Review

Improving Drought Tolerance in Mungbean (*Vigna radiata* L. Wilczek): Morpho-Physiological, Biochemical and Molecular Perspectives

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Abstract: Drought stress is considered a severe threat to crop production. It adversely affects the morpho-physiological, biochemical and molecular functions of the plants, especially in short duration crops like mungbean. In the past few decades, significant progress has been made towards enhancing climate resilience in legumes through classical and next-generation breeding coupled with omics approaches. Various defence mechanisms have been reported as key players in crop adaptation to drought stress. Many researchers have identified potential donors, QTLs/genes and candidate genes associated to drought tolerance-related traits. However, cloning and exploitation of these loci/gene(s) in breeding programmes are still limited. To bridge the gap between theoretical research and practical breeding, we need to reveal the omics-assisted genetic variations associated with drought tolerance in mungbean to tackle this stress. Furthermore, the use of wild relatives in breeding programmes for drought tolerance is also limited and needs to be focused. Even after six years of decoding the whole genome sequence of mungbean, the genome-wide characterization and expression of various gene families and transcriptional factors are still lacking. Due to the complex nature of drought tolerance, it also requires integrating high throughput multi-omics approaches to increase breeding efficiency and genomic selection for rapid genetic gains to develop drought-tolerant mungbean cultivars. This review highlights the impact of drought stress on mungbean and mitigation strategies for breeding high-yielding drought-tolerant mungbean varieties through classical and modern omics technologies.

Keywords: drought; genome editing; high throuhput trait phenotyping; multi-omics approaches; stress tolerance

1. Introduction

   Mungbean is the third most important grain legume after chickpea and pigeon pea. It is predominantly cultivated across the Asian countries and has also expanded to some parts of Africa, Australia and South America [1,2]. It is a diploid, self-pollinating, fast-growing and short-duration crop and helps in the effective utilization of summer fellows to enhance the cropping intensity and crop production [3]. Mungbean has a wider adaptability and low input requirements [4]. It has a strong root system architecture, which is actively

involved in fixing the atmospheric nitrogen into the soil (about 58–109 kg/ha) via symbiosis with *Rhizobium* [5,6]. Therefore, it plays a vital role in improving soil fertility and sustaining productivity [7,8]. It is an excellent source of vegetable proteins, micro-nutrients and antioxidants like flavonoids and phenolics [9–11] and has multifarious uses as a food [12,13], feed, fodder [14] and green manure crop. Despite being an economically important crop, the productivity of mungbean is stagnant due to erratic weather conditions coupled with various biotic and abiotic stresses [15,16]. Among the abiotic stresses, drought is the most limiting factor for mungbean cultivation that hampers its growth and yield. However, varieties respond deferentially to drought stress as per duration of the stress, crop growth stage and genetic potential of a variety that lead to moderate to severe yield loss [17]. Drought stress affects various morpho-physiological processes associated with growth and molecular functions, which lead to poor grain yield [18–21]. At the initial stage, drought stress affects seed germination and impaired seedling establishment due to affected cell division and cell elongation, leading to poor crop growth [22]. It also limits cell growth due to the function of loss of turgor pressure [23]. Drought stress leads to imbalanced assimilates and decreases sucrose content, ultimately reducing the export rate from source to sink and dry matter partitioning by stress [24]. Zare et al. [25] observed 51% to 85.50% yield reduction due to drought stress in the mungbean. The flowering and the post-flowering stages have been found most sensitive than the vegetative stage in drought [26].

Yield is a complex character, which is highly affected by the genotype and its interaction with environmental factors [3,27–30]. Simultaneously, it also depends upon the expression of different morpho-physiological functions. These morpho-physiological processes are highly affected by drought stress, which exhibit impact on yield. The characters like plant height, leaf size, pod filling index, seed weight, root architecture and crop yield are significantly reduced under the drought stress conditions in mungbean and other legumes [31]. Drought stress also greatly impacts the nutrients up-taken by plant roots system along with water [32,33] due to reduced root growth in drought conditions. Furthermore, symbiotic association plays an important role in nutrient relations of legumes, which also affects the nitrogen-fixing ability and plant growth. Due to interactive effects, the nutrient relations are more complicated; therefore, this requires detailed research at molecular level. Hence, there is an utmost need to develop drought-tolerant varieties to improve crop productivity to ensure farmers' nutritional and livelihood security, especially under the changing climate. The diverse mechanisms such as drought escape, drought avoidance, and drought tolerance are involved in the adoption of drought stress that enables the plants to survive, accumulate dry matter and produce seed [34].

In the last two decades, we moved from "Mendelian era" to the "Omics era", which made several novel omics tools available to us to elucidate the genetics and mechanisms of stress tolerance. DNA and RNA sequencing are no longer constraints as several sequencing platforms are now available. Understanding the gene functions is also possible through these omics and bioinformatics tools [35]. Nair et al. [16] highlighted the effect of various biotic and abiotic constraints and breeding progress made so far. They also emphasized the impact of *RNAi*-technology for improving the stress tolerance in the mungbean and suggested utilizing high throughput phenotyping platforms against particular stress to develop a suitable mitigation strategy. In this review, we summarize the progress made on drought stress tolerance in the mungbean by previous workers and highlight the gaps along with mitigation strategies for future research.

