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Breeding banana (*Musa* spp.) for drought tolerance: A review

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Abstract

Drought is a major abiotic stress affecting banana production worldwide, leading to yield losses of up to 65%. Consequently, numerous efforts to understand and mitigate drought effects that include developing tolerant crop varieties are ongoing in several banana breeding programmes. The breeding efforts, however, have been greatly slowed down by inherent banana problems (polyploidy and male or female sterility) and complexity of drought tolerance (reportedly controlled by several genes). This review summarizes the pertinent research findings on water requirements of banana for its proper growth and productivity, symptoms of drought-sensitive varieties and field management strategies to cope with drought stress. The coping strategies deployed by resistant cultivars include high assimilation rates and water retention capacity as well as minor losses in leaf area and gaseous exchange. Reduced bunch weight, leaf chlorosis, wilting and strangled birth are underlined to be directly associated with drought susceptibility. Integration of conventional, molecular breeding and biotechnological tools as well as exploitation of the existing banana genetic diversity presents a huge opportunity for successful banana improvement.

KEYWORDS
banana water requirement, drought stress, drought tolerance, molecular markers, *Musa* spp., phenotyping

1 | INTRODUCTION

Banana (*Musa* spp.) is a major staple and commercial crop with a global production of 113.9 million tons (FAOSTAT, 2017). It is grown in several countries, mainly in the warm and humid tropical regions of the world with abundant rainfall, including Africa, Latin America, Caribbean, Asia and Pacific. In Africa, over 70 million people derive 25% of their dietary energy from banana and plantain (Edward & Fredy, 2012). Bananas are consumed in various forms including raw, cooked, baked, steamed or fermented (Fungo & Pillay, 2011). However, their production in major growing regions is greatly affected by a complex of biotic and abiotic stresses, ultimately threatening the livelihoods of smallholder farmers in the developing world. Prominent biotic stresses include pests such as banana weevil (*Cosmopolites sordidus*) and nematodes (*Pratylenchus coffeae* and *Radopholus similis*) (Gold, Kagezi, Night, & Ragama, 2004; Ocan, Mukasa, Rubaihayo, Tinzaara, & Blomme, 2008; Speijer, 1999), while diseases include banana bacterial wilt (caused by *Xanthomonas campestris* pv. *musacearum*) (Ocimati, Nakato, Fiaboe, Beed, & Blomme, 2014; Tripathi, Tripathi, Tushemereirwe, Arinaitwe, & Kiggundu, 2013), black leaf streak disease (caused by *Mycosphaerella fijiensis*) (Barekye, Tongoona, Derera, & Tushemereirwe, 2009; Marín, Romero, Guzmán & Sutton, 2003), fusarium wilt (caused by *Fusarium oxysporum* f.sp. *cubense*) (Ploetz, 2015) and banana bunchy top virus disease (causal agent, banana bunchy top virus), (Niyongere et al., 2012). Among the abiotic stresses, salinity (Ravi & Uma, 2011), heat, low soil fertility (Bekunda & Woomer, 1996; Wairegi, van Asten, Tenywa, & Bekunda, 2010) and drought (van Asten, Fermont, & Taulya, 2011; Taulya, van Asten, Okech, & Gold, 2006) are the most prevalent.

As a result of climate change, adverse effects of drought have become more pronounced in the tropics and subtropics of the world

(Ravi, Uma, Vaganan, & Mustaffa, 2013). Tuberosa (2012) defines drought as "a condition in which the amount of water available through rainfall and/or irrigation is insufficient to meet the transpiration needs of the crop". For optimal production, bananas require a minimum of 100 mm of evenly distributed rainfall every month (Robinson & Sauco, 2010). Bananas are very sensitive to drought, which may cause yield reductions of up to 65% when the annual rainfall falls below 1,100 mm per annum (van Asten et al., 2011). Therefore, banana varieties which can produce reasonable yield with less water offer the most promising alternative to protecting the banana crop against daunting drought effects.

