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ORIGINAL ARTICLE

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Effects of post-fire heating on germination and early growth of two congeners of *Dimorphandra* species from Cerrado and Atlantic Forest

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Abstract

Plants in the Atlantic Forest are not adapted to fire. On the other hand, in the Cerrado, fire occurs naturally, favoring species morphophysiologically adapted to its seasonality. However, little is known about the influence of the post-fire scenario on the germination of woody species in these two biomes. The objective of the present study was to evaluate the impact of post-fire heating on the germination and early growth of two species of the genus *Dimorphandra*. The seeds of *Dimorphandra mollis* (Fabaceae, Cerrado) and *D. exaltata* (Atlantic Forest) underwent three pre-germination treatments: control at ambient temperature, 30 days of heating (simulating fire in the mid-dry season), and 7 days of heating (simulating fire at the end of the dry season) at 45°C day and 10°C night in a Biochemical Oxygen Demand Incubator. *Dimorphandra mollis* seeds had a shorter germination time than *D. exaltata* in heating treatments. A higher hypocotyl–root axis was found in *D. mollis* seedlings under control temperature, but this species showed a decrease in the hypocotyl–root axis in both heating treatments. Reduced root growth could decrease the ability of this species to compete for resources under the soil. The germination interval in *D. exaltata* seeds in the heating treatments may be slower, scattering recruitment over time in such conditions, but this could be a survival strategy for plants in disturbed environments. The post-fire scenario was detrimental to germination and early development, delaying germination and impairing the growth of the hypocotyl–root axis in plants of the genus *Dimorphandra*.

KEYWORDS

biomass allocation, disturbance, fire ecology, heating, hypocotyl–root axis

1 | INTRODUCTION

Temperature fluctuations throughout the year play a central role in the germination and recruitment of plants, especially those adapted to fire-prone ecosystems (Pausas & Lamont, 2022). Recent studies indicate that fire in the Cerrado is responsible for the increase in plant recruitment in the seed bank, both due to its occurrence and the alternation of temperatures caused by the post-fire scenario (Dairel & Fidelis, 2020, 2024). In the

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Atlantic Forest, fire is less frequent, resulting in biomass loss and a decreased native species richness (Guedes et al., 2020; Singh & Huang, 2022). Similarly, soil temperatures close to 45°C were found at the forest edges (Geisler et al., 2017) and post-fire scenarios on Cerrado soils (Miranda et al., 1993, Miranda et al., 2009; Musso et al., 2015). Therefore, it is necessary to understand how temperature alternation may influence seed recruitment in the soil, especially with the increase in fire events of anthropogenic origin (Guedes et al., 2020; Silva et al., 2005; Singh & Huang, 2022). It is also important to understand the effects of post-fire temperature on the germination and early development of tree species, both in the Cerrado and the Atlantic Forest.

In the Atlantic Forest, fire is a mostly anthropogenic disturbance (Guedes et al., 2020). Therefore, plants from the Atlantic Forest are not resistant to fire, which results in the destruction of vegetation and a reduction in the natural floristic composition of the biome after fire events (Hardesty et al., 2005; Singh & Huang, 2022). On the other hand, the Cerrado is characterized by a marked climatic seasonality (dry winters and rainy summers, Adámoli et al., 1987; Klink et al., 2020; Marcuzzo et al., 2012). This precipitation pattern, combined with the high biomass of herbaceous plants accumulated on the soil during the dry season (Pilon et al., 2021), allows fire to be present seasonally (at the beginning of the wet season) as an ecological and evolutionary factor for at least 10 million years (Coutinho, 1990; Keeley et al., 2011; Simon et al., 2009). Thus, fire is a selective pressure for Cerrado plants that are highly resilient (Dantas & Pausas, 2013; Hoffmann et al., 2009; Pilon et al., 2021).

