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Building a better Mungbean: Breeding for reproductive resilience in a changing climate

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Abstract

Mungbean (*Vigna radiata* (L.) R. Wilczek var. *radiata*) is a significant food and cash crop grown in tropical and subtropical regions. Mungbean production and consumer demand have increased substantially over the last two decades, owing to its agronomic, nutritional and economic benefits. Despite increased breeding efforts and the expansion of mungbean production in various agro-climatic regions, further production is hindered by low yield and variability, which is partly attributed to the impacts of abiotic stress. Abiotic stress impacts on the physiology, morphology and reproductive ability of mungbean which influences yield. Exposure to abiotic stresses at the reproductive stage is considered the most critical for yield production. In this review, we evaluate how abiotic stress impacts mungbean growth and productivity when occurring during the reproductive stage and traits that may confer adaptation. We present the limitations of current research including limited number of genotypes, lack of field experiments and detailed experimental information. We highlight the opportunities to exploit new tools and technologies, such as high-throughput phenotyping platforms, gene editing, and genomic selection, to accelerate breeding efforts to develop more resilient mungbean cultivars for today and tomorrow.

KEYWORDS

abiotic stress, breeding, drought, heat, physiology, *Vigna radiata*

1 | INTRODUCTION

Mungbean (*Vigna radiata* (L.) R. Wilczek var *radiata*), also known as green gram or moong, is an important food and cash crop grown in tropical and subtropical regions (Kim et al., 2015). Mungbean seed is a rich source of easily digestible dietary protein, minerals and vitamins that can aid in supplementing and diversifying cereal-based diets (Hou et al., 2019). Mungbean has become an important choice for double and intercropping systems, particularly between cereals, due to its short growing season (e.g., 55–100 days depending on cultivar and season) and ability to fix atmospheric nitrogen ($58–109 \, kg^{-1} ha^{-1}$) to improve overall soil fertility (Ilyas et al., 2018; Yaqub et al., 2010).

Mungbean has a diverse market and is consumed in a variety of ways around the world, some of which require specific grain quality properties. For example, in East and Southeast Asia, mungbean dry grains are used for dahl, the sprouts are used for garnishing, and it is also processed to make transparent noodles. Whereas in East African countries, mungbean is typically consumed as a key ingredient in beef stew (Nair et al., 2020; Sequeros et al., 2021).

The agronomic, nutritional and economic benefits of mungbean are becoming more apparent globally, thus production and consumer demand has increased substantially over the past two decades (Kim et al., 2015). Mungbean is currently grown across a range of latitudes and seasons and the production area now exceeds 6 million hectares (ha) globally (Chauhan & Williams, 2018). The majority of mungbean production occurs in Southeast Asia, with the top producers, India and Myanmar, producing 1.6 million tonnes (Mt) and 1.597 Mt respectively (Nair et al., 2020). Other major regions producing mungbean now include East Africa and Australia (Figure 1).

Despite increased research and development efforts, further expansion of mungbean production is expected to be limited due to low average yield and poor yield stability (Tripathi et al., 2020; Yimram et al., 2009). Currently, the average production of mungbean globally varies from $<1–1.5 \, t \, ha^{-1}$ depending on the growing conditions (Nair et al., 2020; Sequeros et al., 2021), which is substantially lower than yield recorded in research plots (Chauhan et al., 2017; Rachaputi et al., 2019) and predicted yield from crop models such as the Agricultural Production Systems sIMulator (APSIM) (Chauhan & Williams, 2018; Geetika, Hammer, et al., 2022).

Over the past decade, substantial efforts have been made to develop improved cultivars. Most crop improvement to date has focused on establishing biotic tolerance and increasing yield potential (Nair et al., 2020). However, agricultural losses worldwide are also caused by abiotic stress, which negatively impacts crop growth and productivity through biochemical and physiological changes. Climate change is exacerbating this issue by increasing climatic variability and the frequency of extreme weather events (Jägermeyr et al., 2021). Consequently, there is an urgent need to improve abiotic stress tolerance and enhance yield stability in mungbean.

Abiotic stress, such as drought and heat, can have a detrimental effect on the physiology, morphology and reproductive ability of mungbean, thus impacting yield and grain quality. While a crop can experience abiotic stress
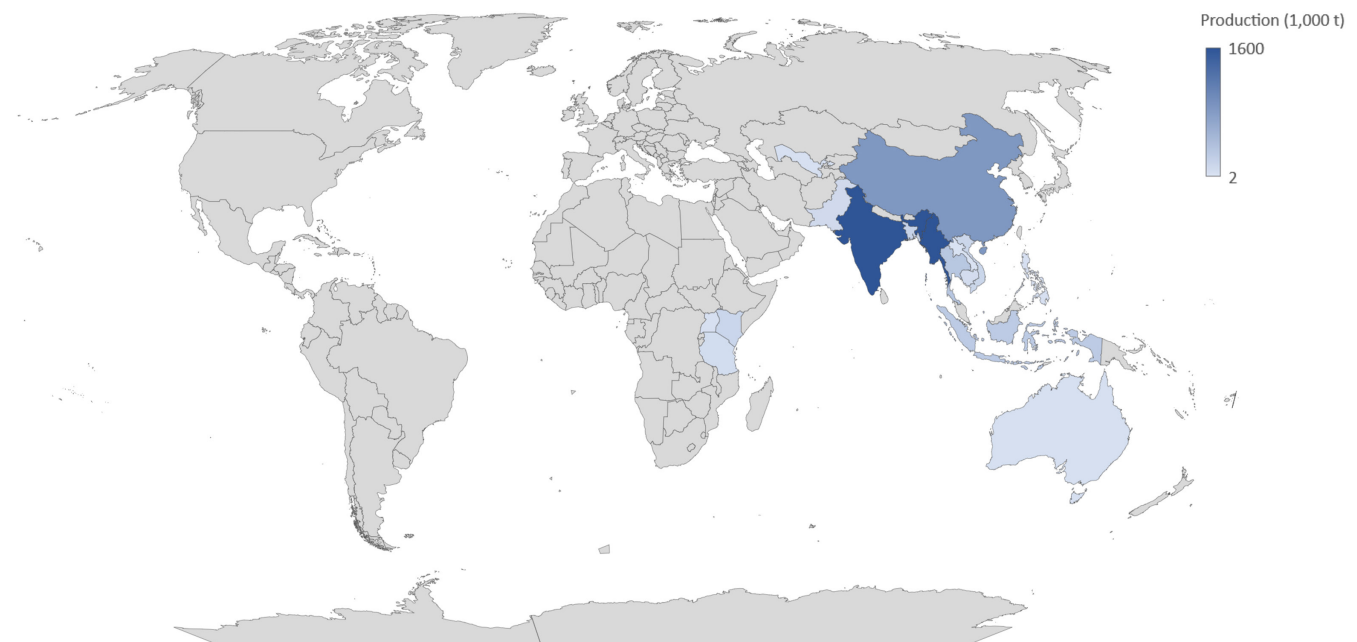

FIGURE 1 Global mungbean production.
Data source: Nair et al. (2020).

at any growth stage, mungbean is particularly vulnerable at the reproductive stage (De Costa et al., 1999; Hanif & Wahid, 2018).

