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# Productive and morphological responses of *Megathyrsus maximus* hybrids subjected to water deficit and waterlogging

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**ABSTRACT** - This study aimed to characterize the response mechanisms and evaluate the resistance of *Megathyrsus maximus* hybrids to water deficit and waterlogging. The experiment was conducted in a greenhouse using a randomized block design with an 8 × 3 × 2 factorial arrangement. Treatments were a combination of eight genotypes of *M. maximus*, three water conditions (control, waterlogging, and water deficit), and two harvest times (20 days of water stress and 12 days post-recovery). Productive and morphological traits were evaluated at the end of the stress period and after the recovery period. All hybrids subjected to water deficit showed reduced aerial and root mass. However, a survival response was observed post-stress, with recovery of approximately 28.4% of the aerial part and 16.3% of the root system in all genotypes. Hybrid PM409 showed potential for adaptation to waterlogging, as suggested by the observed greater root production (41.2%) compared with the average production of other genotypes. In addition, there was no reduction on leaf and stem mass production compared with the control condition. The results suggest that no material showed to be resistant to water deficit. On the other hand, hybrid PM409 showed promising traits for waterlogging stress resistance.

**Keywords:** biomass production, root recovery index, root to shoot ratio, root volume

## 1. Introduction

The increasing concern about climate change projections has raised awareness within the scientific community, mainly due to the impacts of these changes on agriculture and livestock (IPCC, 2014). Among the predicted extreme events, the frequent occurrence of intense droughts and heavy rains represents a major challenge for Brazil's agricultural sector (IPCC, 2018; OCHA, 2020). In cattle production systems where pastures are important, the vulnerability to climate risks is evident (Lesk et al., 2016). A study by Pezzopane et al. (2017) highlights the increasing seasonality in the production of *Megathyrsus maximus* cv. Tanzania, focusing on soil water availability challenges.

In this context, the search for strategies to mitigate the impacts of water stress on pastures is critical. Forage cultivars resistant to water deficit and waterlogging are promising to minimize adverse effects on forage production and animal performance (Euclides et al., 2016). This approach is crucial, as degraded pastures, one of the main obstacles in tropical systems, are often linked to abiotic stresses (Teixeira Neto et al., 2000; Dias-Filho, 2005; Dias-Filho and Andrade, 2005).

However, beyond immediate stress resistance, the recovery capacity of plants post-stress is poorly characterized. Pasture persistence under water deficit or waterlogging significantly depends on plant survival mechanisms and recovery ability (Dias-Filho and Andrade, 2005). The effects of water deficit and waterlogging on forage plants vary widely, impacting physiology and morphology, thus affecting productivity. Facing water deficit, plants may adopt drought resistance, survival, and escape strategies. Drought resistance involves physiological adaptations such as solute accumulation and deeper root system production to maintain cell turgor and productivity (Wasson et al., 2012). Drought survival is linked to reduced or temporarily halted growth during dry periods, resuming when conditions become favorable (Lelièvre et al., 2011; Saud et al., 2017). Drought escape allows plants to complete their reproductive cycle before water deficit onset (Levitt, 1980; Nilsen and Orcutt, 1996).

Waterlogging presents distinct challenges, leading plants to adopt adaptive strategies for better gas exchange between roots and the environment and to maintain energy production (Armstrong et al., 1994). Plants develop resistance mechanisms such as anaerobic metabolism and the formation of adventitious roots and aerenchyma to survive under anoxic soil conditions (Colmer, 2003; Sasidharan and Voesenek, 2015; Loka et al., 2019). Waterlogging also results in stomatal closure, reduced photosynthesis, and decreased leaf area, directly affecting aerial mass production (Cardoso et al., 2013; Voesenek and Bailey-Serres, 2015; Ploschuk et al., 2017; Sasidharan et al., 2017).

In this context, understanding the responses of forage plants to water stress and waterlogging, as well as their recovery capacity, is fundamental for developing efficient management strategies in tropical pasture-based systems. Despite advances in previous research, significant gaps remain, especially concerning *Megathyrsus maximus* hybrids. This study aims to characterize response mechanisms and evaluate the resistance of these hybrids to water deficit and waterlogging.

## 2. Material and methods

### 2.1. Plant material

Eight genotypes of *Megathyrsus maximus*, seven from the breeding program (PM407, PM408, PM409, PM411, PM414, PM415, PM427) coordinated by Embrapa, and the spontaneous hybrid (*M. maximum* and *M. infestum*) Massai cultivar were used. These forage materials were selected based on their productive potential determined in a preliminary field study. The Massai cultivar was used as a control due to its good productive capacity, relative resistance to water deficit and waterlogging stress (Volpe et al., 2008; Ribeiro-Júnior et al., 2017; Veras et al., 2020), and wide use in Brazilian pastures.

### 2.2. Experimental design and plant measurements

The experiment was conducted in a greenhouse at Embrapa Gado de Leite in Juiz de Fora, Minas Gerais, Brazil (21°46'56.4" S and 43°22'12.7" W; 882 m asl). The experimental design was randomized blocks with factorial arrangement 8 × 3 × 2 (eight genotypes, three water conditions, and two harvest times), using three replications. The water conditions were as follows: control – sufficient water (maintained at 100% of the field capacity; no water stress)—this condition was provided as previously reported by Bernardo et al. (2019); water deficit – irrigation interrupted on day 0 (March 17, 2022); and waterlogging – provided by watering the soil until saturation (set as 3 cm of water above the ground) from day 0. The waterlogging condition was assured via the double pot system with a plastic bag to prevent water leakage. The water lost via evapotranspiration was replaced daily. The first harvest was performed after 20 days of water stress and the second after 12 days of recovery.

Polyethylene pots (4 dm$^3$) filled with soil (4 kg) collected from the arable layer (first 20 cm) were used. Before filling the pots, the soil was crushed to pass through a 5-mm screen sieve and then air-dried. The soil had a sandy clay loam texture, with 29% clay, 13% silt, and 58% sand (analyzed via pipette method). The soil had the following chemical traits: pH$_{(H2O)}$, 5.4; organic matter, 2.18 dag kg$^{-1}$; Ca, 1.5 cmolc dm$^{-3}$; P, 2.5 mg dm$^{-3}$; K, 51 mg dm$^{-3}$; Mg, 0.8 cmolc dm$^{-3}$; H + Al, 3.14 cmolc dm$^{-3}$; Al, 0.3 cmolc dm$^{-3}$; effective cation exchange capacity, 2.5 cmolc dm$^{-3}$; total cation exchange capacity, 5.6 cmolc dm$^{-3}$; base saturation, 44%; aluminum saturation, 4%; and total exchangeable bases, 2.4 cmolc dm$^{-3}$. Based on the soil chemical analysis, 0.496 g kg$^{-1}$ of limestone, 26.158 mg kg$^{-1}$ of phosphorus, and 6.741 mg kg$^{-1}$ of potassium were added, according to the recommendations for using correctives and fertilizers in Minas Gerais – 5th approximation (Cantarutti et al., 1999).

The seeds were planted directly in the pots (January 7, 2022), and thinning was performed after 30 days, leaving two plants per pot. After the plant reestablishment, a cut (at 20 cm from the soil) and a top-dressing fertilization (0.085 g kg$^{-1}$ of N and 0.042 g kg$^{-1}$ of K per pot) diluted in water were performed (March 7, 2022). During the establishment phase, the soil in the pots was kept close to field capacity to ensure proper plant development.