Drought tolerance is a complex trait whose expression is controlled by many genes and environmentally varies over location and time, which complicates the development of a standard for drought (Ravi et al., 2013). Despite these challenges, the banana gene pool is very diverse and hence presents a great opportunity for the enhancement of complex quantitative traits, including drought tolerance. Currently, the *Musa* International Transit Centre (ITC) in Belgium hosts and maintains over 1,500 *Musa* accessions in vitro including cultivated banana varieties, wild relatives and improved hybrids (Swennen et al., 2011). These accessions require screening as only a fraction of the collection has been assessed in vitro for reaction to drought stress (Vanhove, Vermaelen, Panis, Swennen, & Carpentier, 2012). From this germplasm collection, appropriate male and female parents can be selected and crossed to produce segregating populations from which drought-resistant banana genotypes can be obtained. The challenge, however, is that banana is by nature a clonally propagated crop and every attempted successful cross results in new genotypes, often accompanied by co-inheritance with undesirable growth and fruit characteristics (Ramirez, Jarvis, Van den Bergh, Staver & Turner, 2011). Consequently, fixation of drought tolerance in banana through conventional breeding would require several generations of backcrossing. Co-inheritance of undesirable genes on the other hand can be minimized through the use of genetic modification techniques, whereby only the desirable genes are inserted into the genome of the genotype which requires improvement (Tripathi, Mwaka, Tripathi, & Tushemereirwe, 2010). The objective of this review is to provide a summary of research efforts that have been directed towards understanding and breeding for drought tolerance in bananas. The following research questions will be addressed in the review: (a) "What are the physiological, biochemical and molecular changes that occur in banana under conditions of moisture stress?", (b) "What is the molecular basis of drought tolerance in banana?" and (c) "What prospects do the current research findings, technology advancements and banana genetic diversity present for banana drought tolerance improvement?".

2 | WATER REQUIREMENTS FOR BANANA GROWTH

Banana is a large perennial fruit shrub which requires at least 1,300 mm of rainfall per year for optimal growth (Mustaffa & Kumar, 2012). However, major production systems such as the East African highland banana are often small-scale, completely rainfed, and irrigation is not practiced. The area experiences bimodal rainfall patterns with an average of 900–1,100 mm per year and includes larger parts of Eastern Rwanda, south-western districts of Uganda and the western Kagera Region of Tanzania (van Asten et al., 2011). Moreover, such rains are unevenly distributed, which makes bananas prone to drought stress, thereby limiting production in large areas of Eastern Africa. In addition, with the changing climate, longer and more severe dry spells can be anticipated in eastern Africa (Hulme, Doherty, Ngara, New, & Lister, 2001), and these will ultimately lead to increased moisture stress, which affects banana productivity and production. Accordingly, over 65 per cent of global commercial and/or export banana production is supplemented with irrigation (Carr, 2009).

TABLE 1 Previously used irrigation regimes in banana

Irrigation treatments	Source
0.25 to 1.25 ET[a] in increments of 0.25	Goenaga and Irizarry (2000)
40%, 65%, 85% and 100% Standard maximum ET	Shongwe, Tumber, Masarirambi, and Mutukumira (2008)
33%, 66%, 99% and 120% (ET)	Coelho, de Oliveira, and Pamponet (2013)
25%, 50%, 75%, 100%, 125% and 150% (ET)	D'Albuquerque, Gomes, de Sousa, & de Sousa (2013)
0%, 50%, and 100% (ET)	Fandika et al. (2014)
0.5, 0.75 and 1 (ET)	Ali et al. (2015)

[a] ET, evapotranspiration from a class A pan.

Irrigation needs may differ between locations due to environmental variations which are influenced by temperature, latitude and elevation, as well as seasonality and rainfall amounts and distribution during the growing season. Crop water requirements may also be influenced by the crop type and growth stage, with advanced stages requiring more water than the initial development stages (Brouwer & Heibloem, 1986). Irrigation requirements of horticultural crops like melon, green beans, watermelon and pepper have been estimated using drainage lysimeters which measure evapotranspiration (Orgaz, Fernández, Bonachela, Gallardo & Fereres, 2005). Similarly, banana evapotranspiration has been estimated using the pan evaporation method (Goenaga & Irizarry, 2000). Table 1 summarizes the different irrigation treatments formerly investigated on banana, which can be used as references in drought tolerance studies. Although a substantial amount of research has been carried out to determine the water requirements of drip-irrigated bananas, specific information on the amount of irrigation to be applied is still lacking. Nonetheless, Goenaga and Irizarry (1998) recommended a pan factor of 1.0 (100% evapotranspiration) as the adequate water consumption for optimum banana production after reporting a significant improvement in banana yield components of the mother plant and two ratoon crops.

3 | PHENOTYPIC SYMPTOMS OF DROUGHT-SENSITIVE BANANA CULTIVARS

Drought effects on banana are manifested at various growth stages including early vegetative stage, floral primordial initiation, flowering and bunch/finger development (Robinson & Alberts, 1986; National Research Centre for Banana (NRCB), 2008). However, the intensity of this damage depends on the growth stage of the plant and duration of stress (Ravi et al., 2013). Drought-sensitive banana cultivars exhibit characteristic symptoms both externally and internally (Mahouachi, 2007; Uma, Sathiamoorthy, Singh, & Dayarani, 2002). Such symptoms may either be common across all sensitive genotypes or are genotype-specific. Internal symptoms are manifested as physiological and biochemical changes which occur at cell level (Surendar, Devi, Ravi, Jeyakumar, & Velayudham, 2013b). The most prominent external symptoms include wilting and/or drying of leaves resulting from overheating and dehydration of cells (Ravi & Vaganan, 2016) and a significant reduction in bunch yield (van Asten et al., 2011). For instance, when banana plants were deprived of water at flowering for four weeks, a reduction in the bunch weight, fruit length and circumference was observed at harvest in cultivars 'Robusta', 'Karpuravalli' and 'Rasthali' (NRCB, 2008). Such significant decline in crop yield may be attributed to the reduction in the plant's photosynthetic rate, which is greatly influenced by the leaf chlorophyll content as well as closure of the stomata (Flexas & Medrano, 2002).