2. Morpho-Physiological Trait Variations for Improving Drought Tolerance

Mungbean is sensitive to drought stress at all the crop growth stages, which hampers the crop yield [2]. However, it is more sensitive at the reproductive stage, which represents a series of events from anthesis to maturity. Drought stress witnessed during any of these critical stages leads to severe yield reduction. Therefore, the selection of genotypes at targeted crop growth stage(s) would be an important measure of drought tolerance (Table 1). Exploring natural variations in germination-related traits under drought stress will offer the

chance to select stress-tolerant genotypes. Polyethylene glycol (PEG) has been frequently used to artificially induce drought stress in various legumes like mungbean [36–38], urdbean [39,40], cowpea [41], pigeon pea [42] and soybean [43]. PEG has a high molecular weight, preventing water from penetrating the cell wall [44]. Dutta and Bera [45] evaluated 15 mungbean genotypes through the application of PEG and reported that the drought tolerance index of the seedlings was a highly stable parameter for screening of genotypes for their response to drought. The significant reduction in tap root length and diameter under drought stress have been reported by Bibi et al. [46] and Ali et al. [47]. This indicated that the root length would be an excellent marker to assess drought tolerance [47,48]. Aslam et al. [49] screened 17 mungbean genotypes for drought tolerance at the seedling stage, and they observed that the early growth proved to be the best selection criteria to tag drought tolerant genotypes. Jincya et al. [50] evaluated 108 greengram genotypes for drought under laboratory conditions using PEG for drought tolerance-related traits at the seedling stage and found the genotypes COGG 1332, VGG 16069, VGG 17003, VGG 17004, VGG 17009, VGG 17019 and VGG 17045 as drought tolerant.

Table 1. Key morpho-physiological traits for improving drought tolerance in mungbean.

Sl. N.	Key Traits	Stage of Tolerance	References
1	Early vigour, relative water content (RWC)	Seedling/vegetative stage	[51]
2	Seedling biomass, stress tolerance index	Seedling stage	[45]
3	Photosynthesis rate, stomatal conductance, transpiration rate, relative leaf water content (RLWC), leaf temperature	Vegetative/reproductive stage	[52]
4	Biomass, harvest index	Reproductive stage	[53]
5	RLWC	Vegetative stage	[54]
6	Root length	Reproductive stage	[26]
7	Number of floral buds, shoot dry weight, number of lateral roots, root length, number of root nodules, dry matter weight of root system	Seedling, vegetative/reproductive stage	[26]
8	Shoot length, root length, root shoot ratio, stem diameter, shoot weight, dead leaf percent, emergence percent, energy of emergence	Seedling stage	[49]
9	Early flowering, specific leaf area	Vegetative/reproductive stage	[55]
10	Yield components	Reproductive stage	[56]
11	Root length, shoot length, root volume, root diameter, root and shoot weight	Vegetative/reproductive stage	[57]
12	Shoot length, root length, number of roots, root diameter	Vegetative/reproductive stage	[58]
13	Survival rate of seedling, wilt index, RWC, stress index	Seedling stage	[59]
14	leaf area, RLWC	Seedling stage	[60]
15	Stomata size, net photosynthesis, osmotic stress injury, Biomass	–	[61]
16	RWC, relative injury (RI), chlorophyll stability index (CSI), specific leaf area (SLA), chlorophyll content	Vegetative/reproductive stage	[56]
17	Germination percent, root length, shoot length	Seedling stage	[62]
18	SPAD chlorophyll meter reading and specific leaf area	Vegetative/reproductive stage	[63]
19	RWC, membrane stability index (MSI)	Vegetative/reproductive stage	[17]
20	Germination percentage, promptness index, radicle length, root length stress index, germination stress index, seed vigour	Seedling stage	[50]
21	Shoot length, biomass, leaf area index, RWC, stomatal conductance	Vegetative/reproductive stage	[64]

Another important aspect for physiological regulation of drought tolerance is water use efficiency, which should be taken into consideration [65]. Physiologically, drought tolerant cultivars have a potential to have higher water use efficiency under drought stress than the susceptible cultivars and produce higher dry matter by the mechanism of low water consumption and low transpiration rate [66]. Leaf wilting and stay green are also

important criteria and should be considered in drought screening experiments that have great significance [67–70]. Gurumurthy et al. [71] evaluated the response of drought stress on morpho-physiological characters of urdbean genotypes at flowering stage and four genotypes PGRU95016, COBG05, IPU99209, IPU941 and IPU243 were found as drought tolerant based on parameters like photosynthesis, stomatal conductance, transpiration rate and total chlorophyll content. This suggests that the crop growth stage and screening techniques should be focused to identify the potential donors.

Exposure to drought stress alters various morpho-physiological functions like change in flowering time, maturity duration, plant architecture, pod number, seed weight, stomatal conductance, relative water content (RWC), leaf and canopy temperature, transpiration rate and chlorophyll content [72,73]. Abiotic stresses also induce anthesis and shorten the reproductive phase in the mungbean [15]. Several kinds of research have demonstrated ample genetic variations among key traits that confer drought tolerance (Table 2). Evaluation of natural genetic variation and drought tolerance-associated traits, including morpho-physiological and adaptive traits, and yield attributes, would help to develop drought-tolerant varieties [74]. The effect of drought stress by extension in irrigation on growth and yield parameters in mungbean has been studied by Tawfik [75], who noticed a significant reduction in fresh weight, dry weight and yield under drought stress. Hossain et al. [76] evaluated 27 mungbean genotypes under drought stress and noticed significant reduction in pod number, days to flowering, plant height, seeds per pod as well as yield per plant. Kumar et al. [58] evaluated some crosses of mungbean along with their parental lines under drought stress. They focused on key characters like shoot length, root length, number of roots and root diameter. Baroowa and Gogoi [77] evaluated the response of mungbean and urdbean genotypes under drought stress imposed at vegetative, early reproductive and pod filling stages, and they found that drought stress had a significant inhibitory impact on all the traits studied. They identified two genotypes *viz.*, T9 and Pratap as drought tolerant with higher extant of drought tolerance index, mean productivity and harvest index. Ranawake et al. [26] screened the mungbean genotypes against drought stress, and results revealed that the water stress significantly affects the flowering and pod filling period. Ghanbari and Javan [78] evaluated thirty mungbean genotypes under drought conditions using multivariate analysis to assess the effect of drought stress on morpho-phenological traits. These parameters could be included in breeding programs for developing drought-tolerant cultivars.