Water conditions were applied ten days after the standardization cut. After treatment implementation, the pots under water deficit were weighed on days 0, 5, 10, 15, and 20 to monitor the water content in the soil via the gravimetric method (Figure 1).

The experimental period was from March 17 to April 18, 2022. At the end of the stress period, plants from half of the pots were harvested to assess productive and structural traits. The other half of the pots were kept under 100% of the field capacity to assess plant recovery after the water stress period.

On the day plants were subjected to water conditions, one tiller was identified per pot to assess morphogenic traits. Measurements were performed twice a week during the stress and recovery period. In the selected tillers, information on the appearance and length of the leaf blade and stems was recorded as previously described by Sbrissia et al. (2020). From these records, the leaf appearance rate, leaf elongation rate, and leaf senescence rate were calculated. In addition, the stem elongation rate, phyllochron, leaf lifespan, leaf length, total leaf number, and live leaf number per tiller were determined.

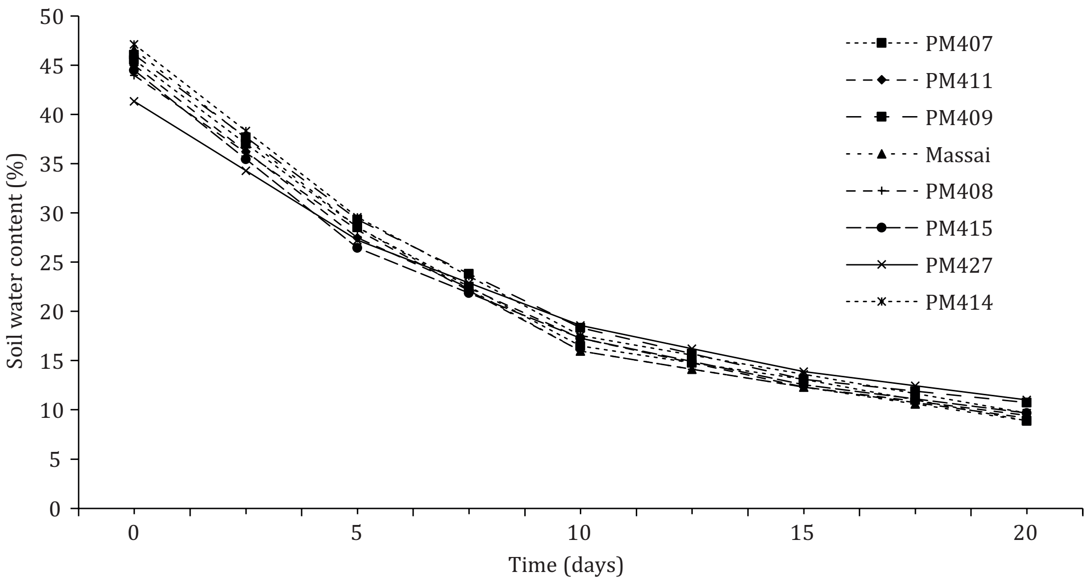


**Figure 1 -** Soil water content (%) in pots containing genotypes of *Megathyrsus maximus* (PM407, PM411, PM409, PM408, PM415, PM427, PM414) and cv. Massai under water deficit condition.

The SPAD index (relative chlorophyll content determined based on the intensity of the green color of the leaves) was measured in three youngest fully expanded leaves per pot using a portable chlorophyll meter (SPAD-502, Konica-Minolta, Osaka, Japan). Readings were performed on days 0, 5, 10, 15, 20, and after 12 days of recovery.

The aerial plant components were cut to assess aerial mass at 20 cm from the soil. Samples were separated into leaf blades and stem, then dried in a forced-air oven at 55 ± 5 °C for 72 h. Subsequently, samples were weighed to determine the leaf and stem (stems + sheath) mass.

Roots were placed on sieves and washed in running water to withdraw all soil particles completely after the water stress and the recovery period. The root volume was estimated by measuring the displacement of water in a graduated cylinder, that is, by the difference in the known volume of water. The direct response of the root volume was obtained using unit equivalence (1 mL = 1 $cm^3$). Roots were dried at 55 ± 5 °C in a forced-air oven for 72 h and then weighed to determine dried mass.

Before each cut, the number of tillers was counted. The height of the plants was measured from the ground level to the end of the highest leaf (i.e., the fully extended plant) using a graduated ruler.

After collecting materials, the leaf area was determined using a leaf area integrating unit (LI-COR Model LI-3100). The specific leaf area was calculated by dividing the leaf area by the leaf dry mass (Radford, 1967).

In addition, information on the leaf dry mass:stem dry mass ratio, the root dry mass:aerial dry mass ratio, and the root recovery index (root dry mass after recovery/root mass after water stress) were measured.

### 2.3. Statistical analysis

Statistical analyses were performed using R Software version 3.6.1 (R Core Team, 2019), and the data were initially tested for the mathematical assumptions with Shapiro–Wilk test and Bartlett tests. The statistical model used was:

$$Y_{ijlk} = \mu + b_k + G_i + W_j + H_l + (G*W)_{ij} + (G*H)_{il} + (W*H)_{jl} + (G*W*H)_{ijl} + e_{ijlk},$$

in which $Y_{ijlk}$ represents the observation in the $k$-th block, in $i$-th genotype, in $j$-th water conditions, and in the $l$-th harvest times; $\mu$ = the overall mean; $b_k$ = the block effect $k$; $G_i$ = fixed effect of the genotype $i$; $W_j$ = fixed effect of water conditions $j$; $H_l$ = fixed effect of harvest times $l$; $(G*W)_{ij}$ = interaction of the effects of genotype $i$ on water conditions $j$; $(G*H)_{il}$ = interaction of the effects of genotype $i$ on harvest times $l$; $(W*H)_{jl}$ = interaction of the effects of water conditions $j$ on harvest times $l$; $(G*W*H)_{ijl}$ = interaction of the effects of genotype $i$ on water conditions $j$ at harvest times $l$; and $e_{ijlk}$ = random error associated to $Y_{ijlk}$ [$e_{ijlk} \sim$ NID (0, $\sigma^2$)].

Data were analyzed as repeated measurements using a randomized block design with an 8 × 3 × 2 factorial arrangement. Comparisons among means were performed according to Tukey's test, and significant differences were set at $P \leq 0.05$.

## 3. Results

### 3.1. Productive traits

An interaction between water condition and genotype was observed ($P<0.001$) for leaf dry mass production. Water deficit reduced leaf mass in all genotypes. In the same way, except for PM409, waterlogging reduced leaf mass production (Table 1). In addition, a harvest time effect ($P<0.001$) on leaf mass was observed. Plants showed a greater leaf mass (10.70 g pot $^{-1}$) in the second harvest (i.e., after the recovery period) than in the harvest performed after a period of 20 days of stress period (8.33 g pot$^{-1}$).