A comprehensive understanding of the impact of abiotic stress on growth during reproductive development, as well as the key adaptive mechanisms, is essential for informing management strategies and improving the adaptation of new cultivars. Genetic improvement through breeding offers the potential to target traits associated with adaptation or tolerance to abiotic stress during the reproductive stage. By gaining a deeper understanding of how stress influences growth at this critical stage, along with the underlying adaptive mechanisms, we can enhance the effectiveness and efficiency of selection in breeding programs. This review highlights the major abiotic stress specifically; heat stress, cold stress, drought, waterlogging and salinity that impact mungbean during the reproductive stage from a physiological perspective. We also demonstrate the importance of applying new tools and technologies to accelerate the development of future mungbean crops with enhanced climate resilience.

2 | MUNGBEAN DEVELOPMENT

Cultivated mungbean is a short duration crop that matures within 60–110 days after sowing (DAS) depending on the cultivar and environmental conditions (Gentry, 2010). Studies underpinning the development of the mungbean crop growth model have proposed nine distinct phenological phases (Chauhan et al., 2010; Robertson et al., 2002). These phenological phases are (i) sowing to emergence, (ii) emergence to the end of juvenile period (basic vegetation), (iii) floral initiation, (iv) first flower, (v) start of pod filling and (vi) physiological maturity (Figure 2). These stages are utilised in the current APSIM mungbean model (Holzworth et al., 2018). However, due to the indeterminate nature of many mungbean cultivars, there is often an overlap between

the vegetative and reproductive development phases (Bushby & Lawn, 1992; Mondal, Fakir, et al., 2011).

The dominant drivers that influence development are temperature and photoperiod. Temperature accelerates the rate of all phenological phases with mungbean having a base temperature (T_b) of 7.5°C, an optimum temperature (T_{opt}) of 30°C and a maximum temperature of 40°C (T_{max}). Temperatures outside the base and maximum temperatures will cease mungbean development (Chauhan & Williams, 2018; Poehlman, 1991). However, as mungbean reaches the reproductive phase, particularly floral initiation, the crop becomes sensitive to both photoperiod and temperature. Lengthening of photoperiod typically results in prolonged vegetative growth and delayed flowering and maturity (Rebetzke & Lawn, 2006). Some genotypes are highly photoperiod sensitive and will not commence flowering under increased photoperiod conditions (Vas Aggarwal & Poehlman, 1977). Sensitivity to photoperiod and temperature influences the development of mungbean sown at different times and in different regions globally. Further understanding of the role of photoperiod and temperature on mungbean flowering behaviour is required to optimise sowing windows to successfully avoid abiotic stress which can be a useful strategy for drought and heat stress (Yadav et al., 2022).

Reproductive development in mungbean occurs from the initiation of flowering until physiological maturity and these stages play a critical role in yield formation (Figure 2). During this period, resources are directed from vegetative to reproductive organs such as flowers and pods (Cohen, 1976). Mungbean typically has an indeterminant growth habit as accumulation of vegetative biomass (both root and shoot) and development of flowers and pods occurs simultaneously (Fakir et al., 2011; Wang et al., 2020). Recent research on Australian mungbean cultivars demonstrated that canopy development ceases at the mid-pod fill stage when pods transition to be the dominant sinks (Geetika, Collins, et al., 2022), highlighting the importance of source-sink dynamics in yield development (Smith et al., 2018).
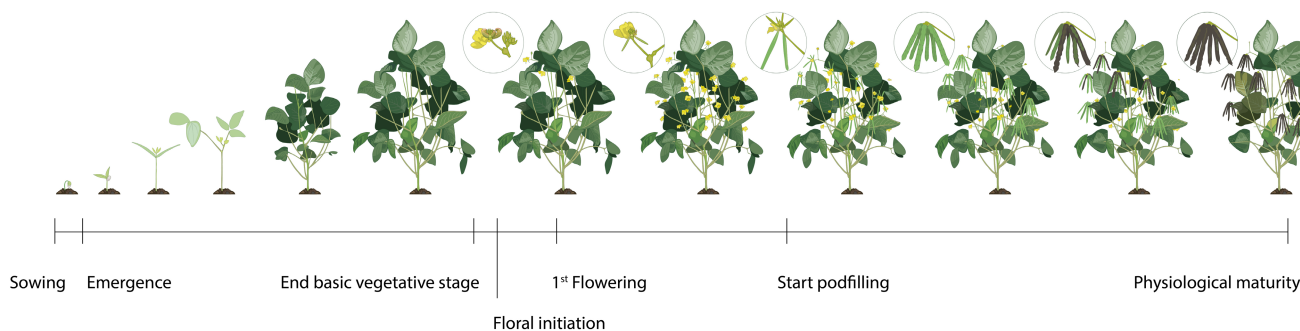

Sowing   Emergence   End basic vegetative stage   1ˢᵗ Flowering   Start podfilling   Physiological maturity