In addition to being resilient, some Cerrado plant species require the occurrence of fire to flower, sprout, and produce fruits (Conceição & Orr, 2012; Munhoz & Felfili, 2007). However, fire is a controlling agent for the development of young trees in the Cerrado, negatively affecting the early stages of the plant's life by burning the crown of those individuals that are not taller than the flame level (Dantas & Pausas, 2013; Gomes et al., 2014; Hoffmann & Solbrig, 2003). On the other hand, in Semideciduous Seasonal Forests, the fire results in the death of woody plants, especially those with smaller diameters (Pereira et al., 2017; Silva et al., 2005; Wade & Lundsord, 1990). Therefore, in this phytophysiognomy of the Atlantic Forest, plant species do not have adaptive strategies to resist fire, as the native Cerrado trees (Singh & Huang, 2022). Thus, studies indicate that fire events in forests reduce tree density by up to 42% (Silva et al., 2005), as well as benefiting the colonization of these environments by invasive graminoid species (Pereira et al., 2017; Reis et al., 2018; Singh & Huang, 2022).

In recent years, studies have shown how fire influences the germination of plant species in the Cerrado (Dairel & Fidelis, 2020; Musso et al., 2015). During fire events, the seeds of woody and herbaceous plants exposed directly to the fire died due to high temperatures (±280°C, Andrade & Miranda, 2014; Castro-Neves & Miranda, 1996; Shackleton, 2007). However, due to the short fire residence time (±5 min), the soil undergoes significant heating up to 1.0 cm deep, between 29°C and 55°C (Miranda et al., 1993, 2009), while at 0.5 cm over the ground, temperatures between 100°C and 110°C were found in the savannas of Venezuela (Silva et al., 1990). For temperatures between 100°C and 110°C, few species showed reduced germination time (González-Rabanal & Casal, 1995; Hanley & Lamont, 2000; Shackleton, 2007; Tarrega et al., 1992).

The influence of fire on the germination of Cerrado plants may not be directly related to heating during its passage but rather to the post-fire scenario (Gashaw & Michelsen, 2002; Scott et al., 2010; Went et al., 1952; Zupo et al., 2016). The accumulation of ashes due to the burning of herbaceous plants increases the daily temperature range on the soil between 10°C and 45°C (Castro-Neves & Miranda, 1996), as well as a reduction in competition for resources (Dayamba et al., 2008; Fichino et al., 2016; Figueroa et al., 2009; Musso et al., 2015). However, little is known about the influence of the post-fire scenario on the germination of seeds of woody species (Parr et al., 2014). Even though the effect of fire has been studied for years, a complete understanding of its influence remains unachieved (Coutinho, 1990; Oliveira et al., 2021; Rodrigues & Fidelis, 2022). For instance, when the fire event occurs at the beginning of the dry season, the soil will be exposed to temperature fluctuations for longer due to the interval between the first natural fires and the first rains. However, when fire occurs later, the soil exposure period to thermal variation will be shorter (Daibes et al., 2017; Moreira & Pausas, 2012).

Dimorphandra mollis Benth. (Fabaceae) is found in Brazil, Bolivia, and Paraguay (Silva, 1986). In Brazil, this species has a wide distribution in central areas of the Cerrado (Borghetti et al., 2019; Lorenzi, 1992; Pacheco et al., 2010; Ratter et al., 2003). Due to *D. mollis* being a woody species typical of savannas, a fire-prone ecosystem, the seeds have a hard cover, which allows the seed to remain viable in the soil for up to 4 years (Bizerril et al., 2005; Borghetti et al., 2019). On the other hand, *D. exaltata* Schott. occurs in the Atlantic Forest and ecotones with Cerrado areas, especially in Minas Gerais, São Paulo, and Rio de Janeiro (Fernandes & Rego, 2014). This species presents seeds with physical dormancy due to their hard cover (Matheus et al., 2017), and Rocha et al. (2024) demonstrated the possible evolutionary origin of

D. exaltata from Cerrado areas, which could result in ecophysiological characteristics like those of Cerrado species. In this sense, many studies worldwide have shown the potential of breaking physical dormancy due to abiotic factors, such as fire (Pausas & Lamont, 2022), especially in savanna plants (Auld & Bradstock, 1996; Ooi et al., 2014) that could present seeds with hard coats.