Table 2. Potential donors for drought tolerance in mungbean.

Sl. N.	Drought Tolerant Genotypes	Screening Method	References
1	V 1281, V 2013, V 3372, VC 2754, VC 2768A	–	[79]
2	WGG 2, MGG 347, EC 396117, MGG 350 and Asha, LGG 450	–	[80]
3	VC 2917	Removal of irrigation for 15 days	[59]
4	HUM 1, VMGG 67, VMGG 82, VMGG 83 and VMGG 90	–	[57]
5	ML 267, MGG 347	Drought induced by PEG	[63]
6	K 851	Drought induced by PEG	[60]
7	C. No. 35, OUM 14-1, OUM 49-2, Pusa 9072, OM 99-3, Banapur local B, Nipania munga, Kalamunga 1-A, TCR 20	Drought induced by PEG	[81]
8	AU-M4	Drought induced by PEG	[61]
9	SML-1411, SML 1136	Drought induced by PEG	[62]
10	ML 267	Drought induced by PEG	[63]
11	Pusa 1131	Drought induced by PEG	[82]
12	*Vigna sublobata*, MCV-1, PLM-32, LGG-407, LGG-450, TM-96-2, and Sattya	Removal of irrigation for 15 days	[17]
13	COGG 1332, VGG 16069, VGG 17003, VGG 17004, VGG 17009, VGG 17019 and VGG 17045	Drought induced by PEG	[50]

Stress indices also play a significant role in identifying tolerant genotypes and can be used as selection criteria for improving the crops under stress conditions. To identify

drought-tolerant genotypes, some indices based on a mathematical equation between stress and non-stress conditions have been proposed by earlier workers [83–86]. Hashemzehi et al. [87] carried out a field study using different indices like mean productivity (MP), geometric mean productivity (GMP), stress tolerance index (STI), tolerance index (TOL), stress sensitivity index (SSI), and harmonic mean of productivity (HARM) to identify the terminal drought tolerant genotypes of mungbean. Principal component analysis (PCA) revealed that MP and GMP contributed more than 99% of variations among all indices. The PCA plotting clearly discriminated the drought-tolerant genotypes from the sensitive ones. Another approach, genotype by trait (GT) biplot analysis, was performed by Paramesh et al. [56] with 31 mungbean genotypes for drought-related traits and was noticed as a powerful statistical tool. They identified the genotypes LGG 450, Pusa 9531, LGG 528, Asha, EC 396117 and MH 565 as ideal cultivars that could serve as potential genetic material for developing drought-tolerant mungbean cultivars. Saima et al. [36] evaluated seven mungbean crosses at different levels of drought stress induced by polyethylene glycol (PEG) and calculated different indices such as germination stress tolerance index (GSI), shoot and root weights, root length stress index (RLSI), dry matter stress index (DMSI) and plant height stress index (PHSI). It was reported that the increased level of PEG concentration, resulted in reduced germination percentage, shoot weights, PHSI and DMSI, however, root weights and RLSI were affected positively. Mafakheri et al. [88] also studied drought tolerance indices *viz.*, tolerance index (TOL), mean productivity (MP), geometric mean productivity (GMP), stress susceptibility index (SSI), yield stability index (YSI), yield index (YI), and stress tolerance index (STI) to identify drought resistant varieties of cowpea. As per study reported, STI, MP and GMP indices probably are best for discrimination of drought tolerant and susceptible genotypes. Kumar et al. [89] evaluated various stress tolerance indices to identify heat tolerant promising genotypes of mungbean using eight heat stress indices on the basis of seed yield in normal and heat stress environment. Significant positive correlations were observed among MP, GMP, STI and yield indices. However, these indices are based on seed yield under controlled and stress environments, which might be an effective approach for screening of large panel of the genotypes. Based on morpho-physiological and biochemical traits, some potential donors for drought tolerance in mungbean are presented in Table 2, which might be utilized in generating new variability and further offer the scope for selection of new drought tolerant recombinants.