Floral initiation

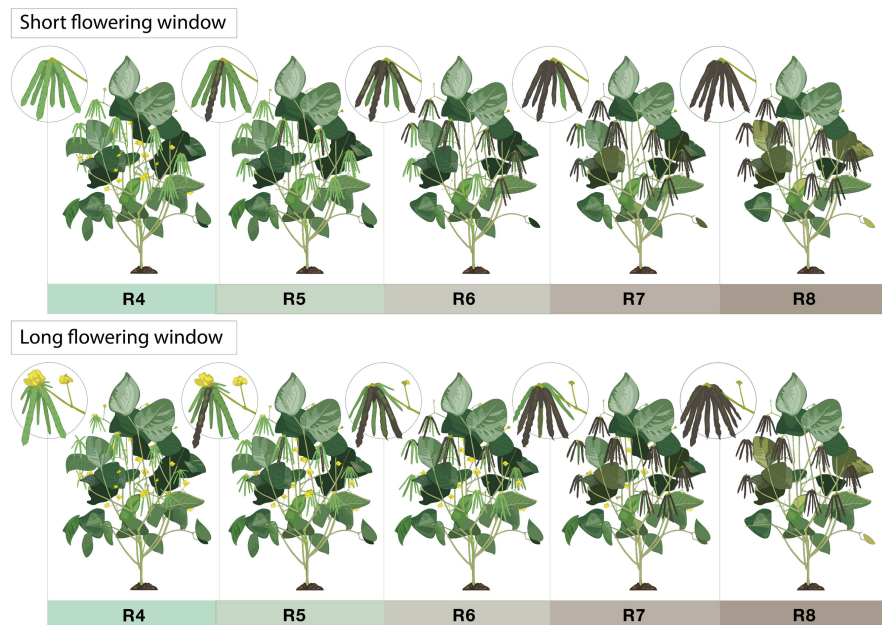**FIGURE 2**   The developmental stages of mungbean.

FIGURE 3 Reproductive stages for mungbean genotypes differing in flowering duration.

Some mungbean accessions may exhibit an extended flowering duration which can involve multiple flowering flushes occurring in close succession (Figure 3). Multiple field studies have determined that an extended flowering duration is associated with increased flower number and yield (Mondal, Fakir, Prodhan, et al., 2011; Mondal, Hakin, et al., 2011). However, a long flowering window leads to staggered pod maturity and pods that are produced in multiple flushes, which is an unfavourable trait for large-scale mechanical harvesting systems (Ha & Lee, 2019). Additionally, pods formed during second and later flushes tend to contribute less to yield compared to those produced during the first flush (Mondal, Fakir, Prodhan, et al., 2011). With staggered maturity, pods formed earlier are vulnerable to pests and are more likely to shatter, which can result in major yield loss (Gentry, 2010). As in other legumes, the probability of floral and pod development may be dependent on the timing of development and nodal position that the cluster forms (Weller & Ortega, 2015). Further research on the role of abiotic stress on flowering and pod abscission is required to determine the impact on individual reproductive components based on timing and location on the plant with greater accuracy.

3 | ABIOTIC STRESSES IMPACTING MUNGBEAN AT THE REPRODUCTIVE STAGE

At a global scale, the main abiotic stresses that are limiting mungbean productivity are related to high and low temperatures, drought, waterlogging and salinity (Chauhan & Williams, 2018). This section describes the impact of abiotic stress at the reproductive stage and in cases where limited research is available, we refer to successful research conducted in other crops to highlight traits that may be studied to improve adaptation in mungbean.

3.1 | Heat stress

Mungbean is produced in regions with relatively warm climates (Chauhan et al., 2010). Despite this, heat stress caused by a period of very high temperatures (e.g., >40°C) during flowering and pod development can dramatically impact growth and productivity and frequently occurs across production regions (Rachaputi et al., 2019). Heat stress directly affects flower and pod development. Depending on the timing and severity of heat stress, the consequence on yield components, such as pod set plant^{-1}, total pods plant^{-1} and total seeds plant^{-1}, can reduce yield by 10%–80% (Hanif & Wahid, 2018; Sharma et al., 2016).

Under ideal conditions, mungbean plants produce flowers prolifically, but only a small portion set pods (Mondal, Hakin, et al., 2011). This is a result of high levels of floral abscission (70%–90%; Kumari & Varma, 1983) similar to other sub-tropical legume crops such as soybean (60%–92%; Heindl & Brun, 1984; Saitoh et al., 2004) and pigeon pea (70%–96%; Rahman et al., 2011; Togun & Tayo, 1990). Abscission of reproductive organs under heat stress is common in grain legumes (Rainey & Griffiths, 2005). Under high temperatures, flower abscission is further amplified which makes it a key driver of yield under heat stress (Khattak et al., 2009; Tickoo et al., 1996). If heat stress occurs during pod development it can also

cause pod abortion and significantly reduce pod filling (HanumanthaRao et al., 2016; Tzudir et al., 2014) with high rates of pod abortion and reductions in grain fill reported under heat stress in mungbean (Kaur et al., 2015).

Abscission is likely caused by damage to the stigma or ovaries, or to pollen viability which leads to infertility. Patriyawaty et al. (2018) found that exposing mungbean to 45°C for 10 days at flowering reduced pollen viability by up to 60%, which could be a result of reduced pollen size and distorted pollen grains. High temperatures can also distort the length and size of pollen tubes which are critical for delivering sperm cells to the female gametophyte (Basu et al., 2019). Similar findings were reported by Kaur et al. (2015) with lower pollen load and stigma receptivity found in cultivars that experienced heat stress.

Canopy development can also be substantially impacted by high temperature at the reproductive stage. Owing to the indeterminate growth habit exhibited in some genotypes, high temperatures during the reproductive phase may inhibit vegetative growth and maintenance. A reduction in canopy biomass in mungbean may be linked to the impact of heat stress on photosynthetic machinery including reductions in chlorophyll fluorescence (20%; Priya et al., 2019), reduction in chlorophyll content (11%–65%; Chand et al., 2018; Hanif & Wahid, 2018), reduction in stomatal conductance (Hanif & Wahid, 2018; Patriyawaty et al., 2018; Priya et al., 2019) and limitation to synthesis and transport of sucrose (Awasthi et al., 2014). In a recent study, RuBisCO activity was 40% lower in mungbean grown under heat stress, which was likely a result of lower stomatal conductance or decreased rates of RuBP regeneration (Priya et al., 2019). Impacts are further aggravated by leaf scorching, chlorosis, wilting and premature senescence of leaves (Priya et al., 2019; Sharma et al., 2016).

Furthermore, as mungbean phenological development is largely driven by temperature (Chauhan et al., 2010), high temperature can lead to an acceleration of flowering time and shortened flowering duration (Sharma & Dhanda, 2014; Sharma et al., 2016). In some scenarios, a hastening of flowering initiation and duration can lead to yield penalties as it can reduce the duration of vegetation growth limiting assimilate supply to support pod development as well as reducing overall duration for pod initiation and maturity (Basu et al., 2019).

