


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

Moureen Nansamba<sup>1,2</sup>  | Julia Sibiya<sup>2</sup> | Robooni Tumuhimbise<sup>3</sup> | Deborah Karamura<sup>1</sup> | Jerome Kubiriba<sup>3</sup> | Eldad Karamura<sup>1</sup>

<sup>1</sup>Bioversity International, Kampala, Uganda

<sup>2</sup>College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg, South Africa

<sup>3</sup>National Agricultural Research Laboratories, National Agricultural Research Organization, Kampala, Uganda

## Correspondence

Moureen Nansamba, Bioversity International, Kampala, Uganda.  
Email: m.nansamba@cgiar.org

## Funding information

CGIAR Research Program on Roots, Tubers and Bananas; CGIAR

Communicated by: Yehoshua (Shuki) Saranga

## 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 & Fredey, 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, & Mustafa, 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 (Mustafa & Kumar, 2012). However, major production systems such as the East African highland

**TABLE 1** Previously used irrigation regimes in banana

Irrigation treatments	Source
0.25 to 1.25 ET <sup>a</sup> 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)

<sup>a</sup>ET, evapotranspiration from a class A pan.

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).

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,

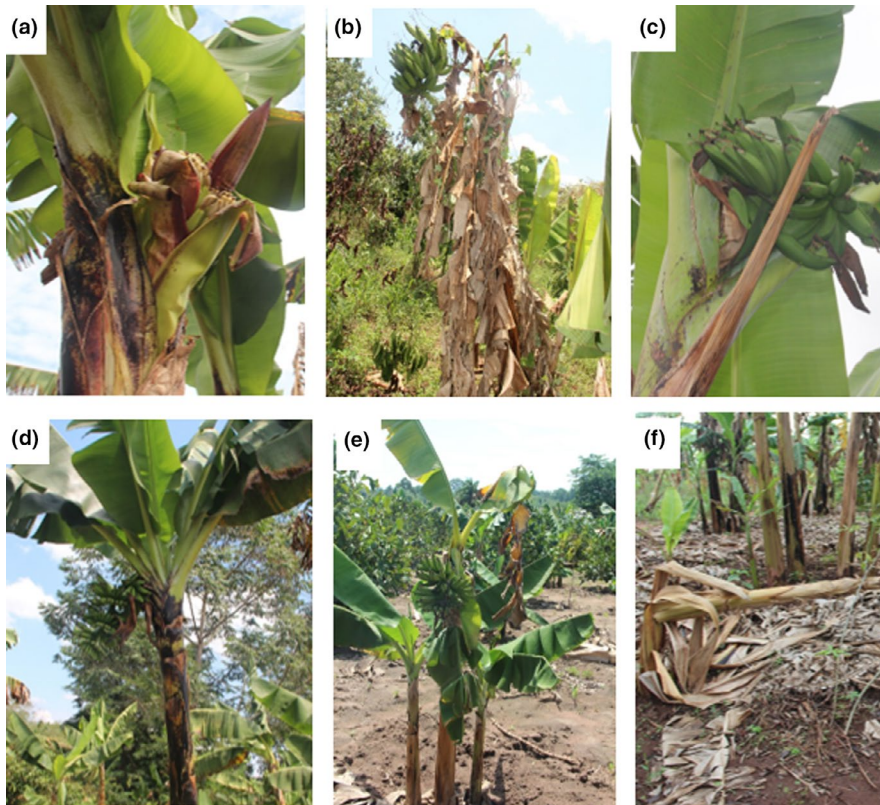
marker-assisted selection and exogenous application of hormones and osmoprotectants to seed or growing plants (Farooq, Wahid, Kobayashi, Fujita, & Basra, 2009). Banana farmers, on the other hand, cope with drought stress by practicing the following management practices to replenish and maintain soil 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 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

## 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 high water-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 & Saucó, 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 (Martinez, 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<sub>2</sub> and O<sub>2</sub><sup>-</sup>), 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<sub>2</sub><sup>-</sup> 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)	<i>MaPIP1;1</i>	Drought, salt	Reduces membrane injury, improves ion distribution and maintains osmotic balance	Xu et al. (2014)
	<i>MaPIP1;2</i>	Drought, cold, salt	Lowers malondialdehyde levels, elevated proline and relative water content and higher photosynthetic efficiency	Sreedharan, Shekhawat, and Ganapathi (2013)
	<i>MaTIP1;2</i> (Promoter)	Drought, salt	Controls the flow of water and other small molecules through biological membranes	Song et al. (2018)
Copper Chaperone Gene	<i>MaCCS</i> 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)	<i>Musa acuminata</i> CAMTA1 ( <i>MuCAMTA1</i> ) transcription factor	Drought	No systematic study has been conducted yet on <i>MuCAMTA</i> transcription factors to identify their role in drought stress in banana plants	Meer, Mumtaz, Labbo, Khan, and Sadiq (2019)
Leucine zipper ( <i>bZIP</i> ) transcription factor gene family	<i>MabZIP</i> 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 ( <i>SWEET</i> )	<i>M. acuminata</i> <i>MaSWEET</i> 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	<i>M. acuminata</i> root hair defective 3 ( <i>MaRHD3</i> )	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, & Mustafa, 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 morphophysiological 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.

## ACKNOWLEDGEMENTS

The authors thank the CGIAR Research Program on Roots, Tubers and Bananas and CGIAR fund donors for supporting to publish this article.