Water stress results in reduced production and increased breakdown of chlorophyll in leaves, which is manifested as leaf senescing or chlorosis (Dekov, Tsonev, & Yordanov, 2000). Moreover, a correlation between leaf area and yield suggests the importance of leaf area and chlorophyll content as major determinants of the harvestable yield (Surendar, Devi, Ravi, Krishnakumar, Kumar, et al., 2013a). A decline in photosynthesis also results in reduced biomass production and allocation (Delfin et al., 2016; Mahouachi, 2009) to major plant tissues like the pseudo-stem, which weaken and eventually snap or collapse. Other drought susceptibility symptoms such as stunted growth, strangled birth and formation of leaf petiole rosette (Figure 1) become more apparent when severe water stress occurs throughout the entire crop cycle. Screening banana germplasm in the field is important as it unveils the reaction of assessed genotypes under stress conditions which are consistent with reality in nature. However, this requires the use of large rainout shelters, screening in multiple locations, lengthy observations due to the long crop cycle (10–12 months), controlled water application as well as large human and monetary resources required.

4 | CULTURAL PRACTICES FOR MANAGEMENT OF DROUGHT STRESS

Drought tolerance in plants could be achieved by incorporating research technologies such as genetic engineering, screening of large amounts of germplasm and breeding for tolerance, marker-assisted selection and exogenous application of hormones and osmoprotectants to seed or growing plants (Farooq, Wahid, Kobayashi, Fujita, & Basra, 2009). Banana farmers, on the other hand, cope with drought stress by practicing the following management practices to replenish and maintain soil moisture to levels optimum for banana production;

4.1 | Mulching

Mulching, as a cultural management option, is often practiced to reduce evaporation, control weeds, reduce the displacement of topsoil by running water, reduce compaction of soil particles and nourish soil with green manure (Govindappa & Pallavi Seenappa, 2014). Common mulch options include the use of dried weeds, grass (*Pennisetum purpureum*) (Swennen, 1990) and other crop or banana plant residues, for example banana peelings, pseudostems and pruned dry or fresh leaves (Bekunda, 1999). In addition, cover crops including chickpeas (*Cicer arietinum*), mucuna (*Mucuna* spp.) and lablab (*Lablab purpureus*) can be used as "living mulch" (Blomme et al., 2018). Integration of such shade- and drought-tolerant leguminous cover crops in banana-based production systems would contribute to a reduction in yield losses induced by drought stress. Moreover, such crops have the capacity to bind atmospheric nitrogen in the soil and protect the soil as ground cover (Raemaekers, 2001) while preventing weed growth and enriching the soil.

4.2 | Irrigation

As indicated in Section 2 above, banana plantations require a large amount of water for irrigation. Supplementary irrigation is particularly vital during floral primordial initiation and development, flowering and one month postflowering to ensure successful bunch emergence and fruit filling (Ravi & Vaganan, 2016). Moreover, increased irrigation boosts banana yield and quality (Fandika, Kadyampakeni, Mwenebanda, & Magombo, 2014). Large-scale commercial banana farmers supplement the available rainfall with drip or sprinkler irrigation, while for small-scale growers (form the majority and are often resource-limited), irrigation is often constrained by water scarcity and cost of water (Blum, n.d.) as well as limited access to irrigation facilities (Kabunga, Dubois, & Qaim, 2012). Even those smallholder growers that irrigate their plantations, the irrigation intensity remains rather low and less frequent (Kabunga et al., 2012). Supplementary irrigation, in many environments, can be made more effective if the water is applied before planting (Blum, n.d.). Preplanting irrigation allows the crop to have a sufficient water supply early in the season, thereby ensuring its proper establishment and growth in spite of unexpected rainfall variations. As the atmospheric conditions become warmer and drier, irrigation is required to maintain a high moisture content while ensuring free movement of water molecules within the soil for easy uptake by plant roots (Robinson, 2000).