An interaction between water stress and genotype was observed ($P<0.003$) for stem dry mass (Table 1). A reduction of stem dry mass was observed in all plants subjected to water deficit to the point in which there were no stems in the samples above the cut-off height (20 cm). The waterlogging condition also impaired stem dry mass production. However, PM409 and PM411 genotypes showed similar results to the control group. An interaction between harvest time and genotype ($P<0.005$) was observed for the stem dry mass. Greater stem yield after the stress recovery period (second harvest time) was observed in the genotypes except for PM411 and PM414, which had similar values to those observed in the cut after the stress period. In addition, an interaction between water condition and harvest time was observed for stem dry mass ($P<0.007$). Plants subjected to waterlogging showed greater stem mass yield in the second harvest season (3.84 g pot$^{-1}$) than in the first harvest (1.86 g pot$^{-1}$).

There was an interaction between water condition and genotype for leaf:stem ratio ($P<0.005$). Waterlogging increased the leaf:stem ratio in the PM408 and PM414 genotypes, while the other genotypes showed no difference compared to the control condition (Table 1).

Root dry mass ($P<0.009$) was negatively influenced by water deficit but was not affected by waterlogging. It is important to highlight that waterlogging benefited root production in the PM409 genotype, as it presented a higher root mass value than in the control condition (Table 1). Also, an interaction between water condition and harvest time was observed ($P<0.001$) for root mass. In the second harvest, a greater root dry mass (35.32 g pot$^{-1}$) was observed in plants subjected to waterlogging compared with the first harvest (15.81 g pot$^{-1}$). However, no difference was observed between the first (7.83 g pot$^{-1}$) and the second harvest (9.11 g pot$^{-1}$) in plants subjected to water deficit.

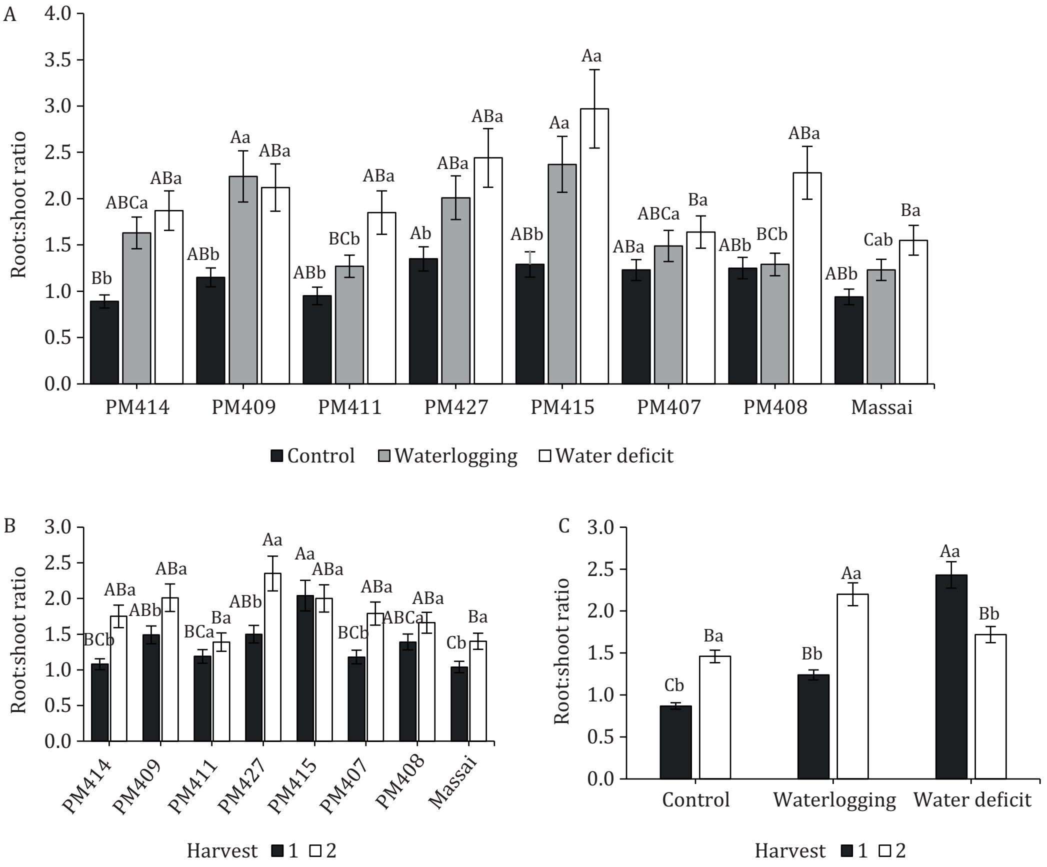
Interactions were observed between water condition and genotype ($P<0.05$), harvest time and genotype ($P<0.04$), and water condition and harvest time ($P<0.001$) for the root:shoot ratio (Figure 2). Water deficit increased the root:shoot ratio in the PM415 genotype. In contrast, no difference was observed in PM408, PM409, PM411, PM414, and PM427 genotypes, while the Massai cultivar and the PM407 genotype showed a lower root:shoot ratio. Waterlogging increased the root:shoot ratio compared with water deficit in the PM409 genotype; however, no difference was observed between the two water conditions (Figure 2A). The root:shoot ratio increased after the stress recovery period. However, PM408, PM411, and PM415 genotypes showed lower recovery potential, resulting in

**Table 1 -** Productive characteristics (g pot$^{-1}$) of *Megathyrsus maximus* genotypes, under three water conditions

| Water condition | Genotype | | | | | | | | SEM |
|---|---|---|---|---|---|---|---|---|---|
| | PM414 | PM409 | PM411 | PM427 | PM415 | PM407 | PM408 | Massai | |
| | Leaf dry mass | | | | | | | | |
| Control | 17.68Aa | 13.87Abc | 17.39Aab | 17.40Aab | 14.67Aabc | 14.31Aabc | 12.56Ac | 14.90Aabc | |
| Waterlogging | 12.8Bab | 12.13Aabc | 13.02Ba | 13.19Ba | 9.91Bbc | 10.77Babc | 9.33Bc | 9.51Bc | 0.39 |
| Water deficit | 2.90Cb | 3.39Bb | 4.05Cab | 3.62Cb | 3.31Cb | 5.57Ca | 4.04Cab | 4.32Cab | |
| | Stem dry mass | | | | | | | | |
| Control | 3.52Acd | 3.38Acd | 2.57Ad | 5.33Aabc | 4.39Abcd | 4.85Abcd | 7.09Aa | 6.44Aab | |
| Waterlogging | 1.47Ba | 3.63Aa | 2.34Aa | 3.72Ba | 2.13Ba | 2.89Ba | 3.60Ba | 3.06Ba | 0.51 |
| Water deficit | - | - | - | - | - | - | - | - | |
| | Leaf dry mass:stem dry mass ratio | | | | | | | | |
| Control | 4.28Bab | 4.25Aab | 6.87Aa | 3.54Aab | 3.61Aab | 3.12Abc | 1.92Bc | 2.53Abc | |
| Waterlogging | 9.11Aa | 4.06Aabc | 6.25Aab | 3.66Abc | 5.10Aabc | 4.11Aabc | 2.92Ac | 3.51Abc | 0.25 |
| Water deficit | - | - | - | - | - | - | - | - | |
| | Root dry mass | | | | | | | | |
| Control | 16.72Ab | 20.63Bab | 25.79Aab | 30.90Aa | 24.33Aab | 24.6Aab | 24.13Aab | 23.29Aab | |
| Waterlogging | 24.10Aabc | 32.87Aa | 20.23Aabc | 32.67Aa | 28.19Aab | 25.39Aabc | 17.04Abc | 15.25Ac | 1.07 |
| Water deficit | 5.69Bb | 7.65Cab | 10.83Ba | 8.69Bab | 10.39Ba | 9.55Bab | 9.26Bab | 6.88Bab | |

SEM - standard error of the mean.
Means followed by a different uppercase letter in the column and lowercase letter in the row differ by Tukey's test ($P<0.05$).