## 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.

## ORCID

Moureen Nansamba  <https://orcid.org/0000-0002-8565-9765>

## REFERENCES

- Agrama, H. A. S., & Moussa, M. E. (1996). Mapping QTLs in breeding for drought tolerance in maize (*Zea mays* L.). *Euphytica*, 9, 89–97. <https://doi.org/10.1007/bf00035278>
- Aguilar Morán, J. F. (2013). Improvement of Cavendish banana cultivars through conventional breeding. *Acta Horticulturae*, 986, 205–208. <https://doi.org/10.17660/ActaHortic.2013.986.21>
- Ahmad, F., Megia, R., & Poerba, Y. S. (2014). Genetic diversity of *Musa balbisiana* Colla in Indonesia based on AFLP Marker. *HAYAT Journal of Biosciences*, 21, 39–47. <https://doi.org/10.4308/hjb.21.1.39>
- Ahmad, M. Q., Khan, S. H., Khan, A. S., Kazi, A. M., & Basra, S. (2014). Identification of QTLs for drought tolerance traits on wheat chromosome 2A using association mapping. *International Journal of Agriculture and Biology*, 16, 862–870.
- Ali, A. B. M., Elshaikh, N. A., Shuang-En, Y., Basheer, A. K., Alnail, M., Alhadi, M., & Altayeb, O. A. (2015). Correlation between water deficiency, yield components and crop productivity of banana. *Journal of Environmental and Agricultural Sciences*, 4, 11–20.
- Amorim, E. P., Vilarinhos, A. D., Cohen, K. O., Amorim, V. B. O., Santos-Serejo, J. A. D., Silva, S. O. E., ... Reis, R. V. D. (2009). Genetic diversity of carotenoid-rich bananas evaluated by Diversity Arrays Technology (DArT). *Genetics and Molecular Biology*, 32, 96–103. <https://doi.org/10.1590/S1415-47572009005000024>
- Anyia, A. O., Slaski, J. J., Nyachiro, J. M., Archambault, D. J., & Juskiw, P. (2007). Relationship of carbon isotope discrimination to water use efficiency and productivity of barley under field and greenhouse conditions. *Journal of Agronomy and Crop Science*, 193, 313–323. <https://doi.org/10.1111/j.1439-037X.2007.00274.x>
- Bananuka, J. A., Rubaihayo, P. R., & Tenywa, M. M. (1999). Reactions of *Musa* genotypes to drought stress. *African Crop Science Journal*, 7, 333–339.
- Barekye, A., Tongoona, P., Derera, J., & Tushemereirwe, W. K. (2009). Variation in diploid (AA) and tetraploid (AAAA) banana populations for black Sigatoka resistance and agronomic traits. *African Crop Science Journal*, 9, 509–516.