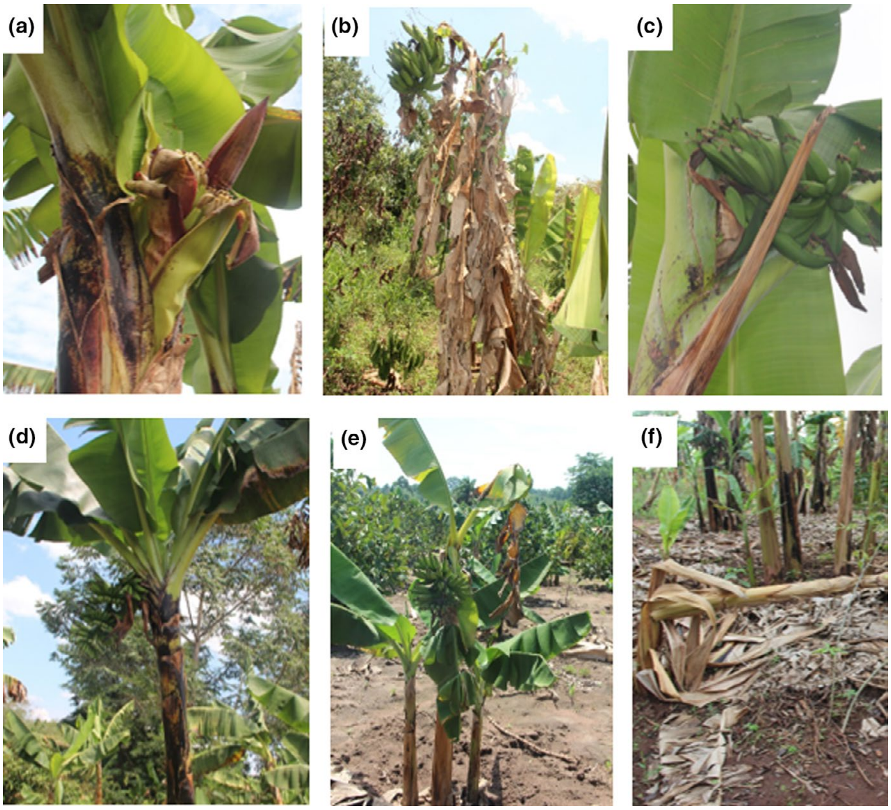

FIGURE 1 Symptoms of drought stress on banana: (a) strangled birth, (b) wilting and drying of leaves, (c) reduced bunch and finger size, (d) formation of petiole rosette, (e) stunted growth and (f) snapping of weak pseudo-stem

5 | PHENOTYPING UNDER DROUGHT STRESS CONDITIONS

5.1 | Physiological analyses

Considering that drought is becoming more and more prevalent in various parts of the world, several authors have demonstrated the physiological changes which occur in banana during such water stress conditions (Bananuka, Rubaihayo, & Tenywa, 1999; Surendar, Devi, Ravi, Jeyakumar, & Velayudham, 2013b). These physiological changes affect processes such as stomatal conductance, water retention capacity, water-use efficiency (WUE) and photosynthesis. Drought-sensitive cultivars show significant reductions in plant dry mass due to reduced biomass production (Mahouachi, 2009), whereas their resistant counterparts have inbuilt mechanisms for drought tolerance such as high assimilation rates and water retention capacity with minor losses in leaf area and gaseous exchange (Bananuka et al., 1999). Similar findings were reported from an experiment conducted under glasshouse conditions in the Philippines (Delfin et al., 2016). The study concluded that genotypes with the highest WUE, root volume, total plant biomass production and root dry weight were drought tolerant. On the other hand, stomatal conductance and photosynthesis are significantly reduced under limiting moisture (Thomas & Turner, 2001).

Inasmuch as prolific vegetative growth is a good indicator of better resistance to drought stress, it is not satisfactory as a sole parameter since a healthy plant absorbs more moisture from the soil and will at times forfeit its inner water balance to allow growth, which ultimately intensifies the stress and reduces development of the final yield (Passioura, 2012). Therefore, one approach is to take both plant growth and efficient use of water during water stress into account. Transpiration efficiency (TE) has been assessed and found to be a useful indicator of drought tolerance in cereal crops including barley, rice and wheat (Anyia, Slaski, Nyachiro, Archambault, & Juskiw, 2007; Cabrera-Bosquet, Molero, Bort, Nogués, & Araus, 2007; Haefele, Siopongco, Boling, Bouman, & Tuong, 2009). In banana, however, only a few studies have assessed the correlation between TE and growth. For instance, Kissel, van Asten, Swennen, Lorenzen, and Carpentier (2015) demonstrated an increase and clear genotypic variation in the transpiration efficiency for six banana cultivars (Mpologoma, Mbwazirume, Sukali Ndizi, Kayinja, Cachaco and Yangambi Km5) when stressed. Nonetheless, selection for high transpiration efficiency did not result in selection of cultivars with slower vegetative growth under watered and mild moisture stress imposition. Therefore, selection of banana cultivars based on the TE during stress conditions could serve as a quick tool for selecting drought-resistant candidates under controlled conditions, thereby reducing the amount of time required for screening and selection under field conditions. There is, thus, a need to evaluate TE for more genotypes which are currently maintained by different banana breeding programmes. It is important, though, to note that a high TE during moisture stress does not necessarily imply drought tolerance for that cultivar or crop (Jones, 2014). A cultivar is only regarded as drought tolerant if it has a highwater-use efficiency accompanied by a minor reduction in growth and yield.