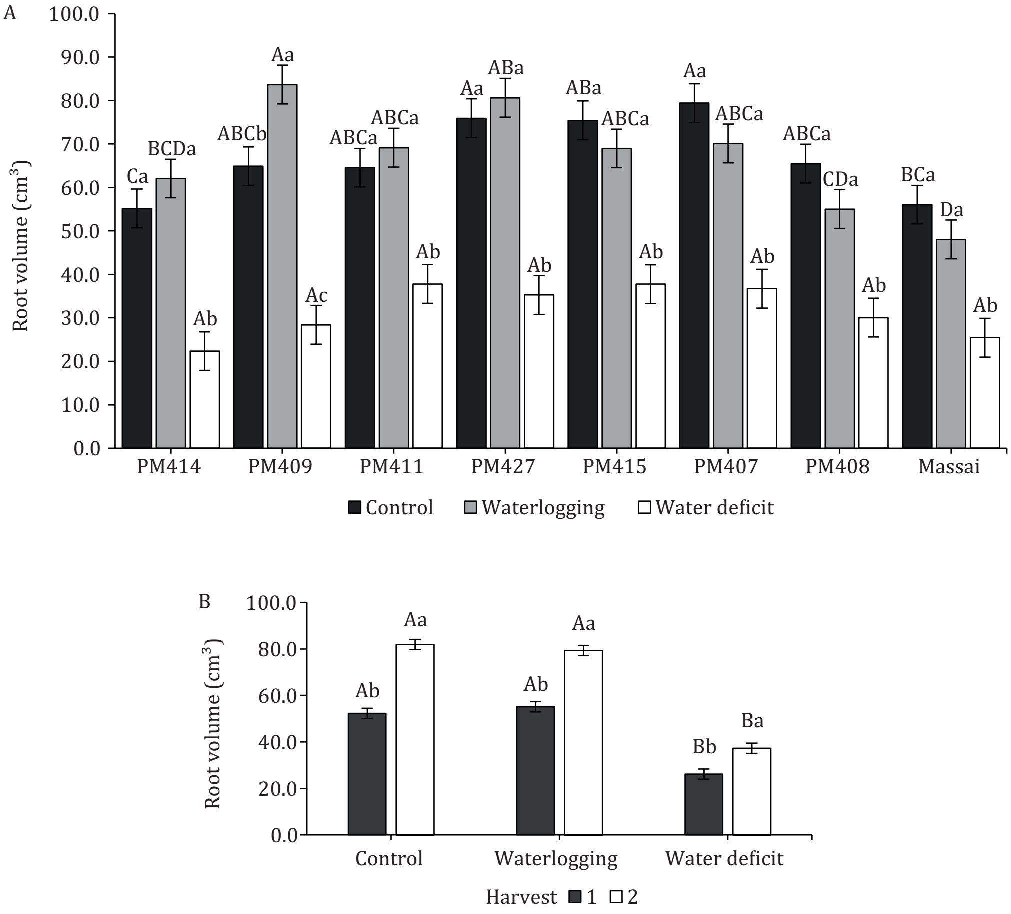
non-significant difference between harvest times (Figure 2B). In control and waterlogging conditions, the root:shoot ratio was greater in the second harvest. On the other hand, this ratio was lower in the second harvest time in plants subjected to water deficit (Figure 2C).



(A) Uppercase letters compare genotypes and lowercase letters compare water condition by Tukey's test (P<0.05); values are the means of eight genotypes and three replicates ± standard error of the means.
(B) Uppercase letters compare genotypes and lowercase letters compare harvests by Tukey's test (P<0.05); values are the means of eight genotypes and three replicates ± standard error of the means.
(C) Uppercase letters compare water condition and lowercase letters compare harvests by Tukey's test (P<0.05); values are the means of eight genotypes and three replicates ± standard error of the means.

**Figure 2** - Root:shoot ratio of *Megathyrsus maximus* genotypes under three water conditions (control, waterlogging, water deficit) (A); root:shoot ratio of *Megathyrsus maximus* genotypes in two harvests (1st harvest: the end of water stress period; 2nd harvest: after recovery period) (B); root:shoot ratio under three water conditions (control, waterlogging, water deficit) and in two harvests (1st harvest: the end of water stress period; 2nd harvest: after recovery period) (C).

Interactions between water condition and genotype (P<0.01) and harvest time and water condition (P<0.001) were observed for root volume (Figure 3). Water deficit reduced the root volume in all genotypes (Figure 3A). However, under waterlogging condition, the PM409 genotype showed greater root volume. In the second harvest (after the recovery period), greater root volume was observed in all stress conditions (Figure 3B).



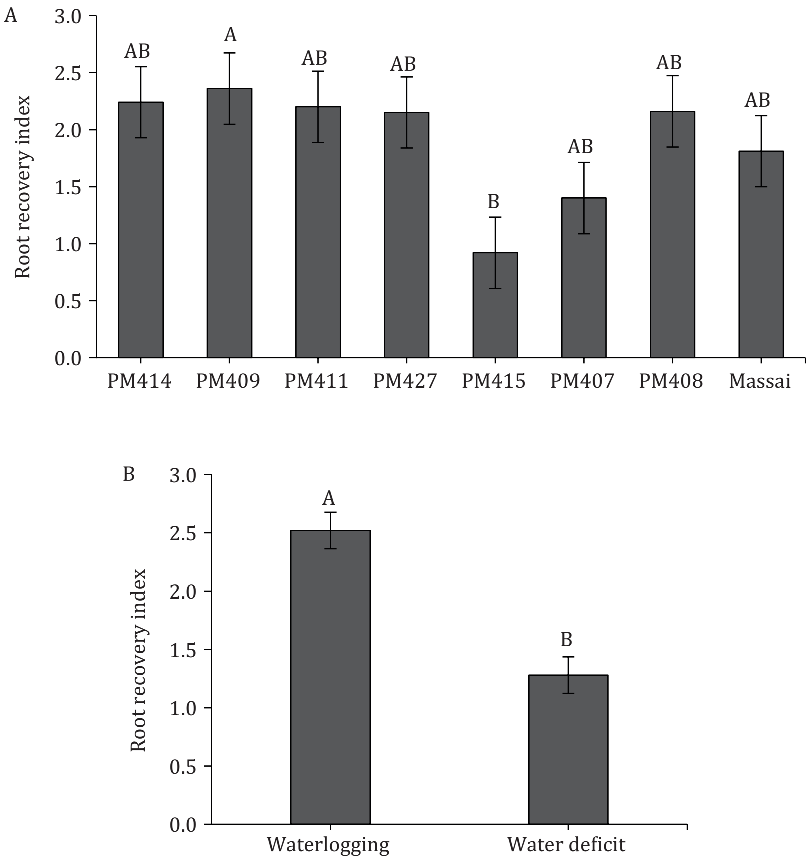
(A) Uppercase letters compare genotypes and lowercase letters compare water condition by Tukey's test (P<0.05); values are the means of eight genotypes and three replicates ± standard error of the means.
(B) Uppercase letters compare water condition and lowercase letters compare harvests by Tukey's test (P<0.05); values are the means of eight genotypes and three replicates ± standard error of the means.