Heat stress is a major threat to production in many crops, leading to a wealth of literature highlighting traits of interest to improve adaptation. Manipulating or reducing phenological development, for instance, by adjusting sowing time, is a successful strategy that enables the crop to avoid heat stress during the critical reproductive period (Yadav et al., 2022). A recent multi-environment study evaluating 80 mungbean genotypes across three agro-ecological zones in Pakistan identified days to flowering,

maturity and seeds per pod as key traits influencing yield under heat stress at the flowering stage (Iqbal et al., 2021). These findings suggest that early maturing genotypes performed best under heat stress conditions. Given similar results have been found in other pulse crops (Devasirvatham & Tan, 2018; Vargas et al., 2021) determining optimal sowing windows to avoid heat stress during the critical period is worthy of further investigation in mungbean.

Optimising root architecture may be another strategy to improve heat tolerance. A 2018 study found that heat tolerant mungbean cultivars had 120% higher root biomass compared to highly susceptible cultivars, which could have supported these genotypes in displaying more favourable water use mechanisms thus supporting shoot growth (Patriyawaty et al., 2018). This highlights the potential to explore the role of roots which may improve access to water in the soil profile (Voss-Fels et al., 2018) during critical periods and enable the crop to reduce yield losses, particularly when heat stress coincides with water stress.

Heat stress is one of the major abiotic stresses that mungbean is exposed to, particularly during reproductive development. The importance of heat stress in mungbean is evident by the number of studies in this area in comparison to the other stresses within this review. Additionally, most of these studies evaluated a large number of genotypes, with few looking at less than five genotypes. This has enabled researchers to identify potential traits of interests to confer adaptation as well as the identification of tolerant genotypes. The vast majority of studies have evaluated heat stress within field conditions, which has confounding effects due to a lack of control of vapour pressure deficit. While these field studies are of immense value, to the best of our knowledge, there has been no investigation of the role of vapour pressure deficit in mungbean. Furthermore, few studies have investigated the impact of heat stress on physiological traits (such as photosynthetic capacity, stomatal conductance) and morphology which would be most accurately examined under controlled environmental conditions. Further evaluation of the timing of heat stress over both the day and night should also be examined as preliminary investigations have suggested a reduction in yield components as a consequence of elevated day and night temperatures (Williams et al., 2022).

3.2 | Cold stress

When growing mungbean outside of its typical region or sowing time, low temperatures can reduce growth and yield. There is limited research on how low temperatures impact yield when exposed at the reproductive stage (Hu et al., 2022). In some environments, such as the northern

grains region in Australia, planting mungbean late may risk exposure to frost during the reproductive stage which may cause plant death, reduce grain quality or yield, particularly when immature pods are exposed (Gentry, 2010). A recent greenhouse study by Hu et al. (2022) in northern China evaluated two mungbean varieties for short-term and prolonged exposure (1–4 days) to cold (15°C) at flowering. Both short- and long-term cold exposure led to decreased yield through a reduction in chlorophyll content and yield components, however, more substantial effects were observed when plants were exposed for longer periods including the downregulation of chlorophyll biosynthesis and leaf cuticle lipid synthesis genes. This highlights a potential mechanism that may be further investigated for improvement of cold tolerance in mungbean. Although it is important to note that the study explored tolerance in only two genotypes in a controlled environment so further studies using genetically diverse material, ideally within the field, are required.

In field pea, it has been observed that frost tolerance is linked to flowering time, where genes associated with delayed flowering were co-located with genes that were upregulated in cold temperature (Lejeune-Hénaut et al., 2008). Similar findings have been observed in wheat and barley (Galiba et al., 2009). As mungbean is typically planted in spring or summer, earlier flowering genotypes are more likely to avoid frost as reproductive development occurs in a time period that reduces the overall risk. With growing interest in expanding mungbean production outside of traditional sub-tropical growing regions and sowing times in Australia, further investigation of the effects of cold stress on growth and productivity, as well as potential tolerance traits, will be required (Christy et al., 2022).

Currently there is limited research evaluating the impact of cold stress on mungbean development when occurring at the reproductive stage. The study available for chilling tolerance in mungbean performed by Hu et al. (2022) had the primary objective to evaluate the application of Uniconazole (UNZ) to improve cold stress tolerance. Further studies are required to evaluate cold stress under different treatments and from a physiological perspective to gain a deeper understanding of how cold stress impacts growth and development and to identify the developmental stage most impacted by this stress. Evaluation of a broader, diverse set of germplasm will enable researchers to identify potential traits of interest that could be incorporated into breeding programs for cold tolerance.

3.3 | Drought stress

Drought frequently affects mungbean production as most crops are grown in rainfed agricultural systems (Sivaji et al., 2021). As a result, the majority of original research articles investigating abiotic stress at reproductive development are focussed on drought, as yield is substantially impacted by water deficit at flowering and pod development stages (Sadeghipour, 2009; Uprety & Bhatia, 1989). For instance, drought can reduce yield by 20%–45% at the vegetative stage compared to 30%–100% at the reproductive stage (De Costa et al., 1999; Hamid et al., 1990; Uprety & Bhatia, 1989). However, Bangar et al. (2019) reported conflicting results with the vegetative stage proving to be more susceptible to drought stress as sufficient above-ground biomass was not accumulated prior to flowering inhibiting yield development. This reinforces the overall importance of canopy development for yield formation in mungbean (Geetika, Hammer, et al., 2022).

In mungbean, water stress results in decreased leaf water potential and can reduce photosynthesis due to the degradation of chlorophyll and stomatal closure (Baroowa et al., 2016). Reduced stomatal conductance limits transpiration, and mungbean typically has a high transpiration rate at flowering. Recovery following a water deficit is possible in mungbean with one study identifying a resumption of photosynthesis and stomatal conductance following drought, although a significant yield reduction was observed (Hamid et al., 1990).

Reduced canopy development is another major effect of drought stress with a substantial reduction in leaf area and plant height (Baroowa & Gogoi, 2015; El-Nakhlawy et al., 2018). Reduction in canopy size is an important mechanism to moderate water use and decrease cell injury during water stress (Basu et al., 2016). However, a smaller canopy size leads to reduced radiation interception which is required to support yield development (De Costa & Shanmugathasan, 1999; Geetika, Hammer, et al., 2022) and maintenance of leaf area under drought has been identified as a trait of interest in mungbean (Hamid et al., 1990).