- Becker, D. K., Dugdale, B., Smith, M. K., Harding, R. M., & Dale, J. L. (2000). Genetic transformation of Cavendish banana (*Musa* spp. AAA group) cv Grand Nain via microprojectile bombardment. *Plant Cell Reports*, 19, 229–234. <https://doi.org/10.1007/s002990050004>
- Bekunda, M. (1999). Farmers' responses to soil fertility decline in banana-based cropping systems of Uganda. *Managing Africa's soils* No. 4. Nottingham: Russell Press.
- Bekunda, M. A., & Woome, P. L. (1996). Organic resource management in banana-based cropping systems of the Lake Victoria basin, Uganda. *Agriculture Ecosystems & Environment*, 59, 171–180. [https://doi.org/10.1016/0167-8809\(96\)01057-2](https://doi.org/10.1016/0167-8809(96)01057-2)
- Blomme, G., Ocimati, W., Groot, J., Ntamwira, J., Bahati, L., Kantungeko, D., ... Tittone, P. (2018). Agroecological integration of shade- and drought tolerant food/feed crops for year-round productivity in banana-based systems under rain-fed conditions in Central Africa. *Acta Horticulturae*, 1196, 41–54. <https://doi.org/10.17660/ActaHortic.2018.1196.5>
- Blum, A. (n.d.). The Mitigation of Drought stress. Retrieved from [http://www.plantstress.com/Articles/drought\\_m/drought\\_m.htm#mitigation\\_irrigation](http://www.plantstress.com/Articles/drought_m/drought_m.htm#mitigation_irrigation)
- Blum, A. (2017). Osmotic adjustment is a prime drought stress adaptive engine in support of plant production. *Plant, Cell & Environment*, 40, 4–10. <https://doi.org/10.1111/pce.12800>
- Bray, E. A. (1997). Plant responses to water deficit. *Trends in Plant Science*, 2, 48–54. [https://doi.org/10.1016/S1360-1385\(97\)82562-9](https://doi.org/10.1016/S1360-1385(97)82562-9)
- Briñez, B., Perseguini, J. M. K. C., Rosa, J. S., Bassi, D., Gonçalves, J. G. R., Almeida, C., ... Benchimol-Reis, L. L. (2017). Mapping QTLs for drought tolerance in a SEA 5 x AND 277 common bean cross with SSRs and SNP markers. *Genetics and Molecular Biology*, 40, 813–823. <https://doi.org/10.1590/1678-4685-GMB-2016-0222>
- Brouwer, C., & Heibloem, M. (1986). *Irrigation water management: Irrigation water needs*. Rome: Food and Agriculture Organization. Retrieved from: <http://www.fao.org/docrep/S2022E/S2022E00.htm#>
- Cabrera-Bosquet, L., Molero, G., Bort, J., Nogués, S., & Araus, J. L. (2007). The combined effect of constant water deficit and nitrogen supply on WUE, NUE and  $\delta^{15}N$  in durum wheat potted plants. *Annals of Applied Biology*, 151, 277–289. <https://doi.org/10.1111/j.1744-7348.2007.00195.x>
- Carr, M. K. V. (2009). The water relations and irrigation requirements of banana (*Musa* spp.). *Experimental Agriculture*, 45, 333–371. <https://doi.org/10.1017/S001447970900787x>
- Champoux, M. C., Wang, G., Sarkarung, S., Mackill, D. J., O'Toole, J. C., Huang, N., & McCouch, S. R. (1995). Locating genes associated with root morphology and drought avoidance in rice via linkage to molecular markers. *Theoretical and Applied Genetics*, 90, 969–981. <https://doi.org/10.1007/bf00222910>
- Chen, Y. F., Dai, X. M., Gong, Q., Huang, X., Xiao, W., Zhao, J. T., & Huang, X. L. (2011). Non-conventional breeding of banana (*Musa* spp.). *Acta Horticulturae*, 897, 39–46. <https://doi.org/10.17660/actahortic.2011.897.2>
- Coelho, E. F., de Oliveira, R. C., & Pamponet, A. J. M. (2013). Water requirements of terra-type banana under coastal tableland conditions. *Pesquisa Agropecuária Brasileira*, 48, 1260–1268. <https://doi.org/10.1590/s0100-204x2013000900010>
- Courtois, B., McLaren, G., Sinha, P. K., Prasad, K., Yadav, R., & Shen, L. (2000). Mapping QTLs associated with drought avoidance in upland rice. *Molecular Breeding*, 6, 55–66.
- Creste, S., Tullmann, N. A., Vencovsky, R., de Oliveira Silva, S., & Figueira, A. (2004). Genetic diversity of *Musa* diploid and triploid accessions from the Brazilian banana breeding program estimated by microsatellite markers. *Genetic Resources and Crop Evolution*, 51, 723–733. <https://doi.org/10.1023/b:gres.0000034578.37951.c4>
- D'Albuquerque, J., Gomes, E. R., de Sousa, V. F., & de Sousa, A. P. (2013). Water requirement and levels of irrigation of banana FHIA-18 in the semiarid region of Piauí state. *IRRIGA*, 18, 756–767.