**Figure 3 -** Root volume of *Megathyrsus maximus* genotypes under three water conditions (control, waterlogging, water deficit) (A); root volume under three water conditions (control, waterlogging, water deficit) and in two harvests (1st harvest: the end of water stress period; 2nd harvest: after recovery period) (B).

The root recovery index was greater in the PM409 genotype regardless of the nature of water stress. It is important to highlight that the PM415 genotype showed the lowest root recovery rate (<1.0; Figure 4A). Regarding water conditions, the root recovery index was approximately 51.0% greater in plants subjected to waterlogging than in those under water deficit (Figure 4B).

### 3.2. Morphological and structural traits

An interaction (P<0.003) between water condition and genotype was observed for leaf area (Figure 5A). All genotypes showed lower leaf area when subjected to water deficit compared with waterlogging and control. On the other hand, two response patterns were observed under waterlogging: lower leaf area in PM407, PM408, PM414, PM415, and PM427 hybrids and Massai cultivar; and no modification of leaf area in PM409 and PM411 hybrids. Furthermore, an interaction (P<0.001) between harvesting time and water condition was observed for leaf area (Figure 5B). Plants under water deficit showed potential five times greater for leaf area recovering between the first and second harvest times than plants under waterlogging (0.08-fold).



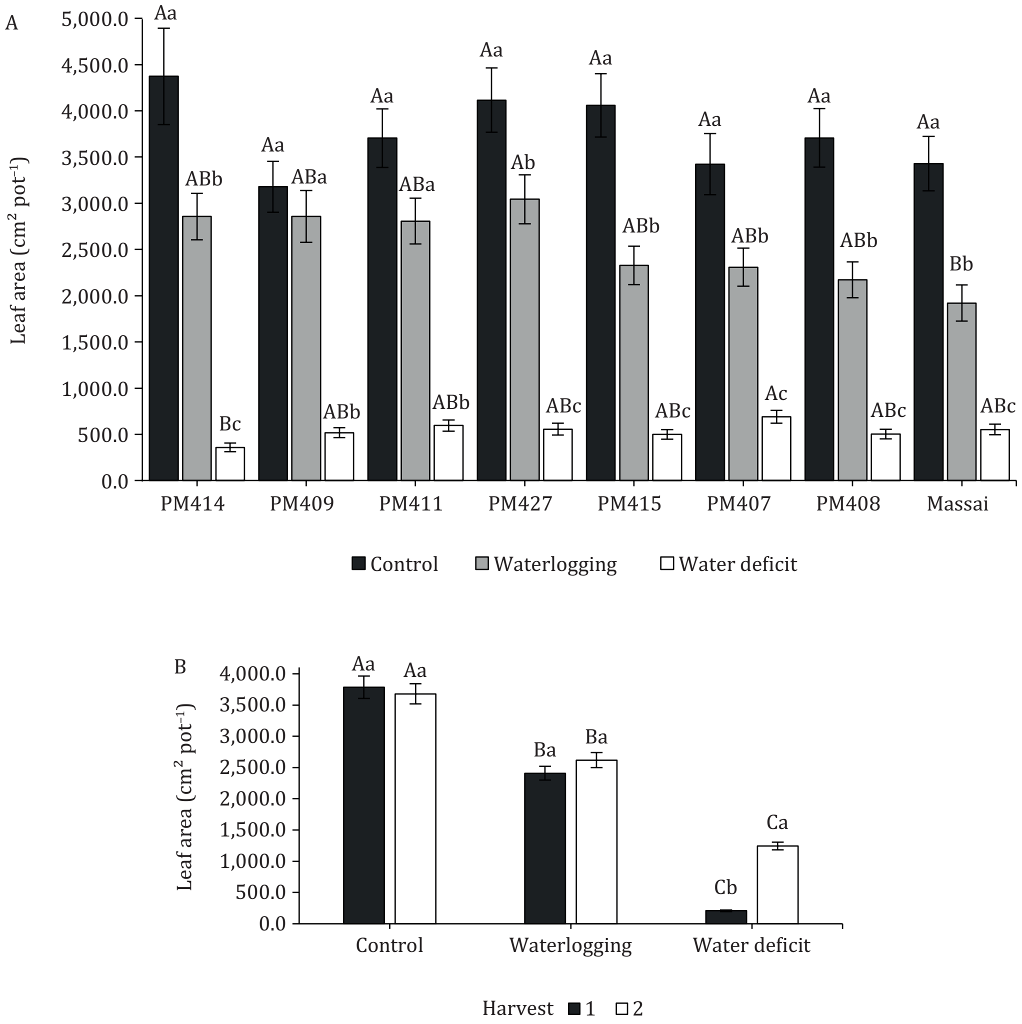
Different letters indicate difference by Tukey's test (P<0.05); (A and B) values are the means of eight genotypes and three replicates ± standard error of the means.

**Figure 4 -** Root recovery index of *Megathyrsus maximus* genotypes (A); root recovery index under two harvests (1st harvest: the end of water stress period; 2nd harvest: after recovery period) (B).

Interactions between water condition and genotype (P<0.001) and water condition and harvest time (P<0.001) were observed for specific leaf area (Figure 6). The water deficit reduced the specific leaf area in all genotypes (Figure 6A). However, it was more pronounced in the PM407 genotype. Nevertheless, waterlogging did not affect the specific leaf area compared with the control conditions. A lower specific leaf area due to water deficit was observed in the first harvest. However, in the second harvest, after the recovery period, plants under water deficit showed on average a specific leaf area 20% higher than plants subjected to waterlogging and control (Figure 6B).

An interaction between water condition and genotype was observed (Table 2) for leaf elongation rate (P<0.001), stem elongation rate (P<0.003), leaf lifespan (P<0.003), and number of live leaves (P<0.02). Water deficit impaired leaf elongation rate in all genotypes evaluated. However, except for the PM415 genotype, no reduction was observed in plants subjected to waterlogging compared with the control. The stem elongation rate was reduced in plants subjected to water deficit. However, for genotypes PM407, PM411, and PM414, there was no significant reduction in relation to the control condition.

A similar effect was observed for leaf lifespan and live leaf number. Indeed, plants subjected to water deficit showed lower values than those on waterlogging and control conditions. The PM411 genotype showed the highest live leaf number per tiller when subjected to waterlogging (Table 2).



(A) Uppercase letters compare genotypes and lowercase letters compare water condition by Tukey's test (P<0.05); values are the means of eight genotypes and three replicates ± standard error of the means.
(B) Uppercase letters compare water condition and lowercase letters compare harvests by Tukey's test (P<0.05); values are the means of eight genotypes and three replicates ± standard error of the means.