Therefore, the objective of the present study was to understand how the post-fire heating time, at the mid-dry season (30 days of pre-germination heating) or the end of the dry season (7 days of pre-germination heating), influences the germination and early development of *D. mollis*, a species belonging to the Cerrado, and *D. exaltata*, a species belonging to the Atlantic Forest. We postulated that the germination traits and seedling early development may remain a niche-conserved trait of the Cerrado in both *Dimorphandra* species or be changed in the forest species, *D. exaltata*, adapted to the new environment.

2 | METHODS

2.1 | Seeds and experimental design

The experiment was carried out from October to December 2022. The seeds of *D. mollis* were purchased from Arbocenter in 2020, while the seeds of *D. exaltata* were collected from 40 adult trees located on a farm close to the urban perimeter of Florestal city in 2022 (−19 862 836° S, −44 446 567° W).

The seeds underwent an aseptic protocol with 5% sodium hypochlorite for 5 min (Freitas et al., 2009). They were then washed successively in deionized water. After drying, the 180 seeds (90 for each species) were placed in brown paper bags and divided into three groups corresponding to the treatments: NH = no heating (control group, $n = 30$ seeds per species); SH = seven days of heating (simulating fire at the end of the dry season, $n = 30$ seeds per species); TH = thirty days of heating (simulating fire at the middle of the dry season, $n = 30$ seeds per species, Musso et al., 2015). First, the TH treatment bags (30 days of heating) were placed in the Biochemical Oxygen Demand incubator (B.O.D.—ELETROLAB, model EL202/4E, São Paulo, Brazil) to be heated at 45°C/10°C (12 h day/12 h night), as mentioned by Castro-Neves and Miranda (1996). After 23 days of heating, at the same B.O.D., the SH treatment bags (7 days of heating) were added. The same temperature and photoperiod were maintained until the end of the heating treatment and monitored twice a day using a thermo-hygrometer (KETOTEK, HTC-2, São Paulo, Brazil).

2.2 | Germination and early growth

After 30 days of pre-germination treatment, the 180 seeds ($n = 30$ per species in each treatment) were removed from the paper bags, manually scarified, and placed in Petri dishes sanitized with 70% alcohol. The Petri dishes with germitest paper were wetted with 2.5 mL of deionized water twice a day for 30 days after the beginning of the experiment. The Petri dishes, identified with their respective treatments and species, were placed into the B.O.D. to germinate at a constant temperature of 27°C with a 12-hour photoperiod, following the usual climatic conditions of the Cerrado (Felippe & Silva, 1984; Fichino et al., 2016). The shelves inside the B.O.D. were rotated weekly (every 7 days for 30 days) to avoid differences between the samples. The temperature and humidity of the air inside the B.O.D. were daily monitored using a Thermo-hygrometer. Also, the light intensity within the B.O.D. was measured with a lux meter (Lux-Meter, model 07137.00, Phywe, Germany).

2.3 | Vegetative morphometry and biomass determination

From the first day after the beginning of the experiment, we monitored the time for germination (in days) and cotyledon emergence (in days). In all germinated seeds, we measured the hypocotyl–root axis (cm), epicotyl length (cm), and leaf number (LN) using a digital caliper (DIGITAL CALIPER, model KQL038, London, UK) during 30 days.

At the end of the germination and early growth period, we divided the seedlings into five segments: cotyledons, hypocotyl, radicle, epicotyl, and leaves. We placed the seedling segments in brown paper bags identified with the respective species and treatment. Afterward, the 120 bags were dried in an oven (TECNAL TE-394/3, São Paulo, Brazil) at 70°C (Perez-Harguindeguy et al., 2013) for 48 h. We used an analytical balance (SHIMADZU-Série BL-320H, Tokyo, Japan) to measure the dry mass of the cotyledons, hypocotyl, radicle, leaves, and epicotyl.