- Dekov, I., Tsonev, T., & Yordanov, I. (2000). Effect of water stress and high temperature stress on structure and activity of photosynthetic apparatus of *Zea mays* and *Helianthus annuus*. *Photosynthetica*, 38, 361–366. <https://doi.org/10.1023/a:1010961218145>
- Delfin, E. F., Ocampo, E. T. M., Cueva, F. M., Damasco, O. P., de la Cruz, F., Dinglasan, E. G., ... Molina, A. B. (2016). Response of wild and edible *Musa* spp. seedlings to limiting moisture stress. *Philippine Journal of Crop Science*, 41(3), 1–12.
- Droc, G., Larivière, D., Guignon, V., Yahiaoui, N., This, D., Garsmeur, O., ... Bocs, S. (2013). The banana genome Hub. *Database* 2013. <https://doi.org/10.1093/database/bat035>
- Edward, E., & Fredy, B. (2012). *Banana Market*. Florida: University of Florida/IFAS extension.
- Fandika, I. R., Kadyampakeni, D., Mwenebanda, B. M. L., & Magombo, T. M. (2014). Banana irrigation management and optimization: A comparative study of researcher-managed and farmer-managed irrigated banana production in Shire Valley, Malawi. *African Journal of Agricultural Research*, 9, 2687–2693. <https://doi.org/10.5897/ajar09.302>
- FAOSTAT (2017). *Food and Agricultural Organization (FAO)*. Retrieved from: <http://www.fao.org/faostat/en/#data/QC>. Accessed on Sat May 04 14:9:42 EAT 2019.
- Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., & Basra, S. M. A. (2009). Plant drought stress: Effects, mechanisms and management. *Agronomy for Sustainable Development*, 29, 185–212. [https://doi.org/10.1007/978-90-481-2666-8\\_12](https://doi.org/10.1007/978-90-481-2666-8_12)
- Feng, X., Chen, F., Liu, W., Thu, M., Zhang, Z., Chen, Y., ... Lai, Z. (2016). Molecular characterization of MaCCS, a novel copper chaperone gene involved in abiotic and hormonal stress responses in *Musa acuminata* cv. Tianbaojiao. *International Journal of Molecular Sciences*, 17, 441. <https://doi.org/10.3390/ijms17040441>
- Flexas, J., & Medrano, H. (2002). Drought-inhibition of photosynthesis in C3 plants: Stomatal and non-stomatal limitations revisited. *Annals of Botany*, 89, 183–189. <https://doi.org/10.1093/aob/mcb027>
- Foyer, C. H., & Noctor, G. (2000). Oxygen processing in photosynthesis: Regulation and signaling. *New Phytologist*, 146, 359–388.
- Fulton, T., van der Hoeven, R., Eannetta, N. T., & Tanksley, S. D. (2002). Identification, analysis and utilization of conserved ortholog set (COS) markers for comparative genomics in higher plants. *Plant Cell*, 14, 1457–1467. <https://doi.org/10.1105/tpc.010479>
- Fungo, R., & Pillay, M. (2011).  $\beta$ -Carotene content of selected banana genotypes from Uganda. *African Journal of Biotechnology*, 10, 5423–5430. <https://doi.org/10.5897/ajb10.1047>
- Galeano, C. H., Cortés, A. J., Fernández, A. C., Soler, Á., Franco-Herrera, N., Makunde, G., ... Blair, M. W. (2012). Gene-based Single Nucleotide Polymorphism Markers for genetic and association mapping in common bean. *BMC Genetics*, 13, 48. <https://doi.org/10.1186/1471-2156-13-48>
- Gill, S. S., & Tuteja, N. (2010). Reactive oxygen species and antioxidant machinery in abiotic tolerance in crop plants. *Plant Physiology and Biochemistry*, 48, 909–930. <https://doi.org/10.1016/j.plaphy.2010.08.016>
- Goenaga, R., & Irizarry, H. (1998). Yield of banana growth with supplemental drip irrigation on an ultisol. *Experimental Agriculture*, 34, 439–448. <https://doi.org/10.1017/s0014479798004062>
- Goenaga, R., & Irizarry, H. (2000). Yield and quality of banana irrigated with fractions of class A pan evaporation on an oxisol. *Agronomy Journal*, 92, 1008–1012. <https://doi.org/10.2134/agronj2000.9251008x>
- Gold, C. S., Kagezi, G. H., Night, G., & Ragama, P. E. (2004). The effects of banana weevil, *Cosmopolites sordidus* (Germar), damage on highland banana growth, yield and stand duration in Uganda. *Annals of Applied Biology*, 145, 263–269. <https://doi.org/10.1111/j.1744-7348.2004.tb00382.x>
- Govindappa, M., & Pallavi Seenappa, C. (2014). Importance of mulching as a soil and water conservative practice in fruit and vegetable