3. Biochemical Traits Modulating Drought Tolerance

Besides the morpho-physiological traits, drought stress also affects plants' biochemical processes and molecular functions [90,91]. Drought resistance is a complex quantitative trait involving interactions of many metabolic pathways related to stress-resistant genes [92]. It mainly affects the root production as compared to the shoot [26,93]. Alderfasi et al. [94] evaluated two genotypes of mungbean, namely, Kawmay-1 and VC2010 using some of the key components *viz.*, stomata conductance, shoot water content, chlorophyll content and enzymes involved in anti-oxidant photo-protection for drought tolerance. Dutta et al. [60] evaluated 16 mungbean genotypes for seedling stage drought stress tolerance through various morpho-physiological traits, in which K-851 exhibited greater drought tolerance due to outstanding leaf water balance and chlorophyll stability. Chlorophyll florescence technology is a unique and powerful tool for identifying drought-tolerant germplasm [95]. Several plant breeders and physiologists widely used it to measure the photo-oxidative damage, and transpiration and photochemical efficiency, which are useful indicators for drought tolerance [96]. Rahbarian et al. [97] noticed that the genotypes having higher PS-II photochemical efficiency are drought-tolerant, and therefore, it might be used as indicator to tag the drought tolerant genotypes. The vital phenomena of photosynthesis are also highly affected by the drought stress environment [90] by reducing leaf area, leaf senescence and improper functioning of the photosynthetic machinery [98]. It impairs the performance of stress-dependent enzymes, leading to a reduction in dry matter accumulation and seed

yield [99]. Moradi et al. [52] concluded that drought treatments at vegetative and reproductive growth stages negatively affected photosynthesis and gas exchange parameters. They noticed that the stomatal factors were responsible for the decline in assimilation capacity in mild water deficit, whereas non-stomatal factors had a role limiting leaf gas exchange and assimilation capacity under severe drought stress. They concluded that the gas exchange parameters measured during and after water stress treatments seem reliable parameters to evaluate the genotypes for their responses to drought. Bangar et al. [17] evaluated twenty-five mungbean genotypes under drought stress at the vegetative and reproductive stage and noticed a significant decline in RWC, membrane stability index (MSI), proline content of leaves, leaf area plant height and yield.

Biochemical markers, especially proteins and isozymes, play a key role in stress tolerance (Table 3). The role of isozyme systems *viz.* superoxide dismutase (SOD), ascorbate-glutathione (AsA-GSH), ascorbate (AsA), cytosolic ascorbate peroxidase (cAPX), dehydroascorbate reductase (DHAR) were well understood for drought tolerance [100]. The efficacy of these isozymes as biochemical markers for the characterization of mungbean genotypes was reported by Sanghani et al. [101]. Alderfasi et al. [94] noticed the significant increase in antioxidant enzymatic activity of *SOD, catalase (CAT), ascorbate peroxidase (APX) and polyphenol oxidase (PPO)* in water stress condition. It was also evident that the elevated expression of antioxidant enzymes inhibits oxidative damage (*ROS*) due to environmental stress. Ali et al. [40] screened various mungbean genotypes based on the seed germination traits and recorded a significant increase in soluble protein, *malondialdehyde (MDA)*, under drought stress condition. The activities of *CAT, APX, SOD*, total flavonoid content (TFC) and *peroxidase (POD)* were observed with significant increase. In contrast, ascorbic acid (AsA) and TPC decreased due to severe drought stress. These parameters can be used as selection criteria for developing drought tolerant mungbean genotypes. Kumari et al. [61] observed higher proline accumulation and lower osmotic stress injury in mungbean by inducing drought stress. Tawfik [75] noticed a significant increase in osmoprotectants such as total soluble sugars, proline and glycine betaine in plants subjected to water stress.

Table 3. Biochemical responses modulating drought tolerance in mungbean.

Sl. N.	Key Traits	Expression	References
1	H_2O_2	Increased	[102]
2	Glutathione disulphide, GSH, ascorbate peroxidase and glutathione *S*-transferase activities	Increased	[103]
3	Superoxide dismutase (SOD), guaiacol peroxidase (GPOX), ROS	Increased	[82]
4	Cu/Zn superoxide dismutase, oxidoreductase and aldehyde reductase	Increased	[104]
5	Monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and catalase	Decreased	[105]
6	Phenols and ascorbic acid content, H_2O_2	Increased	[60]
7	malondialdehyde (MDA), total soluble sugars (TSS) and proline contents	Increased	[64]
8	Proline content	Decreased	[17]
9	Soluble protein content	Decreased	[64]
10	Globulin seed storage protein	12.8 kD band present in drought tolerant genotypes	[81]

Plant tissues predominantly express the Glycine betaine (GB) under drought stress conditions. It is non-toxic at a higher concentration, raises the osmotic pressure in the cytoplasm and stabilizes the function of various proteins and enzymes. Mungbean does not accumulate *GB*; hence, genetic manipulation of these crop plants with genes responsible for *GB* biosynthesis could be an effective mode for developing stress-tolerant plants. Sai and Chidambaranathan [106] assessed the biochemical response to drought tolerance in the urdbean at the flowering stage. They noticed that drought tolerance was modulated by increased ABA synthesis, proline content and lipid peroxidase activity. However, SDS-

PAGE and mRNA expression analysis during drought indicated differential expression of 23 KDa band protein and 1100 bp mRNA band, respectively. Thus, the identified trait of antioxidant accumulation protects membrane stability and contributes the major share of drought stress tolerance in urdbean. Ghallab et al. [107] observed one unique polymorphic band at molecular weight of 39.66 kDa linked with drought tolerance which could be used for improving drought tolerance in mungbean. Gurumurthy et al. [71] evaluated response of drought stress on urdbean genotypes using biochemical characters in a pot culture experiment. Water stress was created at flowering stage and the genotypes, i.e. PGRU95016, COBG05, IPU99209, IPU941 and IPU243 were identified as tolerant to drought stress based on proline content and peroxidase activity. Therefore, the peroxidase activity can be evidently used as biochemical marker for screening of drought tolerant lines in mungbean as well. The role of exogenous application of *glutathione* (*GSH*) on mungbean seedlings modulates the drought response [103].