Several studies have reported banana genotypes with the “B” genome such as AAB and ABB to be more drought-tolerant than those entirely based on the “A” genome, for example ‘Cavendish’

AAA (Robinson, 1996; Robinson & Sauco, 2010). This drought tolerance has been imputed to the belief that the *Musa balbisiana* (*M. balbisiana*) originated from drier parts of South Asia including lower Himalayan ranges (Tenkouano, 2006) unlike *Musa acuminata* (*M. acuminata*), whose origin is the humid forest regions of South-East Asia (Kissel et al., 2015). In a field study by Ravi and Uma (2011), several *M. acuminata* diploids exhibited high susceptibility to drought, which was manifested by bunch choking, fewer hands, ill-filled fruits and no seed set. Conversely, water deficit conditions had little impact on fruit and seed development of *M. balbisiana* cultivars. Under controlled conditions, Thomas, Turner, and Eamus, (1998) reported a higher sensitivity to leaf-air vapour pressure deficit in the cultivar 'Williams' (AAA) than cultivars 'Bluggoe' (ABB) and 'Lady Finger' (AAB). Likewise, an in vitro assessment of banana varieties showed that ABB varieties had the least reduction in growth under slight osmotic stress (Vanhove et al., 2012). As such the B genome may contain drought tolerance genes which can be identified, isolated and introduced in drought-sensitive farmer preferred cultivars.

5.2 | Biochemical analyses

Drought stress elicits a series of biochemical responses including mechanisms of susceptibility to osmotic or moisture stress, transformation of stress signals to cellular signals, transfer of cell signals to the nucleus and transcriptional control of moisture stress-induced genes, resulting in tolerance to the water deficit (Blum, 2017; Bray, 1997). For instance, drought stress specifically induces the synthesis and build-up of organic solutes such as proline, free amino acids, total soluble proteins and carbohydrates, which act as osmolytes (Lacerda, Cambraia, Cano, & Ruiz, 2001; Surendar, Devi, Ravi, Jeyakumar, & Velayudham, 2013b). Such osmolytes, for example proline, may regulate the osmotic balance of the cell thereby countering the osmotic stress induced by drought (Hayat et al., 2012). Osmotic adjustment safeguards major plant cell structures such as chloroplasts and cell membranes (Martìnez, Lutts, Schanck, Bajji & Kinet, 2004). This was corroborated by Surendar et al. (2013c), who concluded that the higher yield observed in resistant banana genotypes may have been due to higher water and osmotic potential, resulting from increased epicuticular wax, proline and free amino acids during stress conditions. On the other hand, accumulated total sugars serve as an important energy source under severe stress in corn (Pimentel, 1999). These biochemical compounds can be used as drought tolerance indices to rapidly select resistant candidates among existing banana cultivars and hybrids.

Drought stress enhances the production of reactive oxygen species (ROS) (including alkoxy radicals, OH, HO_2 and O_2^-), which impair proteins, lipids, carbohydrates, and DNA, and thereby causing oxidative stress (Gill & Tuteja, 2010). To maintain the integrity of cellular structures, such active species of O_2^- are eliminated by a catalase, an antioxidant enzyme which in turn eliminates the hydrogen peroxide produced during plant metabolic processes (Surendar, Devi, Ravi, Krishnakumar, Kumar, et al., 2013a). Literature sources have reported the continuous production and scavenging of ROS molecules by many antioxidative defence mechanisms during drought stress (Foyer & Noctor, 2000). In fact, a close association between drought tolerance and an increment in antioxidant enzyme activity under conditions of drought stress has been observed in wheat genotypes by Sairam, Shukla, and Saxena (1997). Considering ROS scavenging reduces oxidative stress caused by moisture deficit, we presume that the enhancement of such antioxidative processes would improve drought tolerance in banana.