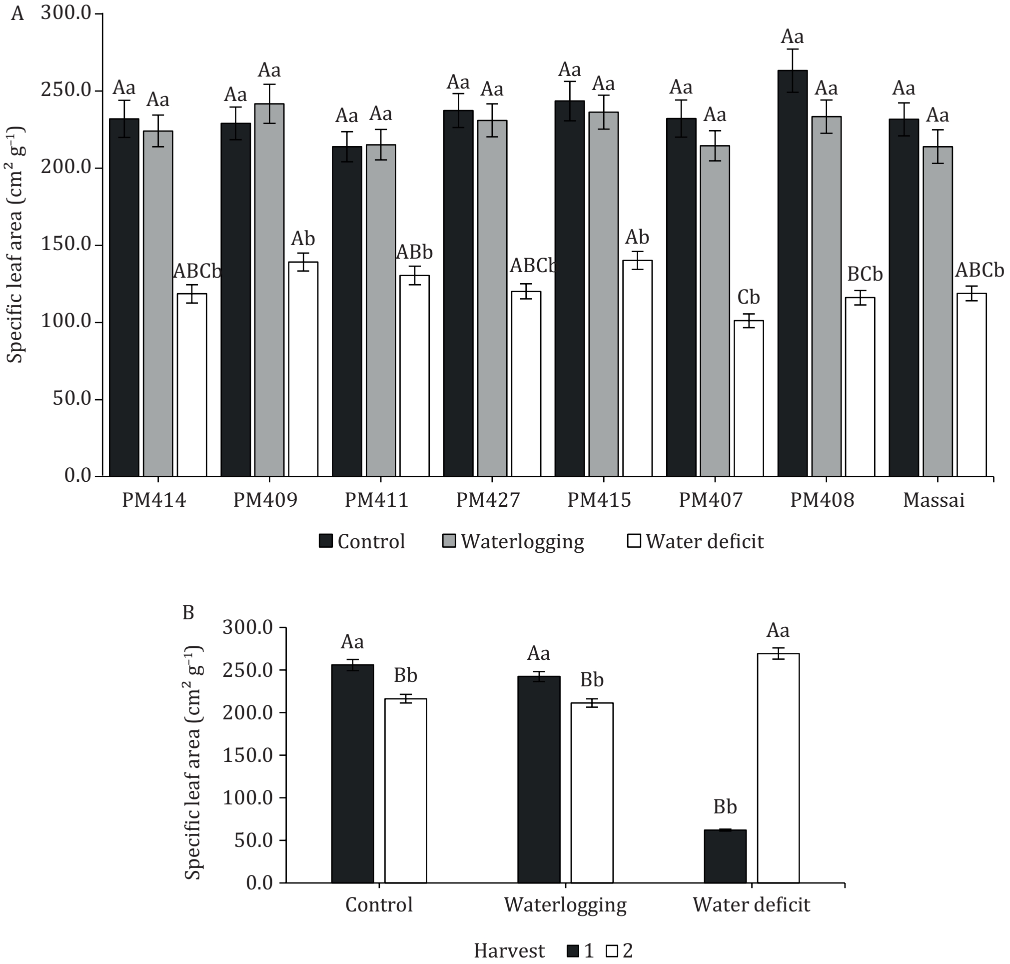
**Figure 5** - Leaf area (cm$^2$ pot$^{-1}$) of *Megathyrsus maximus* genotypes under three water conditions (control, waterlogging, water deficit) (A); leaf area (cm$^2$ pot$^{-1}$) under three water conditions (control, waterlogging, water deficit) in two harvests (1st harvest: the end of water stress period; 2nd harvest: after recovery period) (B).

Leaf senescence rate was affected (P<0.001) by water conditions. Higher values were observed in plants subjected to water deficit (2.85 cm tiller$^{-1}$ day$^{-1}$) than the control (1.88 cm tiller$^{-1}$ day$^{-1}$) and waterlogging (1.13 cm tiller$^{-1}$ day$^{-1}$) groups, which did not differ from each other.

Leaf appearance rate (leaf tiller$^{-1}$ day$^{-1}$) and total leaf number per tiller were also affected by water conditions (P<0.001). Leaf appearance rate was lower in plants subjected to water deficit (0.05 leaf tiller$^{-1}$ day$^{-1}$) than in those under waterlogging and control (0.09 leaf tiller$^{-1}$ day$^{-1}$) treatments. Water deficit reduced the total leaf number per tiller (2.44). However, waterlogging and control showed a similar total leaf number per tiller (4.36 and 4.48, respectively).

Phyllochron was higher (P<0.02) in the Massai cultivar, while no difference was observed in PM407, PM408, PM409, PM414, and PM415 genotypes. Plants subjected to water deficit showed greater phyllochron (19.39 days leaf$^{-1}$ tiller$^{-1}$) ($P<0.001$). Plants under waterlogging and control treatments showed a lower number of days to the appearance of a leaf in the tiller, with values of 10.97 and 11.73 days, respectively. There was no significant interaction between water condition and genotype for leaf length ($P<0.001$). However, in relation to genotypes ($P<0.001$), the lowest leaf length was in the PM408 genotype, but did not differ from the Massai cultivar. Water deficit reduced leaf length (40.91 cm; $P<0.001$) in plants. However, this effect was not observed in plants subjected to waterlogging (58.95 cm), which did not differ from the control group (64.88 cm).

The average number of tillers per pot ($P<0.001$) was greater in PM407 and PM408 genotypes and the Massai cultivar. Water deficit reduced the average tiller number ($P<0.001$) in relation to the control. On the other hand, waterlogging did not influence the tiller number compared with the control.



(A) Uppercase letters compare genotypes and lowercase letters compare water condition by Tukey's test ($P<0.05$); values are the means of eight genotypes and three replicates ± standard error of the means.
(B) Uppercase letters compare water condition and lowercase letters compare harvests by Tukey's test ($P<0.05$); values are the means of eight genotypes and three replicates ± standard error of the means.

**Figure 6 -** Specific leaf area (cm$^2$ g$^{-1}$) of *Megathyrsus maximus* genotypes under three water conditions (control, waterlogging, water deficit) (A); specific leaf area (cm$^2$ g$^{-1}$) under three water conditions (control, waterlogging, water deficit) in two harvests (1st harvest: the end of water stress period; 2nd harvest: after recovery period) (B).

There was an effect of genotypes on plant height (P<0.001). Plant height was higher for the PM409 genotype but did not differ among PM414, PM415, PM427, and the Massai cultivar. Plant height (P<0.001) was reduced in both water stress conditions but more intensely under water deficit (81.22 cm) than under waterlogging (121.57 cm).