The reaction of a plant towards drought stress is an outcome of the expression of regulatory and functional genes [108,109]. However, the knowledge about the insight of stress signals during the initial period is scarce [110]. The common stress signalling pathways have been distinguished into abscisic acid (ABA)-dependent and ABA-independent [111] pathways. Various studies suggested a significant increase in proline content under drought stress conditions, whereas protein content significantly decreased in drought environments [17]. The levels of protein were reported to be reduced because of decrease in nitrate assimilation during stress condition at both, vegetative, as well as reproductive phase in mungbean [92,112]. It is believed that proline acts as an osmolyte and protects the plant against low tissue water potential by osmotic adjustment [113]. High proline with reduced chlorophyll content under water stress have earlier been reported in mungbean [114] and pigeon pea [42]. Fahramand et al. [115] observed the increased proline accumulation in tolerant genotypes than that of other amino acids; therefore, proline can be used as a criterion for screening drought-tolerant varieties. Tripathy et al. [81] detected a specific 12.8 kD protein band responsible for drought tolerance. They recommended such type of polypeptide-based biochemical markers for the identification of drought-tolerant genotypes in mungbean. Further, the role of other protein-based markers *viz. LEA* supergene family [116] and *heat shock proteins* [117] also play a significant role in screening drought-tolerant mungbean lines.

4. Multi-Omics Approaches to Understanding Drought Tolerance

4.1. Genomics Approaches

Understanding the genetics of any trait is very important to any crop improvement programme. As drought stress is a quantitatively inherited trait and is highly influenced by genotype x environment interaction (GEI), it remains a challenge for researchers [118]. Genetic control of drought tolerance-related traits requires integrated approaches to determine the genes/QTLs underlying them at a specific crop growth stage. The stage-specific drought stress-related traits need to be focused upon to improve the drought tolerance. Linkage mapping for QTL detection requires robust drought-tolerant donors. Yuliasti et al. [119] evaluated five mutant lines along with their parents for drought tolerance and found nine SSR-markers *viz.*, MBSS R033; satt137; MBSSR008; MBSSR203; MBSSR013; MBSSR021; MBSSR016; MBSSR136; and DMBSSR013 linked to drought stress tolerance. A recent report by Liu et al. [120] describes the linkage of SSR loci associated with drought tolerance through linkage mapping. They detected two QTLs, *qPHI4.1* and *qPHI4.2* accounting for 7.85% and 21.60% phenotypic variations for each locus. Likewise, two QTLs (*qBMI8.1* and *qPHI8.2*) for drought tolerance index of biomass were mapped on LG08, with each locus accounting for 7.11% and 5.64% of the total phenotypic variations. Nonetheless, very few reports are available on this aspect to our best knowledge, indicating the lack of QTL information for drought tolerance in mungbean. Sholihin et al. [121] identified QTLs for RWC under drought conditions. In contrast, QTL mapping in mungbean for various resistant traits such as resistance to bruchids [122–125], powdery mildew [126,127],

mungbean yellow mosaic virus [128], *mungbean yellow mosaic India virus* [123,129–131] and *Cercospora* leaf spot [132], have been worked out which indicates the efficiency and importance of mapping approach. Despite several studies carried out for biotic stresses, limited information is available for abiotic stress tolerance in the mungbean, therefore requiring more focus.

Although several gene mapping techniques like QTL-hotspot detection, association mapping, nested association mapping, AB-QTL approach have been evolved, the studies on gene mapping for targeted traits for drought tolerance in mungbean are still meagre. Exploring "QTL-hotspot" for drought tolerance could be a milestone for introgression of associated QTLs. Varshney et al. [133] transferred a "QTL-hotspot" for several root and drought tolerance traits through marker-assisted backcrossing into chickpea. Varshney et al. [134] identified a QTL-hotspot region in chickpea that consisted of 13 main-effect QTLs controlling 12 drought-related traits. A similar kind of hot-spot QTL identification and exploitation approach is also needed in mungbean for improving drought tolerance. Furthermore, while earlier workers have reported several QTLs for various traits, only few of them have been characterized, cloned and incorporated in breeding programs [135]. Therefore, to elucidate genetic and molecular mechanisms underlying drought tolerance in mungbean, the identified QTLs need to be cloned and characterized for their effective utilization in a breeding programme.

Genotyping by sequencing (GBS) is one of the most powerful approaches in plant breeding [136,137], which will allow plant breeders to implement GWAS, molecular diversity analysis, linkage analysis, marker discovery and marker-assisted selection [138–143]. GBS has proven to be robust for genotyping and SNP discovery [136,144]. GWAS detects marker–trait associations with higher precision by combining genotypic and phenotypic data on the natural population [145]. Sai et al. [106] prepared the GBS-based linkage map for *MYMIV*-resistance in mungbean. Mathivathana et al. [146] used the genotyping-by-sequencing (GBS) platform to develop the genetic linkage map using an interspecific population of *V. radiata* × *V. umbellata* (mungbean × rice bean), comprising of 538 SNP markers, with an average marker distance of 2.40 cM. Likewise, Schafleitner et al. [125] adopted GBS approach for detecting QTLs for bruchid resistance in mungbean. Noble et al., [147] characterized a mungbean panel consisting of 466 cultivated and 16 wild accessions by conducting a pilot genome-wide association study of seed coat color. Thiel et al. [148] developed SSR markers using MISA tool, which can be used in molecular breeding of mungbean against biotic and abiotic stresses. Jiao et al. [149] performed resequencing of two accessions, namely Salu and AL127, via the Illumina HiSeq 2500 platform (Illumina Technologies) for mapping *lma* locus. Genomic selection (GS) is a novel approach compared to MAS, which combines molecular markers with phenotype and pedigree to increase the breeding accuracy and efficiency of genomics-assisted breeding [136,150,151].

