have been reported in purslane (D'Andrea et al., 2015). The study showed that three important genes, namely, *Ribosomal protein S15A* (*RPS15A*), *Ribosomal protein L2* (*RPL2*), and *ω-6-fatty acid desaturase 2* (*FAD2*) were induced at higher levels following rewatering/recovery of purslane, suggesting their important roles in imparting stress tolerance. FAD2 and stearoyl-acyl-carrier-protein desaturase (SAD) are also important genes involved in ω-3 fatty acid biosynthesis, and there differential expression is reported in stem and leaves of *P. oleracea* (Du et al., 2021). C4/CAM switching is one of the most important mechanisms reported from purslane in response to the differences in environmental conditions. It uses C4 machinery at normal irrigated conditions whereas it switches to CAM when water scarcity is sensed. The enzymes that are activated during C4 and CAM environmental conditions have been studied (Lara et al., 2003, 2004; D'Andrea et al., 2014, 2015). However, the identification of genes governing C4/CAM switch which enables plants to survive under different environmental conditions would be immensely helpful to manipulate this mechanism in purslanes by genetic engineering.

TABLE 1 | Some traditional food systems based on purslane from different countries.

Sl. No.	Country	Traditional food	Preparation/uniqueness	References
1	Turkey	Salad	Used as salad or side dish.	Borelli et al., 2020
2	Spain	Special soup "sop salem korkat"	Sop salem korkat is made by boiling it with local celery, leek, and citrus and sweet soy sauce.	Tarkergari et al., 2013
3	India	"Kulfa ka saag" and papads	Leaves are cut and boiled by adding salt till it becomes paste. Coriander seeds and red chillies fried in mustard oil mixed with this paste. Experience a bit of sour taste.	Kapoor et al., 2010; Renu and Waghray, 2016
4	Indonesia	Oseng-oseng	Leaves cooked with tamarind, *Oseng-oseng* are prepared by stirring and frying young leaves and tender stems along with shallot, garlic, red chilies, palm sugar, salt, salem leaves, and galangal.	Mishra et al., 2020
5	Sri Lanka	Cooked vegetables	Entire plant of purslane is cooked and used as a vegetable.	Ediriweera, 2010
6	Italy	Salad	Plants are eaten as salads and cooked like spinach.	Bosi et al., 2009
7	Mexico	Snacks and sauces	Rolled in omelets and tortillas and added in soups or stews or flowers, leaves, and stems are steamed and consumed.	Irawan et al., 2003; Manzanero-Medina et al., 2020
8	China	Stir fry, pancakes, soups, and sauces	In South China, tender leaves and stems are eaten as stir fry and in egg pancakes, soup, and sauces.	Xu et al., 2020
9	Bulgaria	Salad and soups	Above-ground parts are used for preparing salad and soups.	Nedelcheva, 2013
10	Australia	Roasted roots, raw leaves, and seed floor.	Roots are eaten after roasting. Leaves and stems are consumed raw or in slightly heated form. Seed flour is used in cakes.	Smith, 1991
11	Armenia	Fries, salads, lacto-fermented foods	Fried aerial parts are eaten or pickled in brine. Young leaves and stems are used in salads. Aerial parts are lacto-fermented	Nanagulyan et al., 2020; Pieroni et al., 2021
12	Albania	Raw fresh parts consumed as such. Leaf used to make drinks.	Drink made from leaf juice mixed with milk and sugar.	Pieroni et al., 2005
13	Georgia	Food (Phkhali)	Leaves are used as delicious food.	Bussmann et al., 2016
14	Tunisia	Flours, sauce, and salads	Leaves and stems are used in sauce and salads and seeds crushed into flours.	Ismail, 2013
15	South Africa	Snacks and vegetables	Stem is used as a vegetable, leaves for snacks and vegetables.	Magwede et al., 2019; Welcome and Van Wyk, 2019
16	Madagascar	Soup/salad	Locals use it as salad or soup.	Beidokhti et al., 2018
17	Benin	Cooked vegetables	Locally used as a green vegetable. In Benin, it is used against rheumatism, gynecological diseases, dysentery, fever, and other infections.	Achigan-Dako et al., 2010
18	Greece	Purslane salad	Raw purslane is mixed with potato slices, onions, tomatoes, green chillies, and oil.	Irawan et al., 2003