5.3 | Molecular analyses for drought tolerance in bananas

Drought stress triggers the expression of several genes and transcription factors influencing different plant resistance mechanisms including escape, avoidance, tolerance and acclimatization (Farooq et al., 2009). Such molecular factors are responsible for the production of biochemical compounds which maintain or restore the integrity of plant cells during moisture deficit conditions. Several studies provide insight into the molecular basis of drought tolerance in important cereal crops such as wheat (Ahmad, Khan, Khan, Kazi, & Basra, 2014; Ibrahim, Schubert, Pillen, & Léon, 2012), rice (Shim et al., 2018) and maize (Liu et al., 2013; Wang et al., 2016). In bananas, transcriptomic changes in drought-tolerant (*cv.* 'Saba') and sensitive (*cv.* 'Grand Naine') cultivars have been monitored and compared using mRNA-Seq under well-watered and drought stress conditions (Muthusamy, Uma, Backiyarani, Saraswathi, & Chandrasekar, 2016). Among the upregulated and/or downregulated differentially expressed genes (DEGs), several genotype-specific gene expression patterns were observed for drought stress in both cultivars. Such unique gene expression profiles observed in resistant cultivars could represent candidate drought stress tolerance genes considering their stress association in plants is already known. Also, notable are transcription factors, namely the banana *NAC* transcription factor (*MusaSNAC1*) which imparts drought tolerance by regulating stomatal closure and hydrogen peroxide content after binding to the CGT[A/G] motif in regulatory region of many stress-related genes (Negi, Tak, & Ganapathi, 2018). Table 2 summarizes the different protein/gene families that have been associated with tolerance to drought and other abiotic constraints through molecular characterization and genome wide analysis. Understanding the molecular basis for drought tolerance will provide required genetic information influencing drought resilience in banana.

6 | BREEDING FOR DROUGHT TOLERANCE IN BANANA

Crop improvement involves the creation, selection and fixation of resistance or tolerance against biotic and abiotic constraints into superior plant phenotypes, which meet the needs of farmers and consumers. The wide genetic diversity within *Musa* germplasm is an important

TABLE 2 Protein families and their role in drought and other abiotic stresses affecting banana

Protein/Gene family	Specific protein/Gene	Tolerance to which abiotic stress	Role during stress	Source
Aquaporin (AQP)	*MaPIP1;1*	Drought, salt	Reduces membrane injury, improves ion distribution and maintains osmotic balance	Xu et al. (2014)
	MaPIP1;2	Drought, cold, salt	Lowers malondialdehyde levels, elevated proline and relative water content and higher photosynthetic efficiency	Sreedharan, Shekhawat, and Ganapathi (2013)
	MaTIP1;2 (Promoter)	Drought, salt	Controls the flow of water and other small molecules through biological membranes	Song et al. (2018)
Copper Chaperone Gene	*MaCCS* gene	Drought, copper, heat, cold and light	Delivers copper to its target *Cu/ZnSODs*. Function is not yet so clear	Feng et al. (2016)
Calmodulin-binding transcription activator (*CAMTA*)	*Musa acuminata* CAMTA1 (*MuCAMTA1*) transcription factor	Drought	No systematic study has been conducted yet on *MuCAMTA* transcription factors to identify their role in drought stress in banana plants	Meer, Mumtaz, Labbo, Khan, and Sadiq (2019)
Leucine zipper (*bZIP*) transcription factor gene family	*MabZIP* genes	Drought, cold, salt	They participate in stress signalling, but their function is yet to be confirmed in banana	Hu et al. (2016)
Sugars Will Eventually be Exported Transporters (*SWEET*)	*M. acuminata MaSWEET* genes	Drought, cold, salt	Promote early sugar transport to improve fruit quality and enhance stress resistance in banana	Miao et al. (2017)
Constitutive Banana cDNA	*M. acuminata* root hair defective 3 (*MaRHD3*)	Drought	ROS scavenging enhanced lateral root branching and root hair density	Wonga, Mazumdarb, Laub, and Harikrishna (2018)
	ATPase and heat shock proteins	Drought	Involved in metabolism, responses to stress, growth and development	Mattos-Moreira et al. (2018)

source for disease and pest resistance genes, good agronomic performance and tolerance to abiotic stresses, hence an indispensable resource for banana enhancement. However, identification and characterization of this genetic diversity and putative resistance genes, and utilization of this genetic variation to improve the inherently female and/or male sterile and clonally propagated crop can be a challenge (Ssali, 2016). For banana improvement, conventional cross-breeding and non-conventional breeding approaches including molecular breeding techniques have been deployed (Chen et al., 2011).

6.1 | Genetic diversity in banana

The two principle progenitors of present-day edible bananas are *M. acuminata* Colla, (AA) and *M. balbisiana* Colla, (BB), whose centre of origin is believed to be in South and South-East Asia and Pacific countries (Ravi & Uma, 2011; Simmonds, 1962). These were later introduced to the tropical and subtropical climatic zones, where the crop is now a major food crop. The existing large diversity of banana is a result of natural interspecific hybridization of *M. acuminata* and *M. balbisiana* species, thus forming various genomic groups like diploids (AA, AB, BB), triploids (AAA, AAB, ABB, BBB) and tetraploids (such as AAAB and AABB) (Simmonds, 1966). Over the years, humans have domesticated, selected and perpetuated useful banana genotypes. Such useful diversity includes good agronomic performance as well as resistance or tolerance to several biotic and abiotic stresses (Singh & Uma, 2000). Large collections of banana germplasm including progenitors, wild relatives, landraces and hybrids are currently assembled and maintained in situ and ex-situ by twelve banana breeding programmes spread all over the world. Although only a few species have been domesticated, wild relatives of banana consist of at least 75 species, which originate from India and the Pacific, specifically in the humid tropical forests (Manimaran et al., 2018). From these germplasm collections, resistant candidates can be selected and used to introgress drought tolerance in commercially important but susceptible bananas.