**Table 2 -** Morphological characteristics of *Megathyrsus maximus* genotypes under three water conditions

| Water condition | Genotype | | | | | | | | SEM |
|---|---|---|---|---|---|---|---|---|---|
| | PM414 | PM409 | PM411 | PM427 | PM415 | PM407 | PM408 | Massai | |
| | Leaf elongation rate (cm tiller$^{-1}$ day$^{-1}$) | | | | | | | | |
| Control | 7.00Abc | 8.19Ab | 4.94ABcde | 6.19Abcd | 11.91Aa | 4.79Acde | 3.59Ade | 3.08ABe | |
| Waterlogging | 6.93Aa | 6.41Aab | 5.76Aab | 5.61Aab | 4.86Bab | 4.71Aab | 3.15ABb | 4.34Aab | 0.64 |
| Water deficit | 1.67Ba | 1.89Ba | 2.97Ba | 2.26Ba | 1.69Ca | 2.32Ba | 1.14Ba | 1.92Ba | |
| | Stem elongation rate (cm tiller$^{-1}$ day$^{-1}$) | | | | | | | | |
| Control | 0.50Ac | 0.50ABc | 0.38Ac | 0.88Abc | 0.76Ac | 0.17Ac | 1.80Aa | 1.65Aab | |
| Waterlogging | 0.40Ab | 0.79Aab | 0.51Ab | 0.71Aab | 0.61Aab | 0.26Ab | 1.29Aa | 0.77Bab | 0.16 |
| Water deficit | 0.07Aa | 0.13Ba | 0.04Aa | 0.05Ba | 0.04Ba | 0.10Aa | 0.02Ba | 0.02Ca | |
| | Leaf lifespan (days) | | | | | | | | |
| Control | 36.66Aa | 41.25Aa | 35.75Aa | 36.66Aa | 36.11Aa | 36.66Aa | 38.50Aa | 42.16Aa | |
| Waterlogging | 33.00ABa | 35.75Aa | 42.53Aa | 39.41Aa | 44.91Aa | 42.16ABa | 36.66Aa | 40.33ABa | 3.63 |
| Water deficit | 21.02Bb | 17.30Bb | 21.00Bb | 21.33Bb | 21.03Bb | 49.50Ba | 23.00Bb | 26.69Bb | |
| | Live leaf number | | | | | | | | |
| Control | 3.33Aab | 5.55Aa | 3.00Bb | 3.66Aab | 3.29Aab | 3.00Ab | 3.33Aab | 3.00Ab | |
| Waterlogging | 3.33Aa | 3.66Ba | 4.66Aa | 4.00Aa | 4.00Aa | 3.33Aa | 3.66Aa | 3.66Aa | 0.46 |
| Water deficit | 1.00Ba | 1.66Ca | 1.00Ca | 1.33Ba | 1.00Ba | 3.00Aa | 1.00Ba | 1.33Ba | |

SEM - standard error of the mean.
Means followed by a different uppercase letter in the column and lowercase letter in the row differ by Tukey's test (P<0.05).

### 3.3. SPAD index

Interactions between water condition and genotype (P<0,001), genotype and readings (P<0.02) (Table 3), and water condition and readings (P<0.0001) for the SPAD index were observed. When subjected to waterlogging conditions, a greater SPAD index was observed in the Massai cultivar, while no difference was observed in PM408, PM409, and PM411 genotypes. In plants subjected to water deficit, a greater SPAD index was observed in the PM408 genotype, while no difference was observed in the Massai cultivar and PM409, PM411, PM414, and PM415 genotypes. Regarding genotypes, the SPAD index was lower for all materials in the waterlogging conditions except for PM411 and PM407 genotypes. The PM411 genotype showed no difference when subjected to the water conditions. In contrast, the PM407 genotype showed a similar reduction of the SPAD when subjected to the two water stress conditions.

Regardless of the water condition, the highest SPAD index was observed in the reading performed on day 5 in all genotypes except for the PM415 genotype, which showed the highest SPAD index on day 10. In general, the SPAD index was reduced in all genotypes over time. The lowest result was observed in the last reading performed after the recovery period of water stress (Table 3).

The SPAD index generally decreased in all treatments over time, suggesting an overall reduction in chlorophyll content. Plants subjected to water deficit showed a lower SPAD index than those in the control conditions from the fifth reading. This observation suggests a reduced chlorophyll content due to water deficit, which was recovered after the rehydration period. Similar responses were observed when plants were subjected to waterlogging conditions. However, a lower SPAD index was observed when compared with the other water conditions.

**Table 3 -** SPAD index of *Megathyrsus maximus* genotypes during the stress imposition period with readings on days 0, 5, 10, 15, and 20 and 12 days after recovery from water stress

| Genotype | Reading day | | | | | |
|---|---|---|---|---|---|---|
| | 0 | 5 | 10 | 15 | 20 | 32 |
| PM414 | 37.40Ab | 41.24ABa | 39.78Aab | 37.34ABb | 36.91Ab | 24.33Dc |
| PM409 | 38.65Aab | 42.15ABa | 40.45Aab | 39.64ABab | 37.90Ab | 29.41Cc |
| PM411 | 39.08Aab | 42.42ABa | 41.29Aab | 38.12ABbc | 34.48Ac | 27.70CDd |
| PM427 | 37.46Aab | 40.43Ba | 39.49Aab | 36.48ABb | 36.17Ab | 27.36CDc |
| PM415 | 39.53Aab | 40.85ABab | 41.75Aa | 40.05Aab | 37.06Ab | 29.72BCc |
| PM407 | 37.83Aab | 41.22ABa | 38.86Aab | 36.03Bb | 35.84Ab | 28.88Cc |
| PM408 | 40.08Ab | 44.51Aa | 41.19Aab | 37.63ABb | 38.32Ab | 33.46ABc |
| Massai | 39.96Aab | 42.81ABa | 40.94Aab | 38.58ABb | 38.39Ab | 33.94Ac |

SPAD index - relative chlorophyll content determined based on the intensity of the green color of the leaves.
Means followed by a different uppercase letter in the column and lowercase letter in the row differ by Tukey's test ($P<0.05$).

## 4. Discussion

### 4.1. Water deficit survival mechanism

Our results showed that all genotypes reduced the leaf area development (Figure 5A) and mass production of leaves and stems (Table 1) when subjected to water deficit. These results corroborate previous findings by Verslues et al. (2006), who demonstrated a decrease in development and growth of aboveground components in plants subjected to water deficit conditions. This reduction is one of the first responses of plants to reduced water availability in the soil, resulting in severe physiological water deficit. This deficit reduced water potential and plant turgor, which led to reduction in aerial mass production and increase in leaf senescence rate (Table 2). These effects represent possible mechanisms for reducing transpiration and, consequently, water loss by the plant, characterizing a drought survival process (Volaire and Lelièvre, 2001; Munné-Bosch and Alegre, 2004; Lelièvre et al., 2011; Saud et al., 2017).

Plants that are resistant to water deficit depend on dehydration resistance mechanisms to sustain growth. This involves the accumulation of metabolites, which helps maintain cell turgor (Chaves, 1991), favoring cell expansion and leaf elongation. However, despite these mechanisms, observed responses such as reduced leaf elongation rate (Table 2), reduced tiller number, and increased senescence rate suggest that these mechanisms were not sufficient to sustain plant development.

The root system is one of the components most affected by water deficit, as observed by Kavar et al. (2008). Water deficit impaired the development of root mass (Table 1), showing an average reduction of 51.2% compared with the control conditions after 20 days. This effect could have been enhanced by the physical limitation of the pots, which may have influenced the development in root depth and hence affected the velocity and severity of the water deficit.

It is important to study the root system and root mass:shoot mass ratio, as roots play an important role in water and nutrient allocation to the aerial tissues (Comas et al., 2013). Thus, these characteristics are important for mitigating the limiting effects of stress (Lilley and Kirkegaard, 2011). Increases in the root:shoot mass ratio in response to water deficit reflect the interruption of aerial tissue growth and the simultaneous maintenance of root development, especially in the initial phase of stress (Figure 2A), as also highlighted by Hodge et al. (2009) and observed in Napier grass (*Pennisetum purpureum*) and Mulato grass (*Brachiaria ruziziensis* × *Brachiaria brizantha*) cultivars (Cardoso et al., 2015).

