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Differential Growth and Transpiration Responses Among Banana (*Musa* Spp.) Hybrids—Hope for Breeding Drought Tolerant Bananas?

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Drought stress greatly impacts banana (*Musa* spp.) production (Van Asten et al. 2011), limiting its growth and yield. In the East African Great Lakes region, East African highland bananas (EAHBs) dominate the agricultural production systems (Karamura et al. 2012). They are considered endemic to the region with no clear analogues elsewhere in the world. The existing EAHB genetic diversity is limited, as it is only based on somaclonal mutations and continuous farmer selection (Perrier et al. 2011). The polygenic nature of drought tolerance, coupled with banana's inherent sterility and polyploid nature, is a challenge to the crop's improvement through crossbreeding, but several hybrids with improved pest and disease traits and higher yield have been made (Batte et al. 2019). EAHBs are mainly grown on smallholder farms where they provide food and income security. They only occur at high altitudes (900–2000 m above sea level), which are associated with cooler temperatures and hence a lower evaporative demand (Karamura et al. 2012). Their high-water usage, low water use efficiency, and weak drought avoidance mechanism make them vulnerable to higher evaporative demands (Eyland et al. 2021). Considering this water-spending nature, global warming and market preferences (Akankwasa et al. 2020), it is crucial to improve the resilience of these endemic banana varieties to future environmental conditions through breeding. The objectives of the study were to determine the impact of meiotic recombinations on the variability of water usage and assess the growth behaviour and transpiration responses of secondary banana hybrids and their parental lines to declining soil water content (SWC) in function of light intensity (photosynthetic active radiation, PAR) and vapour pressure deficit (VPD). We hypothesised that despite the narrow genetic diversity observed within the EAHB varieties and the high-water usage, the meiotic recombination would lead to the segregation of reactions of transpiration responses and resulting growth to fluctuating VPD, PAR and SWC. To our knowledge, we present the first study that evaluates the performance of bananas developed purposely for improved drought avoidance and tolerance majorly based on the '*Musa acuminata*' genetic background.

Materials and methods can be found in Supporting Information S2. Two phenotyping experiments were performed concurrently at the Bioversity International phenotyping facility (Phenospex, Heerlen, Netherlands) hosted at KU Leuven, in Leuven, Belgium. Eighteen banana genotypes comprising 16 EAHB progenies and their two parental lines, '917K-2' (female) and 'TMB2x9172' (male), were phenotyped (Supporting Information S3: Table S1). Plant growth and transpiration were monitored as a function of the environment (SWC, PAR and VPD). To disentangle the environmental impacts, transpiration rates were additionally modelled according to the Jarvis–Stewart model (Jarvis 1976; Eyland et al. 2022).

We detected significant genotype-specific responses to declining SWC, varying VPD and PAR (Figure 1a–d, Supporting Information S3: Tables S2–S3, Supporting Information S1: Figures S1). Despite the fact that all plants started the experiment with a comparable leaf area, significant genotypic variations in the average number of days it took for the SWC to drop to −1.92 MPa were observed ($p < 0.001$) (Supporting Information S3: Table S2). The total leaf area after 3 weeks of drought assessment differed significantly across the studied banana genotypes ($p < 0.05$), water treatments ($p < 0.001$) and significant genotype × water treatment interactions were observed ($p < 0.05$) (Supporting Information S3: Table S2). Also, modelled maximum transpiration rates (E_{max}) significantly differed among the genotypes, ranging between 0.8 and 1.9 kg m^{-2} day^{-1} (Supporting Information S3: Table S3).

An artificial X variable was created to objectively quantify the transpiration behaviour using the modelled E_{max}, SWC_{crit} and slope of decline in transpiration rate (SWC_{slope}). A significant correlation was found in the function of leaf damage. The loading scores indicated that transpiration behaviour, and hence water usage, is mainly influenced by the SWC_{crit} and SWC_{slope}. With higher water usage (positive transpiration behaviour value), more 'risk' was taken and consequently, more damage was acquired (Figure 1a). A strong positive correlation was found between E_{max} and SWC_{crit} ($r = 0.71$, $p < 0.001$) and implies that if a genotype has a high transpiration potential (high E_{max}), it might experience water deficit sooner and induce the drought avoidance mechanism at a high soil water content (i.e., high SWC_{crit}).