6.2 | Screening banana germplasm for drought tolerance

For a long time, breeders have focused on breeding for resistance to banana pests and diseases (Aguilar Morán, 2013; Nowakunda et al., 2015), with drought tolerance only considered an important trait along with these traits. Currently, drought is gaining importance and has been considered a primary production constraint by both farmers and researchers. Intrinsic crop-based challenges such as long crop cycle, large green canopy and shallow root system predispose banana to drought stress (Robinson, 1996). Consequently, breeding programmes like that of India, the NRCB, Mexico, the Centro de Investigacion Cientifica del Yucatan (CICY) and Australia (Turner, 2005) have initiated the screening of germplasm for drought. For instance, NRCB has screened 112 out of 340 genotypes for their response to soil moisture shortage under field conditions (Ravi & Uma, 2011). On the other hand, researchers at Katholieke Universiteit, Leven, Belgium, have focused on developing models for in vitro screening of *Musa* diversity for drought tolerance via proteomics (Vanhove et al., 2012), after which, candidates need to be validated at plant level. In such breeding programmes, large amounts of germplasm have been screened for specific phenotypic traits related to plant growth (plant height, dry matter content, leaf emergence rate, leaf area index, root:shoot ratio), plant water status (water-use efficiency, relative water content, water retention capacity) and plant function (such as stomatal conductance, quantification of photosynthetic pigments) (Delfin et al., 2016; Uma & Sathiamoorthy, 2002). However, there is need for more experimentation at different ecological sites to obtain more reliable information regarding drought-sensitive and resistant accessions. Thereafter, cross-breeding could be utilized to produce drought-resistant genotypes. To date, the utilization of identified resistant candidates in banana drought tolerance improvement using conventional cross-breeding has not yet been reported.

6.3 | Application of molecular markers to improve drought tolerance in banana

Over the years, research programmes have deployed several methods for banana improvement, including conventional cross-breeding, marker-assisted selection, genetic engineering, induced mutation breeding, protoplast fusion and selecting somaclonal variants (Chen et al., 2011). Marker-assisted selection is a molecular breeding technique which is becoming popular because it offers the possibility of significantly reducing the amount of time taken for banana improvement when using conventional cross-breeding, which requires one and a half years for the crop to complete its growth cycle and produce new plantlets (Pillay, Hartman, & Tenkouano, 2002). In major cereal crops, genetic markers which co-inherit with specific target traits have been linked to drought tolerance (Agrama & Moussa, 1996; Courtois et al., 2000; Galeano et al., 2012; Sabouri et al., 2018). For instance, various genetic analyses have linked several markers to major effect quantitative trait loci (QTLs) of grain yield, root morphology, leaf rolling and withering degree, under conditions of drought stress (Champoux et al., 1995; Han et al., 2018; Tabkhkar, Rabiei, Samizadeh Lahiji, & Hosseini Chaleshtori, 2018; Yue et al., 2006). In common bean, QTL mapping revealed twenty-two QTLs responsible for leaf temperature, chlorophyll production, days to flowering as well as traits related to yield and biomass production under stress and watered conditions (Briñez et al., 2017). Such phenotypic traits are often associated with drought tolerance in plants.

In banana, however, molecular markers have mostly been used for germplasm characterization. For example, assessment of genetic diversity within *Musa* genotypes has been done using random amplified polymorphic DNA markers (RAPDs) (Pillay, Ogundiwin, Nwakanma, Ude, & Tenkouano, 2001), restriction fragment length polymorphism markers (RFLPs) (Raboin et al., 2005), microsatellites/simple sequence repeats (SSRs) (Creste, Tulmann, Vencovsky, de Oliveira Silva, & Figueira, 2004; Karamura et al., 2016), amplified fragment length polymorphism markers (AFLPs) (Ahmad, Mergia & Poerba, 2014; Ude, Pillay, Ogundiwin, & Tenkouano, 2003) and diversity array technology markers (DArTs) (Amorim et al., 2009; Risterucci et al., 2009; Ssali, 2016). To our knowledge, no banana breeding programme has developed or screened existing mapping populations with such molecular markers and linked them to drought tolerance. Despite its potential to enhance and hasten banana improvement, the application of molecular markers remains largely unexplored because of the intricate genetics, high genetic similarity and high polyploidy nature of bananas as well as the difficulty in developing segregating populations attributable to either male or female sterility (Ortiz & Swennen, 2014; Pillay et al., 2002). Such screening would permit tagging of specific molecular markers to drought tolerance in bananas. Moreover, marker-assisted selection eliminates environmental effects during selection, especially when screening for multigenic traits like drought tolerance (Mwadzingeni, Shimelis, Dube, Laing, & Tsilo, 2016).