IMPROVEMENT OF PURSLANE USING GENOMICS AND GENE-EDITING TOOLS FOR SUPERIOR TRAITS AND URBAN AGRICULTURE

Crop improvement involves strategies for the trait enhancement of the plants for superior characters (Singh et al., 2020). Various strategies including conventional and modern approaches have been used for crop improvement programs (Breseghello and Coelho, 2013). The characterization and identification of diverse germplasm is an important step toward further crop-improvement programs (Ezekwe et al., 1999; Alam et al., 2014b; Egea-Gilabert et al., 2014). Few researchers have attempted and successfully standardized tissue culture protocols and *Agrobacterium*-mediated transformation (Rossi-Hassani et al., 1995; Sedaghati et al., 2019, Sedaghati et al., 2021). Although the advancement of molecular techniques including genomics and other omics technologies enabled the analysis of genomes, proteomes, metabolomes, and ionomes of the crop plants (Salt, 2004; Kumari et al., 2015; Ramalingam et al., 2015), however, such studies are lacking in purslane. The genomics studies in combination with other omics studies such as metabolomics and proteomics will provide useful information about the regulatory networks that contribute to the stress tolerance, diversity of phytochemicals, and other nutritional traits in purslane besides shortening the time required for breeding superior cultivars (Singh et al., 2020). Furthermore, the gene-editing tools can also be exploited for editing the important genes and customization of the purslane cultivars for urban and biosaline agriculture (Abdallah et al., 2015). The purslane improvement studies must focus on traits such as biomass, yield, maturity, flowering, seeds, and stress tolerance (Alam et al., 2014e). Since purslane is highly nutritious orphan crops with a number of superior traits, attempts should be made to decipher its genetic makeup and other regulators such as noncoding RNAs and epigenetic marks using genomics tools. The identification of genes will enable to manipulate and improve desirable traits including enhancement of ω-3-FAs, its CAM pathway, nutritional content, stress tolerance/resistance,

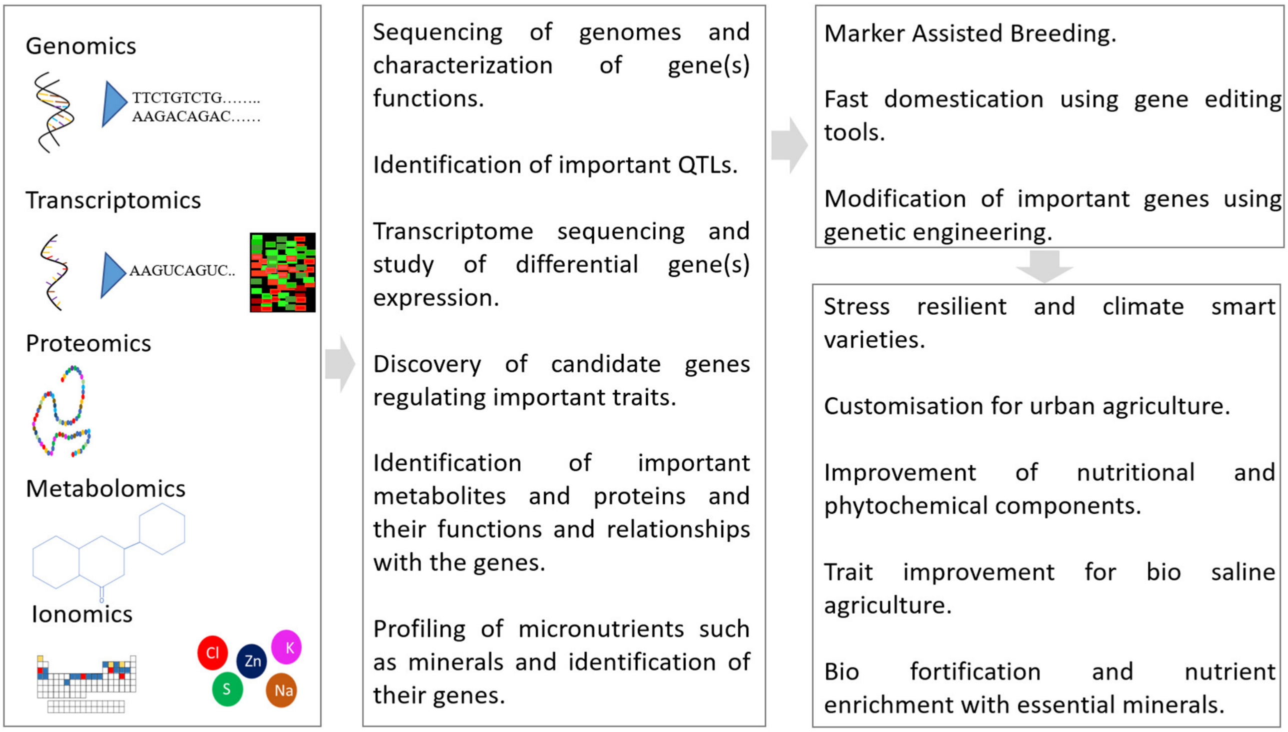

FIGURE 4 | Integrated strategies to improve purslanes using genomics and gene-editing technology.