- production-Review. *International Journal of Agriculture Innovations and Research*, 3, 1014–1017.
- Haefele, S. M., Siopongco, J. D. L. C., Boling, A. A., Bouman, B. A. M., & Tuong, T. P. (2009). Transpiration efficiency of rice (*Oryza sativa* L.). *Field Crops Research*, 111, 1–10. <https://doi.org/10.1016/j.fcr.2008.09.008>
- Han, B., Wang, J., Li, Y., Ma, X., Jo, S., Cui, D. I., ... Han, L. (2018). Identification of quantitative trait loci associated with drought tolerance traits in rice (*Oryza sativa* L.) under PEG and field drought stress. *Euphytica*, 214, 74. <https://doi.org/10.1007/s10681-018-2138-y>
- Hayat, S., Hayat, Q., Alyemeni, M. N., Wani, A. S., John Pichtel, J., & Ahmad, A. (2012). Role of proline under changing environments – A review. *Plant Signaling & Behavior*, 7, 1456–1466. <https://doi.org/10.4161/psb.21949>
- Hu, W., Wang, L., Tie, W., Yan, Y., Ding, Z., Liu, J., ... Jin, Z. (2016). Genome-wide analyses of the bZIP family reveal their involvement in the development, ripening and abiotic stress response in banana. *Scientific Reports*, 6, 30203. <https://doi.org/10.1038/srep30203>
- Hulme, M., Doherty, R., Ngara, T., New, M., & Lister, D. (2001). African climate change: 1900–2100. *Climate Research*, 17, 145–168. <https://doi.org/10.3354/cr017145>
- Ibrahim, S. E., Schubert, A., Pillen, K., & Léon, J. (2012). QTL analysis of drought tolerance for seedling root morphological traits in an advanced backcross population of spring wheat. *International Journal of AgriScience*, 2, 619–629.
- Jones, H. G. (2014). *Plants and microclimate: A quantitative approach to environmental plant physiology*, 3rd ed. Cambridge: Cambridge University Press.
- Kabunga, N. S., Dubois, T., & Qaim, M. (2012). Yield effects of tissue culture bananas in Kenya: Accounting for selection bias and the role of complementary inputs. *Journal of Agriculture Economics*, 63, 444–464. <https://doi.org/10.1111/j.1477-9552.2012.00337.x>
- Karamura, D., Kitavi, M., Nyine, M., Ochola, D., Ocimati, W., Muhangi, S., ... Karamura, E. B. (2016). Genotyping the local banana landrace groups of East Africa. *Acta Horticulturae*, 1114, 67–74. <https://doi.org/10.17660/ActaHortic.2016.1114.9>
- Kissel, E., van Asten, P., Swennen, R., Lorenzen, J., & Carpentier, S. C. (2015). Transpiration efficiency versus growth: Exploring the banana biodiversity for drought tolerance. *Scientia Horticulturae*, 185, 175–182. <https://doi.org/10.1016/j.scienta.2015.01.035>
- Kovács, G., Sági, L., Jacon, G., Arinaitwe, G., Busogoro, J.-P., Thiry, E., ... Remy, S. (2013). Expression of a rice chitinase gene in transgenic banana ('Gros Michel', AAA genome group) confers resistance to black leaf streak disease. *Transgenic Research*, 22, 117–130. <https://doi.org/10.1007/s11248-012-9631-1>
- Lacerda, C. F., Cambraia, J., Cano, M., & Ruiz, H. A. (2001). Plant growth and solute accumulation and distribution in two sorghum genotypes under NaCl stress. *Revista Brasileira De Fisiologia Vegetal*, 13, 270–284. <https://doi.org/10.1590/S0103-31312001000300003>
- Liu, S., Wang, X., Wang, H., Xin, H., Yang, X., Yan, J., ... Qin, F. (2013). Genome-wide analysis of ZmDREB genes and their association with natural variation in drought tolerance at seedling stage of *Zea mays* L. *PLOS Genetics*, 9(9), e1003790. <https://doi.org/10.1371/journal.pgen.1003790>
- Mahouachi, J. (2007). Growth and mineral nutrient content of developing fruit on banana plants (*Musa acuminata* AAA, 'Grand Nain') subjected to water stress and recovery. *The Journal of Horticulture Science & Biotechnology*, 82, 839–844. <https://doi.org/10.1080/14620316.2007.11512315>
- Mahouachi, J. (2009). Changes in nutrient concentrations and leaf gas exchange parameters in banana plantlets under gradual soil moisture depletion. *Scientia Horticulturae*, 120, 460–466. <https://doi.org/10.1016/j.scienta.2008.12.002>
- Manimaran, P., Sanjay, M. R., Senthamaraiannan, P., Jawaid, M., Saravanakumar, S. S., & George, R. (2018). Synthesis and characterization of cellulosic fiber from red banana peduncle as reinforcement for potential applications. *Journal of Natural Fibers*, 16, 768–780. <https://doi.org/10.1080/15440478.2018.1434851>
- Marin, D. H., Romero, R. A., Guzman, M., & Sutton, T. B. (2003). Black Sigatoka: An increasing threat to banana cultivation. *Plant Disease*, 87, 208–222. <https://doi.org/10.1094/pdis.2003.87.3.208>
- Martínez, J. P., Lutts, S., Schanck, A., Bajji, M., & Kinet, J.-M. (2004). Is osmotic adjustment required for water stress resistance in the Mediterranean shrub *Atriplex halimus* L. *Journal of Plant Physiology*, 161, 1041–1051. <https://doi.org/10.1016/j.jplph.2003.12.009>
- Mattos-Moreira, L. A., Ferreira, C. F., Amorim, E. P., Pirovani, C. P., de Andrade, E. M., Filho, M. A. C., ... da Silva Ledo, C. A. (2018). Differentially expressed proteins associated with drought tolerance in bananas (*Musa* spp.). *Acta Physiologiae Plantarum*, 40, <https://doi.org/10.1007/s11738-018-2638-3>
- Meer, L., Mumtaz, S., Labbo, A. M., Khan, M. J., & Sadiq, I. (2019). Genome-wide identification and expression analysis of calmodulin-binding transcription activator genes in banana under drought stress. *Scientia Horticulturae*, 244, 10–14. <https://doi.org/10.1016/j.scienta.2018.09.022>
- Miao, H., Sun, P., Liu, Q., Miao, Y., Liu, J., Zhang, K., ... Jin, Z. (2017). Genome-wide analyses of SWEET family proteins reveal involvement in fruit development and abiotic/ biotic stress responses in banana. *Scientific Reports*, 7, 3536. <https://doi.org/10.1038/s41598-017-03872-w>
- Mustaffa, M. M., & Kumar, V. (2012). Banana production and productivity enhancement through spatial, water and nutrient management. *Journal of Horticultural Science*, 7(1), 1–28.
- Muthusamy, M., Uma, S., Backiyarani, S., Saraswathi, M. S., & Chandrasekar, A. (2016). Transcriptomic changes of drought tolerant and sensitive cultivars exposed to drought stress. *Frontiers in Plant Science*, 7, <https://doi.org/10.3389/fpls.2016.01609>
- Mwadingeni, L., Shimelis, H., Dube, E., Laing, M. D., & Tsilo, T. J. (2016). Breeding wheat for drought tolerance: Progress and technologies. *Journal of Integrative Agriculture*, 15, 935–943. [https://doi.org/10.1016/S2095-3119\(15\)61102-9](https://doi.org/10.1016/S2095-3119(15)61102-9)
- Namukwaya, B., Tripathi, L., Tripathi, J. N., Arinaitwe, G., Mukasa, S. B., & Tushemereirwe, W. K. (2012). Transgenic banana expressing Pflp gene confers enhanced resistance to *Xanthomonas* wilt disease. *Transgenic Research*, 21, 855–865. <https://doi.org/10.1007/s11248-011-9574-y>
- National Research Centre for Banana (ICAR) (2008). 2008 annual report. Trichy, India: Anon.
- Negi, S., Tak, H., & Ganapathi, T. R. (2018). A banana NAC transcription factor (*MusaSNAC1*) impart drought tolerance by modulating stomatal closure and H<sub>2</sub>O<sub>2</sub> content. *Plant Molecular Biology*, 96, 457–471. <https://doi.org/10.1007/s11103-018-0710-4>
- Niyongere, C., Losenge, T., Ateke, E. M., Nkezahizi, D., Blomme, G., & Lepoint, P. (2012). Occurrence and distribution of banana bunchy top disease in the Great Lakes Region of Africa. *Tree and Forestry Science and Biotechnology*, 6, 102–107.
- Nowakunda, K., Barekye, A., Ssali, R. T., Namaganda, J., Tushemereirwe, W. K., Nabulya, G., ... Karamura, D. (2015). 'Kiwangaazi' (syn 'KABANA 6H') Black Sigatoka nematode and banana weevil tolerant 'Matooke' hybrid banana released in Uganda. *HortScience*, 50, 621–623. <https://doi.org/10.21273/hortsci.50.4.621>
- Ocan, D., Mukasa, H. H., Rubaihayo, P. R., Tinzaara, W., & Blomme, G. (2008). Effects of banana weevil damage on plant growth and yield of East African *Musa* genotypes. *Journal of Applied Biosciences*, 9, 407–415.
- Ocimati, W., Nakato, G. V., Fiaboe, K. K. M., Beed, F., & Blomme, G. (2014). Incomplete systemic movement of *Xanthomonas campestris* pv. *musacearum* and the occurrence of latent infections in *Xanthomonas* wilt-infected banana mats. *Plant Pathology*, 64, 81–90. <https://doi.org/10.1111/ppa.12233>