Plants have evolved numerous adaptive mechanisms that enable them to be successful in drought environments. One strategy that plants use to limit water loss in response to decreased water potential is effective stomatal control, which is a key physiological trait evaluated in drought studies (Bennett et al., 1987). An Indian field study observed that the drought tolerant genotype Pratap maintained higher leaf water potential under drought conditions, which contributed to higher yield (Baroowa et al., 2016). Canopy temperature in the field is also a useful tool to evaluate drought adaptation with a relationship between canopy temperature and yield reported in many crops (Karimizadeh & Mohammadi, 2011; Ninanya et al., 2021). However, in mungbean a recent field study did not find a relationship between canopy temperate and yield, instead identifying several tolerant lines that were

able to maintain high chlorophyll fluorescence and high SPAD despite a relatively hot canopy, which is typically associated with reduced stomatal conductance (Raina et al., 2019). Further exploration of physiological traits underpinning crop water use, particularly water demand across development, is required in mungbean to determine trait value in a range of environments.

The ability to access stored soil moisture is critical for drought adaptation. In crops such as wheat, the identification of root architecture traits that improve access to water under drought presents an opportunity for a physiological breeding strategy to develop drought-tolerant cultivars (Ober et al., 2021). However, limited research has been undertaken to evaluate root characteristics in mungbean in the context of drought stress as phenotyping belowground traits is challenging. The root system of a diverse mungbean mini-core collection (296 genotypes) was studied using a modified semi-hydroponic screening method to explore the variation of 14 root traits, such as total surface area and total root length. Within this population, significant root trait diversity was identified (Aski et al., 2021). These findings highlight the diversity in root traits available in existing germplasm collections that could be exploited to improve drought adaptation, however the value of these traits under different drought scenarios has yet to be confirmed in mungbean. To build on this work, it is important to understand how root traits measured under controlled conditions relate to root systems of field-grown plants. Canopy temperature has been used as a proxy trait for water uptake with QTL related to canopy temperature being linked to root distribution in wheat (Pinto & Reynolds, 2015). This provides an efficient phenotyping approach to screen for desirable root traits in the field. However, the value of canopy temperature as a proxy trait for water uptake should be further explored in mungbean to validate its potential for breeding programs.

The development of a root system and, therefore, timing of water uptake is likely to be an important factor in drought adaptation. Under controlled conditions, a mungbean root study observed that early maturing mungbean genotypes displayed enhanced root growth, with rapid root elongation as well as increased root development within deeper soil layers compared to slower maturing genotypes (Singh & Bell, 2021). Coupled with rapid root growth, the early maturing genotypes also had vigorous shoot growth with a higher rate of leaf area development. Although increases in rooting depth and biomass may be useful in some environments, trade-offs have been noted in other legume crops such as chickpea as temporal changes influence water availability later in crop development (Vadez et al., 2007; Zaman-Allah et al., 2011) reinforcing the importance of studying both the environment type and varying crop water use strategies (Akinlade et al., 2022; Blessing et al., 2018).

Drought stress is one of the primary abiotic stresses impacting growth and productivity in mungbean. A shortcoming of the studies conducted to date is the low number of genotypes (in most cases <5) evaluated highlighting the need for future research to explore greater diversity. Furthermore, a more holistic approach that simultaneously considers above- and below-ground development on the same germpasm is required, as most studies in mungbean to date have focused on a few morphological traits, primarily aboveground. Detailed studies on both above- and below-ground traits will be valuable and are a feasible step forward given the rapid development in phenotyping approaches such as multispectral imaging for canopy traits and rhizobox platforms for root traits.

3.4 | Waterlogging

Waterlogging refers to the submergence of the entire root system and potentially parts or the entire plant in water, leading to soil oxygen deficiency (Ikram et al., 2022; Pan et al., 2021). Mungbean can be severely impacted by waterlogging, particularly in Southeast Asia due to high monsoon rainfall during the reproductive stage resulting in low grain quality and yield (Kyu et al., 2021). In Australia, mungbean is typically grown in subtropical regions during summer which can experience extreme rainfall and flooding events, resulting in increased risk of waterlogging. Furthermore, with the effects of climate change extreme weather events including flooding are increasing (Shukla et al., 2019). Therefore, identifying waterlogging-tolerant genotypes is a key priority to ensure adaptation to current and future production environments (Islam et al., 2007).

Mungbean can tolerate some degree of waterlogging without substantial impact on growth and yield (Ahmed et al., 2002). It has been shown that transient flooding (1 day) at any developmental stage, as well as 7 days of flooding at the vegetative stage, does not significantly impact yield (Islam et al., 2008). However, prolonged wet weather as well as heavy rainfall in regions with poor soil drainage can significantly reduce yield in mungbean during reproductive development as seen in other grain legumes, due to the high risk of pod abortion, drop and shattering as well as premature sprouting before harvest (Islam et al., 2008; Nair et al., 2019; Pan et al., 2021). There are conflicting findings as to whether the flowering or pod filling stage is most sensitive which may be the result of different levels of tolerance in the genotypes examined (Ahmed et al., 2002; Islam et al., 2008). Nevertheless, when waterlogging is experienced during reproductive

development, there is a significant reduction of yield components including pods plant^{-1}, seeds pod^{-1} and, therefore, yield. Waterlogging affects the root system of the crop which has a negative impact on aboveground biomass. It has been observed in mungbean that waterlogging during the flowering and pod-filling stages significantly reduces root biomass and length, possibly as a result of root mortality (Garrity & Pernito, 1996). Waterlogging can, therefore, lead to a reduction in nutrient uptake to support aboveground biomass and pod development, reducing pod filling and in some cases increasing pod abortion (Pan et al., 2021).

Crops have evolved several physiological mechanisms that improve adaptation to waterlogging conditions. In faba bean, adventitious roots with aerenchyma can improve tolerance to waterlogging (Solaiman et al., 2007). Similar morphological adaptations may be important in mungbean with an observation that waterlogging tolerant mungbean genotypes developed adventitious roots not observed in the control genotypes (Ahmed et al., 2002). Other traits that were identified in tolerant mungbean lines include the ability to quickly recover photosynthetic activity after waterlogging and maintain high aboveground biomass (Ahmed et al., 2002; Garrity & Pernito, 1996).