and other important traits using conventional and modern genome-editing tools. Furthermore, a large-scale profiling of nutrients and essential mineral elements using metabolomics and ionomics and establishing links with their genes would help us to decipher the importance of genetics of these traits. **Figure 4** represents an integrative strategy involving the use of genomics and gene editing for the improvement of purslane.

CHALLENGES TO CULTIVATION AND IMPROVEMENT OF PURSLANE

Purslane is a nutritionally rich traditionally important orphan crop which is not either cultivated or consumed on a large scale. Although it has multiple desirable traits, it has unpalatable taste due to which it is not widely consumed by people. To increase its production and consumption, awareness programs about its health benefits must be conducted. Although wide variation of purslane is reported, detail collection and characterization to identify potential germplasm to be used in crop improvement has not been reported (Ramanatha Rao and Hodgkin, 2002: Alam et al., 2014a, 2015a). The lack of germplasm collections in different gene/germplasm banks across the globe is also one of the reasons why it remained neglected to date. Furthermore, there are very limited genetic and genomics resources of purslane to date. Future attempts should be made to increase germplasm collections; their characterization, phenotyping, and genotyping using various omics techniques should be attempted for purslane to be used in improvement programs.

CONCLUSION AND FUTURE DIRECTIONS

Purslane, being an important traditional crop with multiple health benefits and inherent stress-tolerant mechanism has tremendous potential to be adopted for cultivation during this time of global climate change, salinity, drought, and urbanization-related problems. The climate-smart crops should be able to grow and adapt in stressful environments such as drought, high temperature, and submergence machinery, and these properties are inherently present in purslane. Purslane uses water-efficient CAM pathway for photosynthesis during drought conditions and switches to C4 machinery when the temperature is very high (Simopoulos et al., 1995; Kamil et al., 2000; Ferrari et al., 2020), which is a potential trait for designing climate-smart crop (D'Andrea et al., 2014). Facultative CAM pathway of purslane and C4 metabolism makes it an important crop for water-scarce regions of the world (Welkie and Caldwell, 1970; Koch and Kennedy, 1980; Ocampo et al., 2013; Winter and Holtum, 2014; Liu et al., 2018). Therefore, its cultivation can also be attempted in the drought-prone regions of the world. Furthermore, its salinity-tolerance character makes it fit for biosaline agriculture where freshwater (normal) is not in plenty (Borsai et al., 2018, 2020). However, the mechanisms of salinity tolerance still need to be investigated in detail. The development of transformation protocols is important for gene editing or genetic modification of crops. A research group has standardized and developed an efficient protocol of *Agrobacterium*-mediated transformation in *P. oleracea* (Sedaghati et al., 2019). The induction of hairy root is a key step toward *in vit*ro production of secondary metabolites, and it has been successfully achieved in *P. oleracea* (Moghadam et al., 2014). Therefore, the availability of *Agrobacterium*-mediated transformation protocol may ensure genetic manipulation experiments once the genes governing important traits are identified. Furthermore, other gene editing technologies may also be attempted in purslane for manipulating genes governing important traits. The application of multi-omics high-throughput technologies such as genomics, transcriptomics, metabolomics, proteomics, and ionomics and their integrated analysis would help to identify genes, understand the regulatory mechanism, and help in manipulation of important traits. Lastly, we suggest and recommend for popularizing the cultivation and consumption of traditional orphan food crop purslane in a large scale owing to its high nutrition and health beneficial compound content and easy to cultivate in less space and multiple stress environments.

AUTHOR CONTRIBUTIONS

All authors have directly and significantly contributed to this work and approved the final draft for publication.

ACKNOWLEDGMENTS

The authors would like to acknowledge Aysha Rooby MK, Aryasree M, Arjun Dinesh M, Vaishnav S. Babu, and Somitta Augusthy for contributions to **Figure 2**. AK extends gratitude to the Central University of Kerala for the support during the work.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.