2.4 | Statistical analysis

Means and standard errors were calculated for all germination, vegetative morphometry, and dry matter production traits determined. To verify possible significant differences ($p < 0.05$) in the variables (germination rate, days to germination, time to cotyledon emergence, hypocotyl–radicle axis length, epicotyl length, leaf number, cotyledon dry mass, leaf dry mass, root dry mass,

hypocotyl dry mass, and epicotyl dry mass), a generalized linear model (GLM) analysis was used, considering species (*D. mollis* and *D. exaltata*) and heating (NH, SH, and TH) as factors. For all GLMs performed, the Gaussian distribution was adopted, and the lowest AIC value was used to choose the models. The Dharma package was used to test the assumptions, and the emmeans package was used to test post hoc differences. The R program, version 3.0.0 (R CORE TEAM, 2024, Vienna, Austria), was used to carry out all statistical tests. All graphs were assembled in OriginPro (v.2016, OriginLab Corporation, Northampton, MA) according to the statistical analysis.

3 | RESULTS

3.1 | Germination and cotyledon emergence

The heating treatments did not affect ($p > 0.05$) the germination rate in both species (Figure 1). The heating treatments (SH and TH) delayed germination in *D. exaltata*, but not in *D. mollis* seeds ($p < 0.05$, interaction between heating and species, Figure 1). The SH treatment delayed cotyledon emergence in both species ($p < 0.05$, simple effect of heating, Figure 2), and *D. mollis* showed a higher time to cotyledon emergence than *D. exaltata* ($p < 0.05$, simple effect of species, Figure 2).

3.2 | Morphometry and dry mass production

D. exaltata seedlings showed higher hypocotyl dry mass than *D. mollis* in all treatments ($p < 0.05$, interaction between heating and species, Figure 3). However, the heating did not affect hypocotyl dry mass in both species ($p > 0.05$, interaction between heating and species, Figure 3). *Dimorphandra exaltata* showed higher cotyledon dry mass than *D. mollis* seedlings in the TH treatment ($p < 0.05$, interaction between heating and species, Figure 3). Also, *D. exaltata* seedlings showed an increased cotyledon dry mass with heating treatments ($p < 0.05$, interaction between heating and species, Figure 3).

D. mollis seedlings showed a higher hypocotyl–radicle axis than *D. exaltata* in the control treatment ($p < 0.05$, interaction between heating and species, Figure 4). However, only *D. mollis* seedlings showed a decreased hypocotyl–radicle axis in heating treatments ($p < 0.05$, interaction between heating and species, Figure 4).

On the other hand, epicotyl length was higher in *D. exaltata* than in *D. mollis* seedlings ($p < 0.05$, simple effect of species, Figure 5), and heating treatments harmed epicotyl growth in both species ($p < 0.05$, simple effect of species, Figure 5). However, seedlings of both species presented more leaf number in the SH treatment than in the control ($p < 0.05$, simple effect of species, Figure 5). Seedlings of *D. exaltata* showed higher dry mass allocation to roots, epicotyls, and leaves