- Orgaz, F., Fernandez, M. D., Bonachela, S., Gallardo, M., & Fereres, E. (2005). Evapotranspiration of horticultural crops in an unheated plastic greenhouse. *Agricultural Water Management*, 72, 81–96. <https://doi.org/10.1016/j.agwat.2004.09.010>
- Ortiz, R., & Swennen, R. (2014). From crossbreeding to biotechnology-facilitated improvement of banana and plantain. *Biotechnology Advances*, 32, 158–169. <https://doi.org/10.1016/j.biotechadv.2013.09.010>
- Passioura, J. B. (2012). Phenotyping for drought tolerance in grain crops: When is it useful to breeders? *Functional Plant Biology*, 39, 377–412. <https://doi.org/10.1071/fp12079>
- Paul, J.-Y., Becker, D. K., Dickman, M. B., Harding, R. M., Khanna, H. K., & Dale, J. L. (2011). Apoptosis-related genes confer resistance to fusarium wilt in transgenic 'Lady Finger' bananas. *Plant Biotechnology Journal*, 9, 1141–1148. <https://doi.org/10.1111/j.1467-7652.2011.00639.x>
- Paul, J.-Y., Khanna, H., Kleidon, J., Hoang, P., Geijskes, J., Daniells, J., ... Dale, J. (2017). Golden bananas in the field: Elevated fruit pro-vitamin A from the expression of a single banana transgene. *Plant Biotechnology Journal*, 15, 520–532. <https://doi.org/10.1111/pbi.12650>
- Pillay, M., Ashokkumar, K., James, A., Kirubakara, S. J., Miller, R., Ortiz, R., ... Sivalingam, E. (2012). Molecular marker techniques in Musa genomic research. In M. Pillay, G. Ude, & C. Kole (Eds.), *Genetics, Genomics, and Breeding of Bananas* (pp. 70–90). USA: Science Publishers Inc.
- Pillay, M., Hartman, J., & Tenkouano, A. (2002). Bananas and plantains: Future challenges in Musa breeding. In M. S. Kang (Ed.), *Crop improvement, challenges in the twenty-first century* (pp. 223–252). New York, NY: Food Products Press.
- Pillay, M., Ogundiwin, E., Nwakanma, D. C., Ude, G., & Tenkouano, A. (2001). Analysis of genetic diversity and relationships in East African banana germplasm. *Theoretical and Applied Genetics*, 102, 965–970. <https://doi.org/10.1007/s001220000500>
- Pimentel, C. (1999). Water relations in two hybrids of corn under two cycles of water stress. *Pesquisa Agropecuária Brasileira*, 34, 2021–2027. <https://doi.org/10.1590/S0100-204x1999001100007>
- Ploetz, R. C. (2015). Fusarium wilt of banana. *Phytopathology*, 105, 1512–1521. <https://doi.org/10.1094/PHYTO-04-15-0101-RVW>
- Raboin, L.-M., Carreel, F., Noyer, J.-L., Baurens, F.-C., Horry, J.-P., Bakry, F., ... Lagoda, P. J. L. (2005). Diploid ancestors of triploid export banana cultivars: Molecular identification of 2n restitution gamete donors and n gamete donors. *Molecular Breeding*, 16, 333–341. <https://doi.org/10.1007/s11032-005-2452-7>
- Raemaekers, R. H. (2001). *Crop production in tropical Africa* (p. 1540). Brussels, Belgium: Directorate General for International Cooperation (DGIC).
- Ramirez, J., Jarvis, A., Van den Bergh, I., Staver, C., & Turner, D. (2011). Chapter 20: Changing climates: Effects on growing conditions for banana and plantain (Musa spp.) and possible responses. In S. Yadav, B. Redden, J. L. Hattfield, & H. Lotze-Campen (Eds.), *Crop adaptation to climate change* (pp. 426–438). Chichester, UK: Wiley-Blackwell Publishing Ltd.
- Ravi, I., & Uma, S. (2011). Phenotyping bananas and plantains for adaptation to drought. In M. Philippe, & R. Jean-Marcel (Eds.), *Drought phenotyping in crops: From theory to practice*. Texcoco, Mexico: CGIAR Generation Challenge Programme/CIMMYT.
- Ravi, I., Uma, S., Vaganan, M. M., & Mustafa, M. M. (2013). Phenotyping bananas for drought resistance. *Frontiers in Physiology*, 4, <https://doi.org/10.3389/fphys.2013.00009>
- Ravi, I., & Vaganan, M. M. (2016). Abiotic stress tolerance in banana. In N. K. S. Rao, K. S. Shivashankara, & R. H. Laxman (Eds.), *Abiotic stress physiology of horticultural crops* (pp. 207–222). New Delhi, India: Springer.
- Risterucci, A.-M., Hippolyte, I., Perrier, X., Xia, L., Caig, V., Evers, M., ... Glaszmann, J.-C. (2009). Development and assessment of Diversity Arrays Technology for high-throughput DNA analyses in Musa. *Theoretical and Applied Genetics*, 119, 1093–1103. <https://doi.org/10.1007/s00122-009-1111-5>