The reduction in the root:shoot ratio during the recovery period (i.e., second harvest season; Figure 2C), coupled with the lowest root recovery index (Figure 4B), suggest a preferential mobilization of reserves for leaf area production (Figures 5B and 6B), aiming for faster photosynthesis restoration (Beloni et al., 2017). The root recovery index (Figure 4) reflects the degree of preservation of meristematic tissues and the integrity of root system membranes, showing that even under severe water deficit conditions, the protection of root meristems allowed rapid recovery of root volume (Figure 3B), promoting the development of the aboveground part with an increase in leaf area (Figure 5B), specific leaf area (Figure 6B), leaf, and stem mass.

It is important to emphasize that a reduced root system and a low recovery rate should not be interpreted as negative aspects of the plant, as they may be associated with a resource conservation strategy. This is due to the fact that a deep root system requires a higher energy investment for root synthesis, maintenance, and absorption (Adiku et al., 2000).

Chlorophyll content assessments have been widely reported in plants under conditions of limited soil water availability. Ebrahimiyan et al. (2013) observed an increased chlorophyll content in *Festuca arundinacea* Schreb. genotypes subjected to mild dry condition; however, the authors observed a substantial reduction in chlorophyll content when subjected to severe water deficit conditions. Similar results were observed in Ryegrass (AbdElgawad et al., 2015) and eleven *Festuca arundinacea* Schreb. cultivars (Sarmast et al., 2015). In the moderate drought condition (onset of water deficit), there was a slight increase in the SPAD index. However, with the worsening of the water deficit (Figure 1), a decrease (compared with the control conditions) in the SPAD index was observed after five days of water stress, coinciding with the drastic drop in soil water content. This outcome is mainly due to the water deficit effects on leaves that inhibit photosynthesis (Farooq et al., 2009).

### 4.2. Resistance mechanisms to excess water

Forage plants that demonstrate greater resistance to waterlogging are generally grasses capable of developing adaptions for transporting oxygen to waterlogged tissues (Dias-Filho, 2013). These adaptations may vary among species or even within the same species, influenced by factors such as intensity, duration, species, growth stage, and plant acclimatization capacity (Bailey-Serres et al., 2012; Striker and Colmer, 2017).

In general, the development of adventitious roots above the soil level was observed in all genotypes, suggesting that this may have favored better absorption of water, oxygen, and nutrients (Armstrong et al., 1994; Dias-Filho, 2006). These morpho-anatomical changes in genotypes influence the rapid growth of the shoot, resulting in increased stem weight and plant height (Bailey-Serres et al., 2012; Beloni et al., 2017). However, contrary to this expectation, this study observed a reduction in canopy height in all genotypes compared with the control, as well as a decrease in stem dry mass, except for hybrids PM409 and PM411, which showed no reduction compared with the control condition (Table 1).

Waterlogging often tends to reduce the total plant mass (Yamamoto et al., 1995; Lopez and Kusar, 1999), especially root production, as plants typically reallocate root reserves to aerial tissues (Dias-Filho and Carvalho, 2000). However, our results showed that all genotypes subjected to waterlogging did not reduce the production of root dry mass (Table 1) and root volume (Figure 3A) compared with the control condition. It is important to highlight that the PM409 genotype showed greater root mass production (37.2%) under waterlogging conditions compared with the control treatment. This effect is possibly a result of intense adventitious root production and root aerenchyma formation (Colmer and Voesenek, 2009; Cardoso et al., 2013). This response of the PM409 genotype influenced the leaf area (Figure 5A) and specific leaf area maintenance (Figure 6A), leaf and stem dry mass production (Table 1), and the main morphogenic variables (Table 2), reflecting in the root:shoot ratio (Figure 2A), indicating that for genotype PM409 under waterlogging stress, there was no preferential reallocation of mass from the root system to the aerial tissues as observed in other studies (Yamamoto et al., 1995; Dias-Filho and Carvalho, 2000).

In the present study, the genotypes of *Megathyrsus maximus* subjected to waterlogging showed the lowest SPAD indexes (Table 3) compared with water deficit and control conditions, differing from the results obtained by Cardoso et al. (2013) and Beloni et al. (2017), in which higher SPAD indexes were found when *Brachiaria* hybrids and *Paspalum* sp. accessions were subjected to waterlogging, these forages being considered resistant to this type of stress. Possibly, the waterlogging caused a denitrification process in the soil that increased chlorosis occurrence in plant leaves. This effect could have reduced the nitrogen absorption by plants (Adams and Akhtar, 1994). Sharp reductions in chlorophyll content were also reported in the studies of Bailey-Serres et al. (2012) and Liu and Jiang (2015) when plants were subjected to conditions of excess water.

In the period after waterlogging stress, unlike water deficit, genotypes prioritized root recovery over aerial tissues (Figure 2C). Furthermore, plants subjected to waterlogging showed a higher root recovery rate (Figure 4B). According to Kato et al. (2014), this effect suggests an effective antioxidant system to cope properly with oxygen re-exposure during the stress recovery period. A similar result was obtained by Puyang et al. (2015), who assessed Kentucky bluegrass cultivars (*Poa pratensis* L.) resistant to waterlogging.

### 4.3. Responses of *Megathyrsus maximus* hybrids to water stress

Assessing the responses of improved forage materials to water deficit and waterlogging is important to determine the resistance capacity, which allows the classification and selection of certain genotypes. Regarding the water deficit stress condition, no genotype, not even the Massai cultivar, proved to be resistant. Despite the Massai cultivar being widely recognized for its relative resistance to water stress (Volpe et al., 2008; Ribeiro-Júnior et al., 2017; Veras et al., 2020), our results indicate that under the acute stress conditions applied in the experiment, even this cultivar could not withstand the severity of the deficit. The limitation of root growth in pot conditions may have exacerbated the effects of water deficiency, highlighting the need for further studies to evaluate the performance of the cultivar under less restrictive conditions, such as in the field. However, we emphasize the existence of a survival mechanism with root and aerial tissues recovery after the stress recovery period (Figures 2C, 3C, and 5B). Given the productive, morphological, and structural responses, the PM409 genotype is a material that showed adaptive characteristics to waterlogging conditions. However, this is not the most productive genotype under ideal soil moisture conditions. In addition, the PM411 genotype also revealed a resource conservation potential when subjected to waterlogging conditions (Tables 1 and 2; Figure 5A).

The results were important for identifying genotypes with promising traits to endure water stress. However, further studies are needed under field conditions to prove the responses of *M. maximus* genotypes to water deficit and waterlogging.

## 5. Conclusions

Water deficit affects the productive and morphological traits of *M. maxim*us genotypes more than waterlogging. Only the PM409 genotype showed stress resistance mechanisms among the materials assessed under waterlogging. On the other hand, none of the materials showed resistance to water deficit.

## Data availability

The entire dataset supporting the results of this study was published in the article itself.

## Author contributions

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## Conflict of interest

The authors declare no conflict of interest.

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