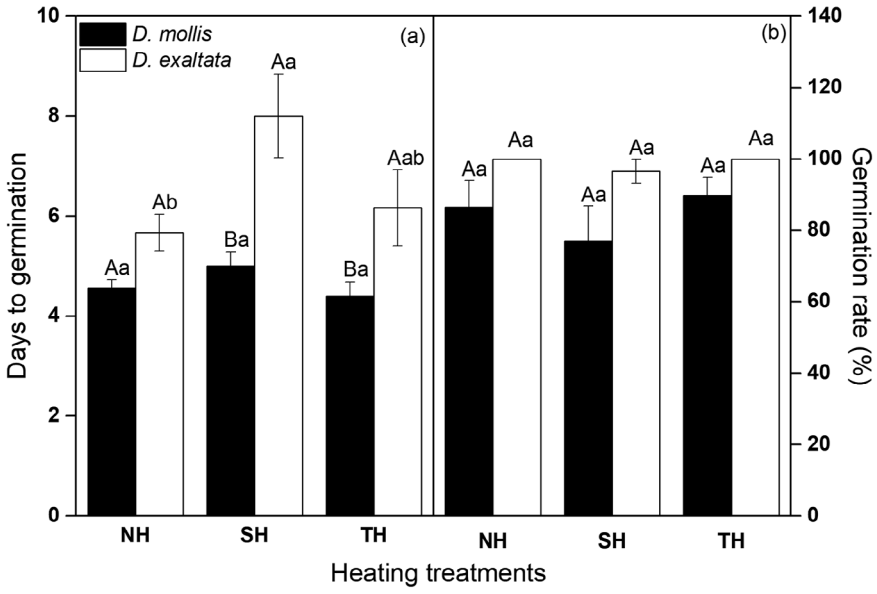

FIGURE 1 Days for germination (a) and germination rate (b) in *Dimorphandra mollis* (black bar) and *Dimorphandra exaltata* (white bar) seeds. Both graphs compare the two species subjected to the same treatments, NH (control), SH (7 days of heating), and TH (30 days of heating). Capital letters compare species within the same treatment, and lowercase letters compare treatments within the same species ($p < 0.05$).

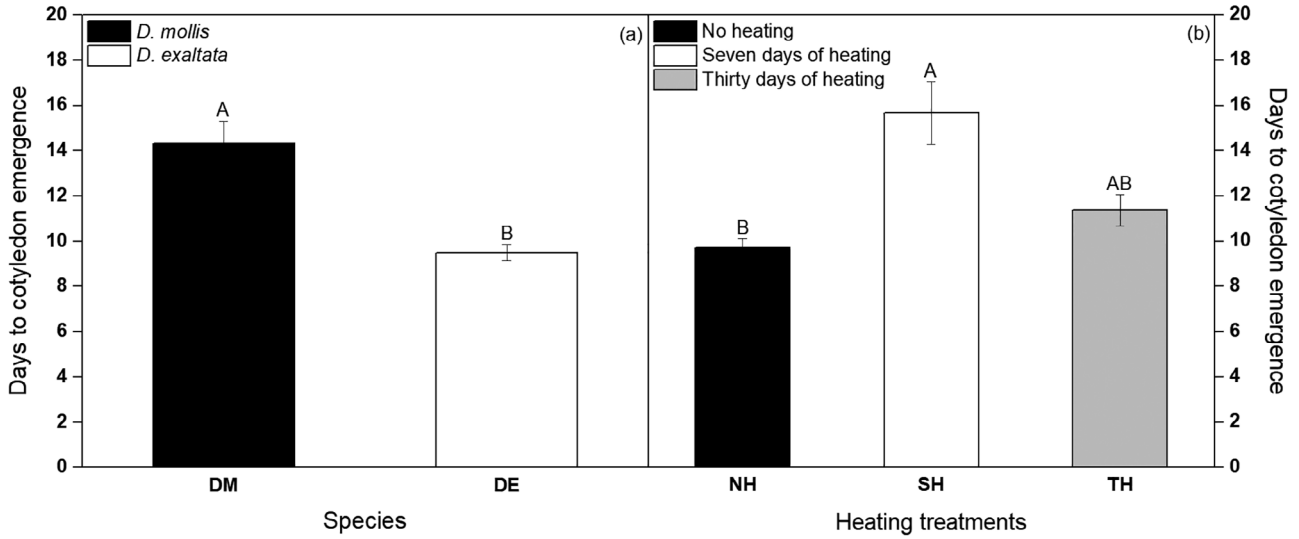

FIGURE 2 Days for cotyledon emergence in *Dimorphandra mollis* (black) and *Dimorphandra exaltata* (white) seedlings. The graph (a) compares the species *D. mollis* (DM) and *D. exaltata* (DE). The graph (b) compares the treatments NH (control, black bars), SH (7 days of heating, white bar), and TH (30 days of heating, gray bar). Capital letters compare species and treatments separately ($p < 0.05$).