- Robinson, J. C. (1996). *Banana and plantains*. Wallingford, UK: CAB International.
- Robinson, J. C. (2000). Banana productivity—the impact of agronomic practices. *Acta Horticulturae*, 540, 247–258. <https://doi.org/10.17660/ActaHortic.2000.540.28>
- Robinson, J. C., & Alberts, A. J. (1986). Growth and yield responses of banana (cultivar 'Williams') to drip irrigation under drought and normal rainfall conditions in the subtropics. *Scientia Horticulturae*, 30, 187–202. [https://doi.org/10.1016/0304-4238\(86\)90097-x](https://doi.org/10.1016/0304-4238(86)90097-x)
- Robinson, J. C., & Saucó, V. G. (2010). *Bananas and Plantains*, 2nd ed. Wallingford, UK: CAB International.
- Sabouri, A., Afshari, R., Raiesi, T., Raouf, H. B., Nasiri, E., Esfahani, M., ... Kumar, A. (2018). Superior adaptation of aerobic rice under drought stress in Iran and validation test of linked SSR markers to major QTLs by MLM analysis across two years. *Molecular Biology Reports*, 45, 1037–1053. <https://doi.org/10.1007/s11033-018-4253-1>
- Sairam, R. K., Shukla, D. S., & Saxena, D. C. (1997). Stress induced injury and antioxidant enzymes in relation to drought tolerance in wheat genotypes. *Biological Plantarum*, 40, 357–364. <https://doi.org/10.1023/a:1001009812864>
- Shim, J. S., Oh, N., Chung, P. J., Kim, Y. S., Choi, Y. D., & Kim, J. K. (2018). Overexpression of OsNAC14 improves drought tolerance in rice. *Frontiers in Plant Science*, 9, <https://doi.org/10.3389/fpls.2018.00310>
- Shongwe, V. D., Tumber, R., Masarirambi, M. D., & Mutukumira, A. N. (2008). Soil water requirements of tissue-cultured dwarf Cavendish banana (Musa spp. L). *Physics and Chemistry of the Earth*, 33, 768–774. <https://doi.org/10.1016/j.pce.2008.06.018>
- Simmonds, N. W. (1962). *The evolution of the Bananas*. London: Longmans.
- Simmonds, N. W. (1966). *Bananas*, 2nd ed. London: Longmans.
- Singh, H. P., & Uma, S. (2000). Genetic diversity of banana in India. In H. P. Singh, & K. L. Chadha (Eds.), *Banana improvement, production and utilization* (pp. 136–156). Proceedings of the Conference on Challenges for Banana Production and Utilization in 21st Century held in Trichy, India.
- Song, S., Xu, Y. I., Huang, D., Miao, H., Liu, J., Jia, C., ... Jin, Z. (2018). Identification of a novel promoter from banana aquaporin family gene (MaTIP1;2) which responds to drought and salt-stress in transgenic Arabidopsis thaliana. *Plant Physiology and Biochemistry*, 128, 163–169. <https://doi.org/10.1016/j.plaphy.2018.05.003>
- Speijer, P. R. (1999). East African Highland banana production as influenced by nematodes and crop management in Uganda. *International Journal of Pest Management*, 45, 41–49. <https://doi.org/10.1080/096708799228030>
- Sreedharan, S., Shekhawat, U. K. S., & Ganapathi, T. R. (2013). Transgenic banana plants overexpressing a native plasma membrane aquaporin MusaPIP1;2 display high tolerance levels to different abiotic stresses. *Plant Biotechnology Journal*, 11, 942–952. <https://doi.org/10.1111/pbi.12086>
- Ssali, R. T. (2016). The identification and characterization of resistance Musa to Fusarium Oxysporum f. sp cubense race 1 (PhD thesis). Stellenbosch: University, Stellenbosch, South Africa.
- Surendar, K. K., Devi, D. D., Ravi, I., Jeyakumar, P., Kumar, S. R., & Velayudham, K. (2013c). Effect of water deficit on yield and epicuticular wax, proline and free amino acid content of banana cultivars and hybrids. *World Journal of Agricultural Sciences*, 9, 201–209. <https://doi.org/10.5829/idosi.wjas.2013.9.2.1725>
- Surendar, K. K., Devi, D. D., Ravi, I., Jeyakumar, P., & Velayudham, K. (2013b). Physiological and biochemical behavior in banana cultivars and hybrids under water deficit. *African Journal of Agricultural Research*, 8, 4198–4208. <https://doi.org/10.5897/ajar2013.7454>
- Surendar, K. K., Devi, D. D., Ravi, I., Krishnakumar, S., Kumar, S. R., & Velayudham, K. (2013a). Water Stress in Banana – A Review. *Bulletin of Environment, Pharmacology and Life Sciences*, 2(6), 1–18.