The female parent ('917K-2') and seven of its offsprings, 'MNK-17-4,' 'MNK-17-5,' 'MNK-17-9,' 'MNK-16-16,' 'MNK-17-7,' 'MNK 16-8,' and 'MNK-16-3' exhibited a high transpiration behaviour and are considered as 'risk-takers' which continue to

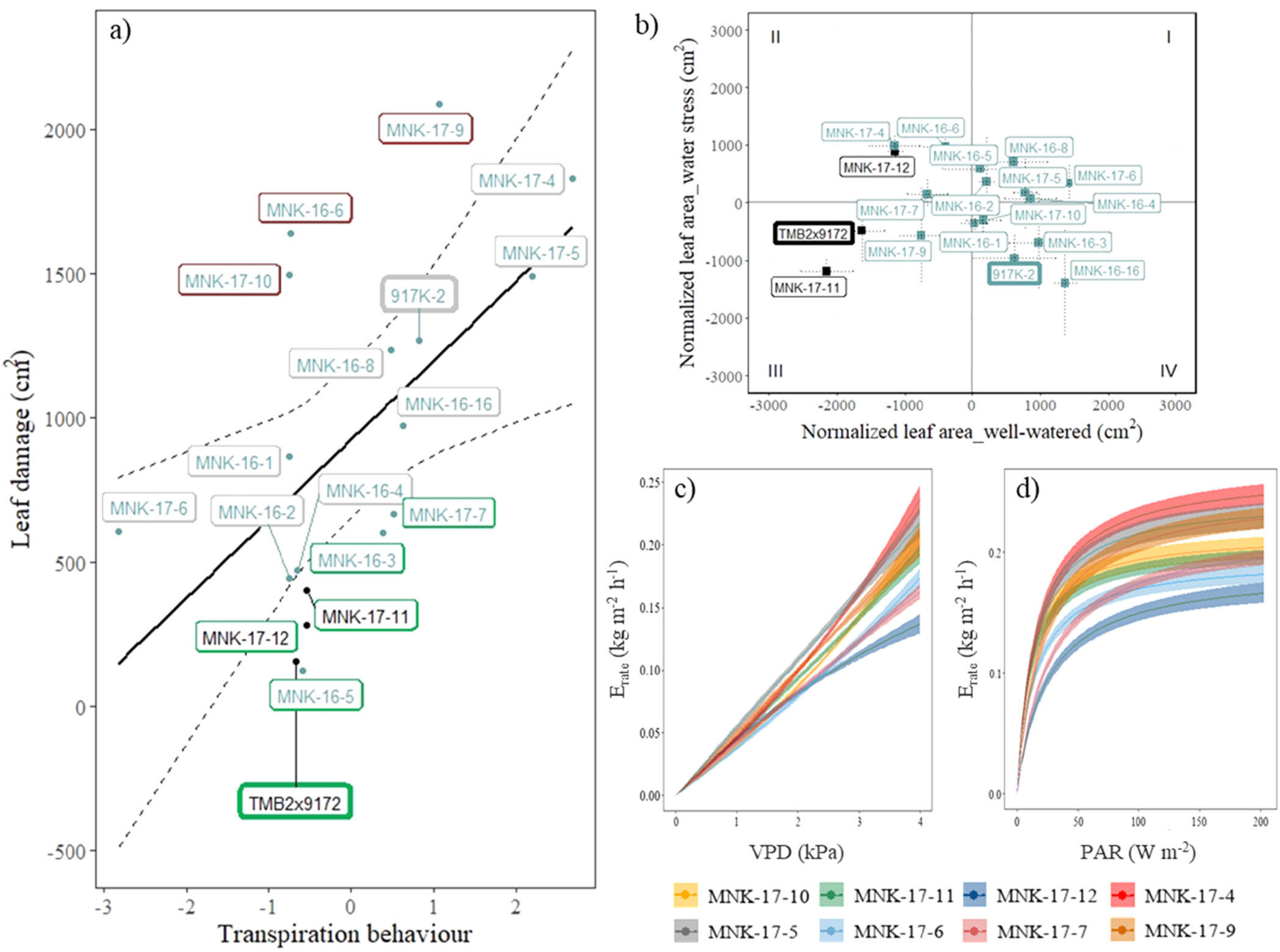

FIGURE 1 | Growth and transpiration responses of 18 test *Musa* spp. genotypes (two parents ['917K-2' and 'TMB2x9172,' indicated by thick boxes in (a) and (b)] and their offspring) deprived of water for 21 days. (a) represents the relationship between modelled transpiration behaviour and observed leaf damage. Dotted lines represent the 9% confidence interval. Genotypes in red and green boxes have more and less damage, respectively, than predicted based on the transpiration behaviour. (b) Quadrant rank at the third week, according to the median total leaf area (cm^2) for each water treatment. Dotted lines represent the standard error. Colour code used for the genotype names in (a) and (b) represent the genetic relationships, as shown in Supporting Information S1: Figure S2. (c) Modelled transpiration rate (E_{rate}) response of eight banana genotypes as a function of vapour pressure deficit (VPD) (at PAR = 100 W m^{-2}, SWC = 3 g g^{-1}, −0.002 MPa) and (d) photosynthetic active radiation (PAR) (at VPD = 2 kPa, SWC = 3 g g^{-1}, −0.002 MPa) ($n = 3$). The shaded area represents the 95% confidence interval. E_{rate} are considered significantly different if the confidence intervals do not overlap.