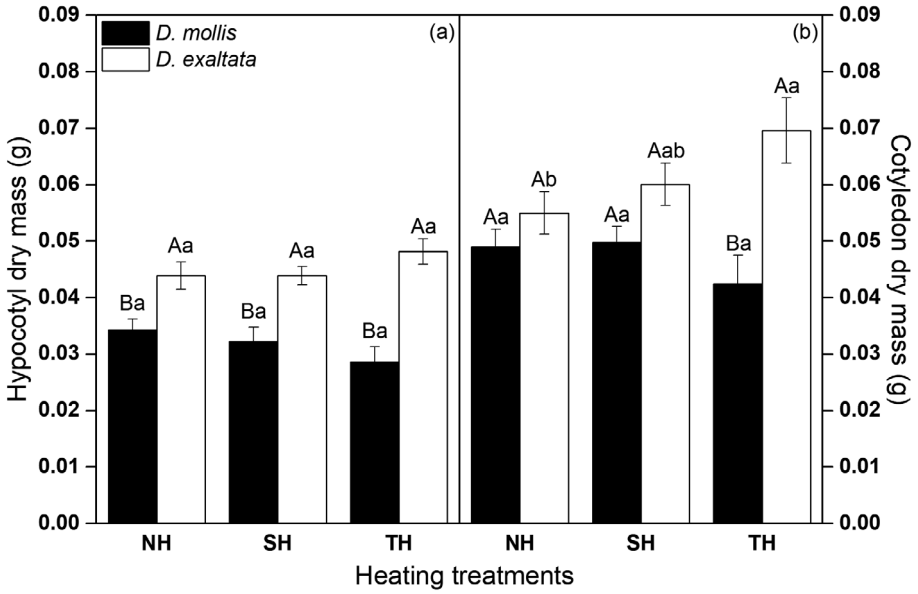

FIGURE 3 Dry mass of the hypocotyl (a) and cotyledons (b) in *Dimorphandra mollis* (black bar) and *Dimorphandra exaltata* (white bar) seedlings. Graphs compare the two species subjected to the same treatments, NH (control), SH (7 days of heating), and TH (30 days of heating). Capital letters compare species within the same treatment, and lowercase letters compare treatments within the same species ($p < 0.05$).

than *D. mollis* ($p < 0.05$, simple effect of species, Table 1).

4 | DISCUSSION

The delayed germination of *D. exaltata* by those temperatures that stimulated the fire event at the end of the dry season was expected, despite the change in the ecological niche of this species, from Cerrado to the Atlantic Forest (Rocha et al., 2024). As a forest species, a negative effect on germination is expected due to high post-fire temperatures (Kaewsong et al., 2022). However, there is no temperature effect on the germination rate in *D. exaltata*, showing that the adaptation to a new ecological niche is still taking place, and some functional traits of fire-prone environments, such as Cerrado, are still preserved. On the other hand, *D. mollis* seeds were not harmed by