In recent years, phenomics has appeared as a novel approach to enhance the efficiency of breeding programs. Modern plant phenotyping methods help to increase the accuracy, precision and throughput at all levels, which reduce the costs through automation, remote sensing, data integration and experimental design [152]. Many next-generation and high throughput plant phenotyping platforms (HTPPs) have been developed to measure various trait values more precisely through imaging techniques to record complex traits [152–157]. These tools will help in improving the phenotyping efficiently as similar to high-throughput genomics tools [158]. Integration of these high throughput phenomics tools with genomics will accelerate the efficiency of breeding programmes.

4.2. Exploring Gene Families and Transcriptional Factors as Drought-Responsive Markers

Functional genomics has revolutionized our understanding of gene function and gene interaction through genome-wide approaches and planning better strategies for improving tolerance towards abiotic stresses [159]. Modern biotechnology tools like transcriptomic and next-generation sequencing technologies have a great role in identification and cloning drought-responsive candidate genes [142,160], which would provide helpful insights into

the molecular mechanisms of stress tolerance [161,162]. Transcriptome studies under various stresses in *Vigna* species have been performed by several workers [163–165], which are summarized in Table 4. The candidate genes from other model and related crops have been presented in Table S1. RNA-sequencing (RNA-seq) is an efficient tool that has been used for gene discovery, their annotation and development of molecular markers including EST-SSRs [166,167]. Tian et al. [164] suggested the possible role of late embryogenesis abundant (*LEA*) and heat shock proteins (*HSPs*), in drought tolerance in mungbean. In this post-genomics era, *Vigna* species have also been engineered against various abiotic stresses [168]. Many studies have suggested that the transcriptional factors consisting of sequence-specific DNA-binding domains bind to the promoter and/or enhancer of target genes and modulate the stress responses [169]. Wang et al. [170] identified 54 and 50 genome-wide *bZIP* proteins in *V. radiata* and *V. angularis*, respectively. Another TF-superfamily *APETALA2/ethylene-responsive element factor binding proteins (AP2/ERF)* are also known to enhance drought-stress tolerance in plants. The *AP2/ERF* superfamily is classified into different subfamilies such as *AP2, ERF, RAV* (related to *AB13/VP*), *DREB* (*dehydration responsive element binding* proteins). Labbo et al. [171] characterized 71 *AP2/ERF* superfamily in the mungbean genome by comparing *Arabidopsis* as a model system using BLAST and prediction of conserved domains with SMART. Out of 71 genes of *AP2/ERF* TF-families, sixteen *VrDREB* genes were significantly upregulated under drought stress, and proved that these genes participate in pathways leading to drought tolerance in mungbean. Similarly, *WRKY* TFs also have great significance acting as positive, as well as negative regulators of stress responses [172]. Srivastava et al. [173] identified 84 *VaWRKY* genes and 85 *VrWRKY* genes in adzuki bean and mungbean, respectively. Besides, there are numbers of transcription factors like *NAC, BZR*, etc. identified in legumes, although such studies in mungbean are yet to be undertaken. *NAC* have been functionally characterized in common bean [174], chickpea [175] and soybean [176]. These studies revealed that NAC expression enhances plant abiotic stresses and defence responses, such as salt, wound, cold and drought. Another gene family, *Brassinazole-Resistant (BZR)*, is reported as a positive regulator in the biosynthesis of brassinosteroids that are actively involved in organ development and respond to drought and salt stresses [143]. Li et al. [177] worked on the expression profile of receptor for activated C-kinase 1 (RACK1) in soybean, a versatile scaffold protein that binds to numerous proteins to regulate diverse cellular pathways *Arabidopsis*. Their analysis revealed that *GmRACK1* was expressed at different levels in all tissues and was strongly down-regulated in drought stress. Manna et al. [178] recently summarized the drought responsive genes in plants and suggested the role of those genes and transcriptional factors such as *bZIP, DREB, DOF, HSF, MYB, NAC-TF, TCP-TF* and *WRKY* gene families in modulating stress response. The *DREB* and *HSFs* are characterized, whereas many more families need to be characterized for elucidating the possible pathways and signalling channels for improving the drought stress tolerance in mungbean.

Table 4. Potential candidate genes and transcriptional factors conferring drought tolerance in *Vigna* spp.