The Banana Genome Hub developed by the French Agricultural Research Centre for International Development (CIRAD) and Bioversity International centralizes databases of genetic and genomic data for the *M. acuminata* crop. It is a valuable resource in banana research as it provides data on the whole genome sequences coupled with gene structures and families, gene product information metabolism, transcriptomics (expressed sequence tags (ESTs), RNA-Seq), molecular markers (SSR, DArT, SNP) and genetic maps (Droc et al., 2013). The ESTs can be used in finding genes, mapping the genome and identification of coding regions in genomic sequences (Fulton, Van der Hoeven, Eannetta, & Tanksley, 2002) as well as developing genetic maps and markers, or to detect functional genes (Pillay et al., 2012). The increasing number of EST databases in different plant species, including *Musa*, is important for developing genetic markers based on ESTs (Ssali, 2016). Furthermore, genetic markers and maps developed from useful sequences can be used in identifying and potentially cloning QTLs and genes of agricultural and biological significance.

6.4 | Integration of biotechnology to improve drought tolerance

Molecular biology and plant tissue culture techniques are applied to enhance the improvement of banana. As such, biotechnology utilizes applications of cell biology such as embryo culture for in vitro seed germination (Uma, Lakshmi, Saraswathi, Akbar, & Mustaffa, 2011), micropropagation for rapid multiplication of banana germplasm and genetic engineering using cell suspensions (Tripathi, Atkinson, Roderick, Kubiriba & Tripathi, 2017). However, the application of genetic engineering requires prior identification and isolation of valuable genes. Since beginning of the 21st century, beneficial genes have been instituted into banana with focus on genes conferring resistance to Fusarium wilt (Paul et al., 2011), black leaf streak disease (Kovacs et al., 2013) and Xanthomonas wilt (Namukwaya et al., 2012) and more recently genes responsible for improved provitamin A content in the banana fruit (Paul et al., 2017). So far, genetic modification techniques including Agrobacterium-mediated transformation and particle bombardment/ biolistic-mediated transformation of banana have yielded stable transgenic lines (Becker, Dugdale, Smith, Harding, & Dale, 2000) and hence can now be deployed to introduce drought tolerance genes in cell lines of drought-sensitive banana cultivars. Similarly, advancements in the efficiency of transformation and regeneration of embryogenic cell suspensions (Wong, Othman, & Khalid, 2008) could be exploited to ensure effective banana drought tolerance improvement. Furthermore, utilization of genetic engineering in banana research could ameliorate deeper understanding of the morpho-physiological and genetic bases of drought tolerance in banana and enable identification of useful putative QTL/gene sequences influencing drought tolerance. Failure to incorporate such biotechnology approaches may not only delay the introgression of drought tolerance genes into banana germplasm but also hinder further understanding of the molecular factors influencing drought tolerance in banana.

7 | CONCLUDING REMARKS AND FUTURE DIRECTIONS

Global banana production is threatened by recurrent drought spells due to its long growth duration. Minimal efforts have been directed towards developing drought-resistant banana cultivars as most research has only gone as far as understanding physiological changes which occur in banana during drought stress, with fewer biochemical and molecular analyses done. Screening efforts have stopped at assessing and reporting drought-tolerant and sensitive cultivars under controlled and field conditions. Therefore, there is a need to develop drought-tolerant cultivars through conventional breeding or identifying candidate genes and integrating them in susceptible cultivars. Systematic studies are required to confirm the role of already identified putative genes and transcription factors such as *M. acuminata* CAMTA1 (*MuCAMTA1*) and *MabZIP* genes in banana drought tolerance. Such molecular factors have potential applications in the genetic improvement of susceptible banana cultivars. Similarly, further refining of phenotypic tools and methodologies to be followed in the field and under controlled conditions is still required. Recent technological developments such as genetic engineering, high-throughput precision phenotyping and marker-assisted selection should also be exploited to hasten improvement of drought tolerance in banana as they permit thorough and precise selection of drought-tolerant candidates. Moreover, genome editing using the CRISPR/Cas9 technology, a type of genetic engineering, can be used to insert drought tolerance genes in the banana genome and silence or knock out genes associated with drought susceptibility.

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CONFLICT OF INTEREST

The authors declare no conflict of interest among them.

AUTHORS CONTRIBUTION

MN prepared the first draft of the manuscript. JS, RT, DK, JK and EK read, revised and approved the submitted version of the manuscript.

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