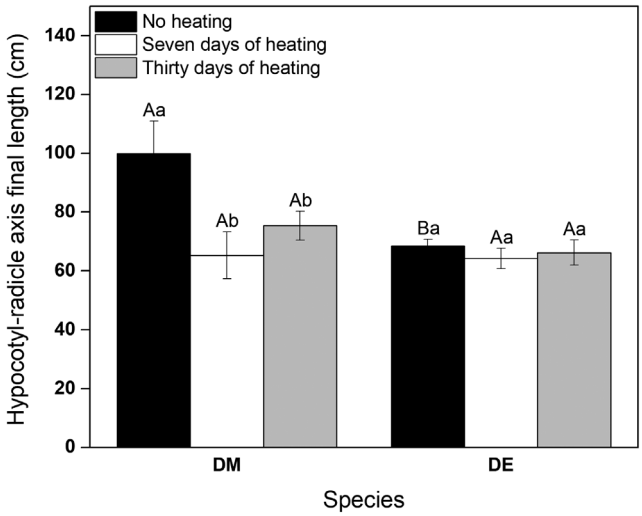

FIGURE 4 Hypocotyl–radicle axis in *Dimorphandra mollis* (DM) and *Dimorphandra exaltata* (DE) seedlings. The graph compares the NH (control, black bar), SH (7 days of heating, white bar), and TH (30 days of heating, gray bar) treatments within species. Capital letters compare different species in the same treatment, and lowercase letters compare treatments in the same species ($p < 0.05$).

heating, showing similar germination traits (interval and percentage) between the different treatments, corroborating the hypothesis that this Cerrado species is tolerant and remains viable in the seed bank after exposure to the post-fire scenario. So, for the forest species, the germination was partially affected by heating, showing that a shift in the ecological niche is still occurring for this species; however, the Cerrado species shows a conservative niche strategy regarding germination. Several studies have demonstrated that Cerrado plants tolerate natural fires at lower temperatures (below 100°C, Fernandes et al., 2021; Fichino et al., 2016; Gorgone-Barbosa et al., 2020). However, fire events of anthropogenic origin have greater intensities and shorter intervals between events (Pivello, 2011). So, based on the results of the germination rate and interval, it is important to highlight that both species from forests and fire-prone environments could be more impacted by anthropogenic fires, mainly endangered species, such as *D. exaltata*.

Even though it was harmful to both species, the 7-day heating treatment was more detrimental to the emergence of cotyledons in *D. mollis*. This species invests more in the growth of the root system than the aerial part, a behavior typical of species occurring in savannas (Hoffmann et al., 2004). The delay in cotyledon emergence in species with fleshy cotyledons, such as *D. mollis*, may negatively impact the establishment and initial growth in savanna areas (Silva et al., 2023), since species with developed cotyledons and embryonic axes could grow faster than species with less differentiated embryonic structures. Thus, to maintain a viable population in Cerrado areas, more studies are necessary to understand the ideal fire frequency for the establishment of *D. mollis* seedlings.

On the other hand, even though *D. exaltata* is a forest species, due to its possible origin in the Cerrado (Rocha et al., 2024), post-fire heating stimulates biomass allocation to the cotyledons, showing that these species have conserved some plasticity from their ancient origin and the change in the ecological niche from Cerrado to Atlantic Forest is still taking place. The increased biomass allocation to the cotyledons (also epicotyl) is an ecological strategy related to the stock of nutrients and water to perform photosynthesis. These functional traits are important for the early growth of seedlings (Kitajima, 1992). The higher cotyledon growth benefits the absorption of light to carry out photosynthesis, resulting in high early growth, which is a competitive strategy for capturing light (Grisi et al., 2019; Macedo et al., 2022).

Post-fire temperatures damaged the final size of the hypocotyl–root axis in *D. mollis*. However, the shorter length of the hypocotyl–root axis was not accompanied by a lower biomass allocation to these compartments in *D. mollis*. The savanna species, such as *D. mollis*, present higher root growth to explore the soil in search of water and nutrients (Hoffmann et al., 2004). Even though the post-fire temperatures do not completely harm the plant, the reduced root growth could negatively affect the ability of this species to compete for below-ground resources with herbaceous and woody species (Gonçalves et al., 2024). The adjustment between seed dispersal and natural fire events may contribute to the *D. mollis* seedlings' escape from disturbances, as fire is a more limiting factor for *D. mollis* seedling recruitment than drought (Borghetti et al., 2019). Therefore, an interval between fire events is necessary for *D. mollis* seedling recruitment in Cerrado, allowing young plants to develop their root and aerial systems to resist fire events and guarantee the resprouting (Borghetti et al., 2019).