In summary, waterlogging is likely to become a more important breeding target in the immediate future with a predicted increase in the frequency of extreme rainfall events. Limited research in mungbean, and research in other closely related species, suggests that waterlogging substantially impacts production when occurring at the reproductive stage. The limited number of studies evaluating waterlogging at reproductive development all showed a thorough approach to data collection which provided detailed insight into how this stress impacts mungbean growth and yield. This provides a useful foundation to expand waterlogging research to explore greater genetic diversity. However, innovative phenotyping methods will be required to support screening larger numbers of diverse genotypes in both controlled and field environments.

3.5 | Salinity

Salinity, the accumulation of salts in soil and water, is an increasing concern for mungbean growers in arid and semi-arid regions due to continued degradation of arable land (HanumanthaRao et al., 2016; Sehrawat et al., 2013). Salinity stress has been shown to impact plant growth through several mechanisms including a reduction in osmotic potential hindering water uptake and salt accumulation in plant tissue increasing toxicity levels (Munns

& Tester, 2008). In legumes an additional impact is reduced symbiotic nitrogen fixation (HanumanthaRao et al., 2016). Almost all studies evaluating the impact of salinity stress on mungbean development have focused on early development in particular at germination and the seedling stage, as salinity can delay or inhibit germination (Misra et al., 1996; Promila & Kumar, 2000) as well as reducing seeding root and shoot growth (Saha et al., 2010). However, in rice and chickpea it has been found that salinity tolerance at seedling and vegetative stages are not necessarily correlated with tolerance at reproductive stages (Mohammadi et al., 2014; Vadez et al., 2007) highlighting the importance of evaluating the effects of salinity at each developmental stage.

Similar to cold stress, limited research is currently available on the impacts of salinity on mungbean during reproductive development. One study noted that salinity during reproductive development resulted in high levels of chlorosis and burning at leaf tips, significantly reduced overall plant dry matter and leaf area as well a reduced leaf mineral and chlorophyll concentrations (Wahid et al., 2004). An additional study investigated the impact of salinity on leaf level gas exchange through leaf assays (Mekhaldi et al., 2008), however, this approach did not examine further impacts beyond gas exchange such as biomass accumulation and yield. While these two studies provide valuable initial insight into the effects of salinity on mungbean reproductive development, the limited scope and number of genotypes tested highlight the urgent need for further research into the future.

3.6 | Concurrent abiotic stresses

A major challenge for mungbean production is the occurrence of multiple simultaneous stresses, such as drought and heat. This is expected to increase in prevalence with climate change. To the best of our knowledge, research evaluating multiple simultaneous abiotic stresses at the reproductive stage have not been undertaken in mungbean. Further research is urgently required to determine key physiological mechanisms involved in adaptation to multiple abiotic stress scenarios and any potential trade-offs associated.

4 | BREEDING FOR ADAPTATION TO ABIOTIC STRESS IN MUNGBEAN

As knowledge of the impact of abiotic stress on mungbean yield development improves, there are increasing opportunities to dissect the physiology and genetics of

traits underpinning adaptation. New breeding tools and technologies can accelerate mungbean breeding efforts to improve yield stability for growers (Figure 4).

4.1 | Mungbean genetic resources

To achieve genetic gain in crop improvement programs, it is important that breeders have access to genetic variation. Since domestication, many agronomically important traits have been selected to improve crop productivity including seed dormancy, phenology-related traits, plant type and 100 seed weight (Isemura et al., 2012). However, current mungbean cultivars have a narrow genetic base (Gupta et al., 2004, 2013; Nair et al., 2020). A recent study found the genetic diversity of cultivars post domestication decreased to 30% of what is available from wild accessions (Ha et al., 2021). Therefore, genebanks are likely to house germplasm with traits not available in elite germplasm that may be used to improve adaptation to abiotic stress in modern cultivars.

Over 43,000 mungbean accessions are maintained at different genebanks around the world with the largest collections held at the Indian Council of Agricultural Research and World Vegetable Center (AVRDC), Taiwan (Nair et al., 2020). These collections have predominantly been studied for biotic stress, however, offer an opportunity to improve adaptation to abiotic stress and yield potential which is a current objective for the International Mungbean Improvement Network (Nair et al., 2020). Many collections also contain wild relatives of mungbean, which could enable access to allelic diversity absent in elite genepools (Kim et al., 2015). Numerous germplasm collections have now been genotyped however a significant bottleneck preventing the utilisation of germplasm in breeding programs is generation of phenotype data for complex traits (Sandhu & Singh, 2021).