Sl. N.	Candidate Gene(s)	Test Species	Stress Condition	References
1	*VabZIP6, VabZIP34, VabZIP50, VrbZIP*	*V. angularis*	Drought	[179]
2	*VaWRKY61*	*V. angularis*	Osmotic stress	[173]
3	*VaWRKY16, VaWRKY45, VrWRKY49*	*V. angularis*	Drought	[173]
4	*VrDREB2A*	*V. radiata*	Drought	[180]
5	*VrbZIP17, VrbZIP27, VrbZIP31, VrbZIP50*	*V. radiata*	Drought	[179]
6	*VrDREB5, VrDREB12, VrDREB13, VrDREB22, VrDREB30*	*V. radiata*	Drought	[171]
7	*VrWRKY73*	*V. radiata*	Osmotic stress	[173]
8	*VrSKP1*	*V. radiata*	Drought	[181]
9	*VrHsfA6a, VrHsfA6b*	*V. radiata*	Drought	[182]

Among different pathways of *GB* synthesis, the most suitable target for metabolic engineering of *GB* is the *COD* pathway that changes choline into *GB* in a single step because of their involvement in the transfer of a single gene *codA*. This study signifies the role of the GB-biosynthetic pathway as accomplished by *codA* gene encoding for choline oxidase for improving stress tolerance in mungbean. It needs hours to accelerate research in the field of molecular biology toward identifying and characterizing different keys gene, which have metabolic or regulatory roles [159,168]. In view of the facts, it is evident that in comparison to other legumes, the genetic and molecular information is still lagging behind. Therefore, an in-depth research is required on identification and characterization of genes involved in detoxification, osmolyte bio-synthesis, proteolysis of cellular substrates, water channel, ion transporter, *heat shock protein (HSP)* and *late embryogenesis abundant (LEA)* protein along with regulatory mechanisms primarily comprising of TFs, signalling protein kinases and protein phosphatases, which synchronize signal transduction and expression of genes during stress responses and that contribute toward drought stress response. Surprisingly, even after more than six years of genome sequencing of mungbean, very little progress has been made in characterizing gene families, which needs to be expedited (Figure 1).
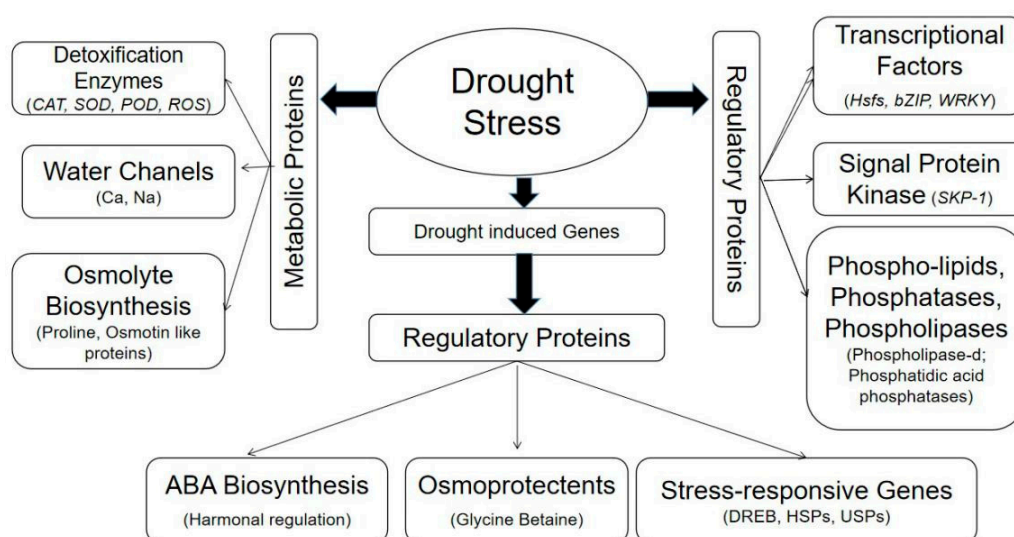

Figure 1. Biochemical and molecular response of plants activated during drought stress.

The candidate genes discovered in grain legumes until date are understood to ameliorate drought stress resistance through enhancing the extent of well suited solutes like proline, starch, sugars and many others, consequently providing cellular osmotic adjustment, stabilization of membrane integrity and various enzymes/proteins and ROS detoxification [183]. Drought stress-responsive candidate genes have been reported in many grain legumes such as chickpea, common bean, soybean, cowpea and pigeon pea [184,185]. However, isolation of such candidate genes has not been reported from mungbean till date [186]. Chen et al. [180] suggested that heterologous expression of *VrDREB2A* isolated from mungbean led to an increased expression of *DREB2A* target, stress-inducible genes and ameliorated salt and drought stress tolerance of transgenic *Arabidopsis*, which provides a useful tool. Bharadwaj et al. [181] cloned a stress-responsive candidate gene *SKP1* from mungbean. Stable transformation and expression of transgene (*codA* gene) for an osmoprotectant glycine betaine have also been achieved in mungbean through *Agrobacterium* mediated transformation system to improve the drought tolerance response [187]. Since drought stress is a quantitatively inherited trait, engineering crop for single gene integration is practically not feasible. In such conditions, engineering of TFs can affect the expression of many genes simultaneously, which will be a more effective approach and therefore, needs to be given a focussed attention.