- Swennen, R. (1990). *Plantain cultivation under West African conditions-A reference manual* (pp. 24). Ibadan, Nigeria: International Institute of Tropical Agriculture (IITA).
- Swennen, R., Carpentier, S. C., Henry, I. M., Vertommen, A., Van den houwe, I., Kovacs, G., ... Panis, B. (2011). From fundamental research discoveries to applications for banana improvement. *Acta Horticulturae*, 897, 47–53. <https://doi.org/10.17660/ActaHortic.2011.897.3>
- Tabkhkar, N., Rabiei, B., Samizadeh Lahiji, H., & Hosseini Chaleshtori, M. (2018). Genetic variation and association analysis of the SSR Markers linked to the major drought-yield QTLs of rice. *Biochemical Genetics*, 56, 356–374. <https://doi.org/10.1007/s10528-018-9849-6>
- Taulya, G., van Asten, P. J. A., Okech, S., & Gold, C. (2006). Effect of drought on the yields of an East African highland banana (cv. 'Kisansa') in Uganda. In: Proceedings of the 23rd Soil Science Society of East Africa conference held in Masaka, Uganda, November.
- Tenkouano, A. (2006). Recent advances and challenges in banana and plantain breeding. In H. P. Singh, & S. Uma (Eds.), *Banana technological advances* (pp. 141–159). India: Trichy.
- Thomas, D. S., & Turner, D. (2001). Banana (*Musa* spp.) leaf gas exchange and chlorophyll fluorescence in response to soil drought, shading and lamina folding. *Scientia Horticulturae*, 90, 93–108. [https://doi.org/10.1016/S0304-4238\(00\)00260-0](https://doi.org/10.1016/S0304-4238(00)00260-0)
- Thomas, D. S., Turner, D., & Eamus, D. (1998). Independent effects of the environment on the leaf gas exchange of three banana (*Musa* spp.) cultivars of different genomic constitution. *Scientia Horticulturae*, 75, 41–57. [https://doi.org/10.1016/S0304-4238\(98\)00114-9](https://doi.org/10.1016/S0304-4238(98)00114-9)
- Tripathi, L., Atkinson, H., Roderick, H., Kubiriba, J., & Tripathi, J. N. (2017). Genetically engineered bananas resistant to *Xanthomonas* wilt disease and nematodes. *Food and Energy Security*, 6, 37–47. <https://doi.org/10.1002/fes3.101>
- Tripathi, L., Mwaka, H., Tripathi, J. N., & Tushemereirwe, W. K. (2010). Expression of sweet pepper Hrp gene in banana enhances resistance to *Xanthomonas campestris* pv. *musacearum*. *Molecular Plant Pathology*, 11, 721–731. <https://doi.org/10.1111/j.1364-3703.2010.00639.x>
- Tripathi, L., Tripathi, J. N., Tushemereirwe, W. K., Arinaitwe, G., & Kiggundu, A. (2013). Transgenic bananas with enhanced resistance against *Xanthomonas* wilt disease. *Acta Horticulturae*, 974, 81–90. <https://doi.org/10.17660/ActaHortic.2013.974.9>
- Tuberosa, R. (2012). Phenotyping for drought tolerance of crops in the genomics era. *Frontiers in Physiology*, 3, <https://doi.org/10.3389/fphys.2012.00347>
- Turner, D. W. (2005). Factors affecting the physiology of the banana root system. In D. W. Turner, & F. E. Rosales (Eds.), *Towards a better understanding of for its productive management* (pp. 107–113). Montpellier, France: International Network for the Improvement of Banana and Plantain (INIBAP).
- Ude, G., Pillay, M., Ogundiwin, E., & Tenkouano, A. (2003). Genetic diversity in an African plantain core collection using AFLP and RAPD markers. *Theoretical and Applied Genetics*, 107, 248–255. <https://doi.org/10.1007/s00122-003-1246-8>
- Uma, S., Lakshmi, S., Saraswathi, M. S., Akbar, A., & Mustaffa, M. M. (2011). Embryo rescue and plant regeneration in banana (*Musa* spp.). *Plant Cell, Tissue and Organ Culture*, 105, 105–111. <https://doi.org/10.1007/s11240-010-9847-9>
- Uma, S., & Sathiamoorthy, S. (2002). *Names and synonyms of bananas and plantains in India*. Trichy, India: National Research Centre for Banana, ICAR.
- Uma, S., Sathiamoorthy, S., Singh, H. P., & Dayarani, M. (2002). Crop improvement in *Musa*-evaluation of germplasm for male and female fertility. *Indian Journal of Plant Genetic Resources*, 15, 137–139.
- van Asten, P. J. A., Fermont, A. M., & Taulya, G. (2011). Drought is a major yield loss factor for rainfed East African highland banana. *Agricultural Water Management*, 98, 541–552. <https://doi.org/10.1016/j.agwat.2010.10.005>
- Vanhove, A. C., Vermaelen, W., Panis, B., Swennen, R., & Carpentier, S. C. (2012). Screening the banana biodiversity for drought tolerance: Can an in vitro growth model and proteomics be used as a tool to discover tolerant varieties and understand homeostasis. *Frontiers in Plant Science*, 3, <https://doi.org/10.3389/fpls.2012.00176>
- Wairegi, L. W. I., van Asten, P. J. A., Tenywa, M. M., & Bekunda, M. A. (2010). Abiotic constraints override biotic constraints in East African highland banana systems. *Field Crops Research*, 117, 146–153. <https://doi.org/10.1016/j.fcr.2010.02.010>
- Wang, X., Wang, H., Liu, S., Ferjani, A., Li, J., Yan, J., ... Qin, F. (2016). Genetic variation in *ZmVPP1* contributes to drought tolerance in maize seedlings. *Nature Genetics*, 48, 1233–1241. <https://doi.org/10.1038/ng.3636>
- Wong, W. C., Othman, R. Y., & Khalid, N. (2008). Improvements in the efficiency of *Agrobacterium*-mediated transformation of embryogenic cell suspensions of banana cv. 'Mas' using a low-antibiotic liquid washing-assisted approach. *Transgenic Plant Journal*, 2, 75–85.
- Wonga, G. R., Mazumdar, P., Laub, S., & Harikrishna, J. A. (2018). Ectopic expression of a *Musa acuminata* root hair defective 3 (*MaRHD3*) in *Arabidopsis* enhances drought tolerance. *Journal of Plant Physiology*, 231, 219–233. <https://doi.org/10.1016/j.jplph.2018.09.018>
- Xu, Y. I., Hu, W., Liu, J., Zhang, J., Jia, C., Miao, H., ... Jin, Z. (2014). A banana aquaporin gene, *MaPIP1; 1*, is involved in tolerance to drought and salt stresses. *BMC Plant Biology*, 14, 59. <https://doi.org/10.1186/1471-2229-14-59>
- Yue, B., Xue, W., Xiong, L., Yu, X., Luo, L., Cui, K., ... Zhang, Q. (2006). Genetic basis of drought resistance at reproductive stage in rice: Separation of drought tolerance from drought avoidance. *Genetics*, 172, 1213–1228. <https://doi.org/10.1534/genetics.105.045062>

**How to cite this article:** Nansamba M, Sibiya J, Tumuhimbise R, Karamura D, Kubiriba J, Karamura E. Breeding banana (*Musa* spp.) for drought tolerance: A review. *Plant Breed*. 2020;139:685–696. <https://doi.org/10.1111/pbr.12812>