consume water by maintaining their maximum transpiration rate (E_{max}) until a low SWC and/or keeping a relatively high transpiration rate after the drought avoidance mechanism kicks in (Figure 1a). With such 'risk-taking' behaviour, generally, genotypes with high water consumption (i.e., positive transpiration behaviour) are predicted to experience high damage in environments with frequent and severe droughts. This fits in general with what is expected from EAHB varieties. However, we found significant variability even in our small set of offspring. The variations in the SWC_{crit} thresholds and the SWC_{slope} indicated genotype-specific stomatal and/or hydraulic control levels (Supporting Information S3: Table S3). The male parent 'TMB2x9172' and its two diploid progenies, 'MNK-17-12' and 'MNK-17-11,' developed relatively low leaf areas and induced the isohydric drought avoidance mechanism relatively early (at a high SWC) (Figure 1b, Supporting Information S3: Table S3). This similar phenotype (i.e., water saving transpiration behaviour, low leaf damage and limited growth vigour) matches their similar genetic profile, as revealed by the DARTseq-based genetic cluster analysis (Supporting Information S1: Figure S2) and might be associated with the presence of '*M. balbisiana*' related SNP markers, inherited from the 'TMB2x9172' parent. Of the 42 '*M. balbisiana*' SNPs identified in the parent, 33 and 34 were present in 'MNK-17-12' and 'MNK-17-11,' respectively. Previous observations already showed '*M. balbisiana*' to exhibit the most pronounced drought avoidance response by strongly decreasing its transpiration rates (Eyland et al. 2022). Nevertheless, our findings also show that a low growth vigour and, hence, lower leaf area, which prevents excessive water loss, is no guarantee for drought tolerance. More specifically, 'MNK-17-10,' 'MNK-16-6,' and 'MNK-16-1' acquired a lot of damage, despite their conservative transpiration behaviour. On the other hand, among the risk-taking genotypes, 'MNK-16-3' and 'MNK-17-7' acquired relatively low damage. While 'MNK-16-3' also had one '*M. balbisiana*' related SNP, no '*M. balbisiana*' Balbisiana-related SNP markers were found in 'MNK-17-7.' Even though some '*balbisiana*' derived influences and differences in ploidy level (Supporting Information S3: Table S2) might tamper with the transpiration behaviour, we have shown that there is genotypic diversity in the responsiveness amongst the solely based '*acuminata*' triploid progenies. This study found four majorly '*acuminata*' based drought-conservative and drought-tolerant progenies, including 'MNK-17-6,' 'MNK-16-2,' 'MNK-16-4,' and 'MNK-16-5.' These progenies had low transpiration behaviour and reduced their E_{max} at relatively high SWC (Supporting Information S3: Table S3). Moreover, 'MNK-16-5' is a promising progeny given its good growth vigour under both well-watered and water stress conditions (Quadrant 1, Figure 1b) and limited leaf damage (Supporting Information S1: Figure S1, Supporting Information S3: Table S2).

The above plant behaviours are inherent genotypic responses to mitigate drought effects. However, the effectiveness and benefits of these different responses will depend on how quickly water becomes available through rain, considering that EAHB production systems are predominantly rain-fed. Further knowledge of the above correlations is useful in determining the most suitable environment for the growth of each progeny evaluated in this study, depending on the current and future drought scenario, particularly in the EAHB region, where drought frequencies are increasing (Haile et al. 2020). Therefore, there is an urgent need for a higher diversity of more drought tolerant varieties on farms to mitigate the risk. In case the dry season is wetter than usual, the triploids with a high growth vigour, including 'MNK-16-2,' MNK-16-3,' 'MNK-16-4,' 'MNK-16-5,' and 'MNK-17-6' would be most suited (Figure 1b). On the other hand, more conservative, slow-growing varieties, such as 'MNK-17-11' and 'MNK-17-12' that managed to stay for more than 30 days in a pot without severe damage (Supporting Information S3: Table S2), would be recommended to sustain growth in EAHB areas with a longer and more extreme drought period.

This study reports the performance of banana hybrids developed purposely for enhanced drought tolerance. Although the number of progenies is rather low for segregation studies, the differential phenotypic behaviour of the study's progenies indicates that genes for drought tolerance or sensitivity may be segregating, and heterosis occurs. Further research is required to check whether the results from these pot assays with small plants provide an accurate account of the response of older plants and how flower and fruit development would be affected by drought. Despite the challenges posed by the complexity of drought tolerance, this study gives hope that developing banana cultivars that can withstand water stress conditions is possible.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the supporting material of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.