4.3. The Role of Long Non-Coding RNA (lncRNAs) and Micro-RNA (miRNAs) in Drought Stress

Considerable progress has been made in the high-throughput sequencing of small RNA libraries than the large-scale identification of non-coding RNA molecules, which has expanded the scope in the era of RNA sequencing [188,189]. It plays an important role in regulating various biological processes, including genome integrity maintenance, and developmental, metabolic and adaptive responses toward environmental stresses [190]. Long noncoding RNAs are the long nucleotide sequence of RNA (~200 nt) without or with less protein-coding potential [191], which serve as precursors of miRNAs and other small RNAs [192]. MicroRNAs (miRNAs) are short (~21-nucleotide), non-coding RNA molecules that play important role in post-transcriptional gene silencing and or translational modification. Evidence suggests the role of long noncoding RNAs (lncRNAs) that modulate the drought stress response in plants [193–195] and are believed to regulate the transcriptional modification of drought-responsive genes [196,197]. The drought-responsive lncRNAs have also been reported in various plant species namely *Arabidopsis* [198], tomato [199], rice [200] and maize [201]. Likewise, Barrera-Figueroa et al., [202] identified 44 drought-responsive miRNAs in cowpea which encode zinc finger family protein, serine/threonine-protein kinase and kelch containing F-box protein. Wu et al. [203] obtained 16 drought-responsive miRNAs and the corresponding target genes related to TFs and protein kinases in common beans. Paul and Pal [204] identified 56 potentially conserved microRNAs and 88 potential miRNA target transcripts belonging to 28 families, in which 3 miRNAs *viz.*, vra-miR160a, vra-miR162b and vra-miR398b were validated. These predicted transcripts were found to be involved in different development, metabolism and stress responses. A literature survey indicated that only a few reports are available about lncRNAs and miRNAs in mungbean, which need to be explored. It provides a unique strategy for modulating differential gene expression under drought stress, thus emerging as the next-generation genetic engineering target for mungbean improvement. It also will facilitate in designing suitable strategies for enhancing drought tolerance with minimum trade-offs in mungbean. Another strategy is use of artificial miRNAs (amiRNAs) to suppress expression of a protein-coding mRNA of interest of target gene [205]. These strategies of integrating multi-omics approaches (Figure 2) will help in improving the breeding efficiency and developing climate smart drought tolerant mungbean cultivars.
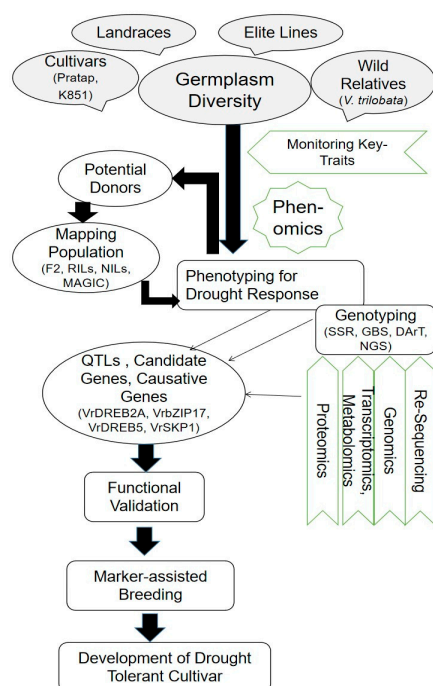
Figure 2. Integrated "omics" approaches for development of drought tolerant mungbean genotypes.

5. Conclusions and Future Prospects

Drought stress affects mungbean at different growth stages with varying severity, which leads to moderate to severe yield loss. A rise in drought incidence and severity is expected in the coming years due to the changing global climate. Hence, there is a need to develop climate-smart mungbean cultivars, which perform better in drought environments. The above discussion clearly stated the involvement of different mechanisms towards drought tolerance at different crop growth stages. Therefore, specific breeding strategies need to be focused upon for improving drought tolerance, while identification and deployment of stage-specific drought-tolerant potential donors are required. Progress made in the insights of mechanisms underlying the physiological and biochemical basis of drought tolerance may also allow for more efficient antioxidants to enhance yield potential and resilience. There is also an urgent need to identify and validate the genes/QTLs/loci from potential intra- and inter-specific donors. Once these genes/QTLs have been tagged, their pyramiding will be the best mitigation strategy. Sometimes, the tracking of previously reported QTLs for stage-specific tolerance may pose an additional challenge, maybe due to the use of different drought-tolerant donors, as well as the screening methods that have been adopted. Like the QTL mapping approach through linkage and association mapping, classical and omics-based breeding approaches have shed light on the inheritance of complex traits like drought. Nonetheless, recent advances in omics technologies offer better opportunities to assess and broaden the genetic base of the gene pool and introduce the valuable QTLs from new sources. The cross-specific genomic resources can also be effectively employed in tagging and mapping of novel QTLs for improving drought tolerance. Furthermore, rising "omics" interventions could substantially improve our present knowledge of the underlying mechanism of drought-tolerance, assisting in development and deploying drought-tolerant mungbean genotypes. Simultaneously, there is a need to enhance the efficiency of the various high-throughput genotyping platforms like GBS, DArT, etc., which might pave the way to discovering high-throughput markers to look for novel genomic variants related to drought tolerance. Characterizing gene families and their expression profiling will also explain the mechanism and novel pathways involved in drought tolerance. The limited gene-families associated with drought tolerance have been characterized in mungbean in the post-genome sequencing era, which need be explored. Implementing genome editing tools for engineering TFs can target the multi-gene expression, facilitating in tapping new insights in stress response. Exploring untapped novel adoptive traits to drought stress from various gene pools and their precise introgression into promising genotypes is urgently required through marker-assisted breeding and other advanced breeding approaches. Harnessing the capabilities of *Vigna* gene pools extensively through omics approaches coupled with advanced techniques, *viz.*, HTPPs, genetic engineering and speed breeding, will facilitate deeper understanding and could effectively accelerate the development of drought-tolerant mungbean cultivars.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/agronomy11081534/s1, Table S1: Potential candidate genes and transcriptional factors conferring drought tolerance in other model plants.

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