4.2 | High-throughput phenotyping

Field-based phenotyping is crucial in breeding programs to characterise and assess complex traits (Pieruschka & Schurr, 2019). Traditional field-based phenotyping methods often involve manual, time-consuming and destructive sampling to capture traits of interest (Borra-Serrano et al., 2020; Furbank et al., 2019). These limitations have hindered the ability to connect genotype to phenotype; creating a bottleneck for researchers and slowing down breeding efforts (Hickey et al., 2019).
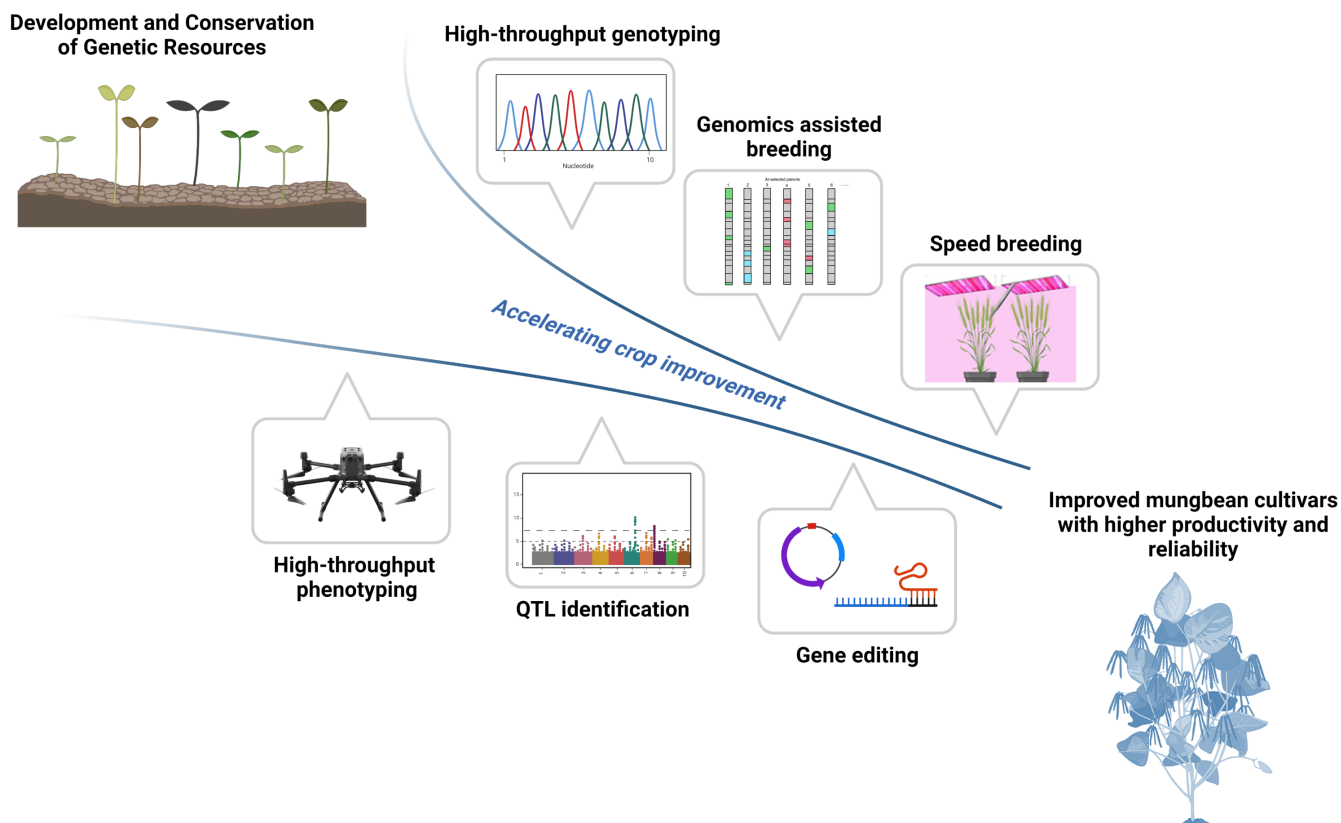

FIGURE 4 Schematic diagram of technologies and methodologies that may be used to rapidly accelerate mungbean breeding for adaptation to abiotic stress.

High-throughput phenotyping platforms offer the opportunity to accelerate trait discovery and gains in crop improvement programs (Potgieter, Watson, Eldridge, et al., 2018; Potgieter, Watson, George-Jaeggli, et al., 2018; Smith et al., 2021). Unmanned aerial vehicles (UAV) in particular have shown great potential for large scale field phenotyping as they are flexible and present low hardware costs (Das et al., 2021). UAVs can have a wide range of cameras and sensors attached to generate high-resolution images of the field. Vegetative and thermal indices can be indicative of ground based physiological traits and have been successfully utilised in a number of crops including sorghum (Gano et al., 2021) and soybean (Roth et al., 2022).

To monitor abiotic stress response, UAVs mounted with sensors can be used to measure proxy traits related to the underlying physiological response. For example, in drought conditions monitoring canopy temperature provides an indication of plant water use in field conditions at scale. This approach has been applied to cereal and legume crops (Crusiol et al., 2019; Das et al., 2021). Similar approaches may be used for a range of abiotic stresses such as salinity, foliar damage from temperature stress and waterlogging. To date, UAV phenotyping approaches have not been published for mungbean. However, another imaging approach has recently been applied to dissect leaf morphology traits in mungbean (Chiteri et al., 2023). This approach involved taking images of the leaves and using image annotation software to calculate traits such as leaf area. These technologies will likely be useful for dissecting canopy dynamics under abiotic stress as data can be captured intensively in a non-destructive manner across the reproductive window allowing for the quantification of rapid changes occurring at the canopy scale.

4.3 | Genomics-assisted breeding for abiotic stress

Knowledge of the underlying genetics of traits associated with abiotic stress adaptation can help breeders to combine traits into improved cultivars. DNA markers linked to traits can enable marker-assisted selection which overcomes phenotyping bottlenecks to track and select the trait of interest within the breeding program. Historically, markers such as simple sequence repeats (SSR), restriction fragment length polymorphism (RLFP), amplified fragment length polymorphism (AFLP) and random amplification of polymorphic DNA (RAPD) have been used for genome analysis in plant breeding. Application of these markers provided early advances in the field, however, they are low-throughput and sometimes have poor reproducibility (Yang et al., 2013). The technology has

now advanced and the cost for genotyping has decreased (Hasan et al., 2021). The advancement in sequencing technologies such as genotype by sequencing (GBS) and single nucleotide polymorphism (SNP) markers have become molecular marker systems of choice in many crops. A popular genotyping service utilised widely in mungbean is the high-throughput Diversity Arrays Technology platform (Kilian et al., 2012). A key advance in mungbean was the first draft of the whole-genome sequence which enabled new genomic research approaches to explore the genome and marker position (Kang et al., 2014).

Using a mungbean recombinant inbred line (RIL) population, researchers have identified several quantitative trait loci (QTL) associated with drought adaptation (Liu et al., 2017). While this approach is powerful for mapping QTL they lack precision and the ability to explore a high degree of genetic variation. Genome-wide association studies (GWAS), provide advantages for exploring variation in SNPs across larger and more diverse populations. GWAS is now a routine approach that has enabled researchers to map the genomic loci associated with economically important traits such as yield and traits underpinning adaptation to biotic and abiotic stress (Hou et al., 2018; Liu et al., 2018). This method utilises SNPs to identify the variation across genomes that affect a particular phenotype based on the statistical significance of the association between the SNPs and the observed phenotype. GWAS can also be used to reveal high resolution and unbiased information about the genetic architecture of the trait, including information regarding the number of causative alleles, distribution of their effects as well as interactions (Hansen, 2006). Several mungbean studies have undertaken GWAS to identify QTL associated with a range of qualitative and quantitative traits such as seed characteristics (i.e. seed coat colour, lustre and texture) (Breria, Hsieh, Yen, Nair, et al., 2020; Noble et al., 2018), total leaf area (Reddy et al., 2020), phenological development (Hwang et al., 2017; Sandhu & Singh, 2021), flower and pod traits and behaviour (Ha et al., 2021; Lee et al., 2021), leaf and canopy characteristics (Chiteri et al., 2023; Ha et al., 2021; Sandhu & Singh, 2021; Sokolkova et al., 2020;), root architecture traits (Reddy et al., 2020) and seed mineral composition (Wu et al., 2020).

Fewer studies have identified QTL associated with traits linked to adaptation under abiotic stress conditions. Evaluation of a mungbean mini-core collection led to identification of two QTL associated with germination under salinity on chromosomes 7 and 9 (Breria, Hsieh, Yen, Yen, et al., 2020). Additional candidate genes for salt tolerance during the seedling stage were identified in a 2022 study (Liu et al., 2022).

GWAS is helpful to understand genetics, and for simple traits, marker-assisted selection is a viable breeding

strategy. However, traits that confer adaptation under abiotic stress are generally complex and quantitative in nature which often results in GWAS revealing many loci with small effect. Another limitation of traditional single marker GWAS approaches is that the associated marker can recombine with the trait. For this reason, haplotype-based GWAS approaches, such as the local genomic estimated breeding value approach (Voss-Fels et al., 2019), can identify a block of markers that are in linkage disequilibrium which can be more suited to tracking and selection in breeding populations. Genomic selection uses all markers across the genome to estimate the overall genetic merit of an individual (Budhlakoti et al., 2022). Genomic selection is a promising approach that has been widely adopted in other crops and presents a more feasible alternative to improve the genome for abiotic stress adaptation traits over time (Redden, 2013). Genomic selection is now routinely used in the Australian National Mungbean Improvement Program (personal communication, Dr Merrill Ryan, QLD Department of Agriculture and Fisheries, 2023), however, no research articles on genomic selection are available at present.

4.4 | Speed breeding

Speed breeding can accelerate crop improvement by reducing the length of the breeding cycle (Watson et al., 2018). Speed breeding involves growing plant populations under controlled environmental conditions such as optimal day length, light intensity, light quality and temperature to accelerate flowering and seed set, therefore, advancing to the next generation faster (Ghosh et al., 2018).

Mungbean crop improvement programs are typically located in the sub-tropics or tropics which often experience an extended period of rainfall, and consequently decreased light intensity, for part of the year. This can delay generation time within regular glasshouse facilities. The control of temperature and light delivery within a speed breeding facility all year round may increase the number of plant generations per year which can greatly accelerate breeding activities. The use of dedicated speed breeding facilities may also increase the reliability of breeding operations in the tropics, as timelines are not interrupted by weather, such as monsoons or heavy rainfall. Speed breeding ensures that new breeding lines can be generated at a fixed time each year ensuring that field testing can be completed on schedule. There is also the additional advantage of increased overall efficiency due to the ability to grow high plant densities in a small space, which can accelerate and expand single seed decent activities. For example, wheat and barley can be grown in 100-cell trays, which equates to a plant density of 900 plants per m^2 (Watson et al., 2018). Speed breeding requires access to suitable facilities that have reliable water and electricity, training staff in the protocol and the ability to adopt major changes to current breeding program designs. Thus, implementation of speed breeding can be a challenge, particularly for underinvested and under resourced crop improvement programs (Chiurugwi et al., 2019; Wanga et al., 2021). While speed breeding protocols for mungbean are not yet published, protocols are now available for tropical legumes, such as soybean (one cycle 77 days; Mobini et al., 2015) and cowpea (one cycle 43–55 days; Edet & Ishii, 2022), which suggests that mungbean would be amenable to speed breeding.

4.5 | Genetic engineering

Genetic modification can be used in conjunction with traditional breeding methods to provide a platform for studying and characterising genes (Massel et al., 2021). This can help to identify the specific genes that are responsible for desired traits. Additionally, these genetic modification platforms (e.g., agrobacterium-mediated transformation and CRISPR/Cas) can be used to produce new varieties that exhibit a desired trait.

Genetic transformation approaches have been applied in mungbean to identify and evaluate genes associated with adaptation to salinity (Baloda et al., 2017; Kumar et al., 2017; Sahoo et al., 2016) and cold stress (Rout et al., 2020). The approach of Kumar et al. (2017) and Sahoo et al. (2016) of overexpressing a gene originally found in Arabidopsis in mungbean highlights the importance of using knowledge from model species to accelerate mungbean improvement. Gene editing approaches are now available in mungbean and have been applied for biotic stress (Talakayala et al., 2022). One advantage of genome editing is that plants generated with gene knockout strategies (classified as SDN1) are now considered non-GM in many jurisdictions (Zhang et al., 2021). However, there are potentially limitations with this approach for abiotic stress adaptation as knockouts may not lead to an optimal physiological phenotype. One strategy to overcome this constraint is to edit the regulatory regions of a gene which can create a spectrum of trait variation (Crisp et al., 2022). Regardless, genome editing technology offers a powerful tool to understand gene function and can be used to evaluate well characterised genes from other species. If editing pipelines are developed using elite varieties, the timeframe to deliver cultivars with improved adaptation to abiotic stress to growers may be reduced.

5 | CONCLUSION

Mungbean crops are significantly impacted by abiotic challenges that occur during reproductive development. Despite the potential impact on production, our extensive search of the literature found a relatively small number of original research articles that focus on the effects of abiotic stress at the reproductive stage in mungbean. This highlights the significant research gap that will need to be bridged in order identify traits that confer adaptation.

Future research is urgently required to expand the application of existing studies to a larger number of genotypes and environments, particularly through the implementation of robust field experiments. Detailed experiments are also required to dissect the physiological and genetic mechanisms underpinning traits involved in adaptation to abiotic stress. To facilitate phenotyping at scale, high-throughput phenotyping platforms such as UAVs mounted with sensors may be utilised however protocols must be validated for specific indices and correlated to traits of interest for each abiotic stress. Advances in genotyping platforms and reduced cost provide opportunities to implement genomic selection for mungbean to accelerate genetic gain for abiotic stress. Gene editing platforms are anticipated to assist in the investigation of traits of interest from model species to advance understanding in mungbean. The current knowledge generated for abiotic stress at the reproductive stage in mungbean, and insights from other crops, provides a useful foundation to guide the research and technological advances required to breed resilient mungbean cultivars for the future.

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