The low initial investment in the biomass allocation to the roots in *D. exaltata* is typical of forest species (Hoffmann et al., 2004). However, this species presents a higher investment in the growth of the aerial part than *D. mollis*. Due to the post-fire heating treatments, it was possible to observe the persistence of the leaf number, but with low linear epicotyl growth in both species. Lower aerial growth in forest species can be detrimental to light capture, a limiting resource in understory areas, affecting tolerance to biotic and abiotic stresses (Valladares et al., 2016). Thus, the competitive ability of young *D. exaltata* plants may be compromised, mainly due to the adverse effect of fire, which is more evident in

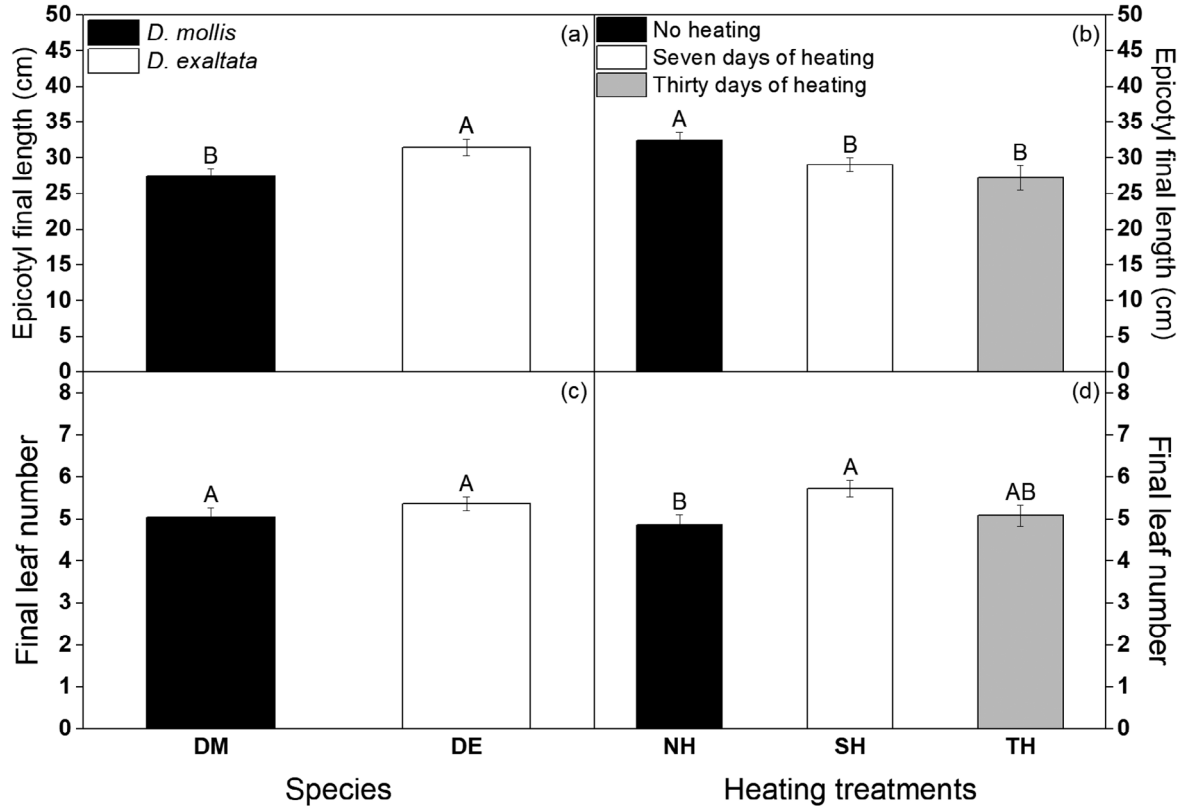

FIGURE 5 Epicotyl length (a and b) and leaf number (c and d) in *Dimorphandra mollis* (DM) and *Dimorphandra exaltata* (DE) seedlings. Graphs a and c compare the species *D. mollis* (black bar) and *D. exaltata* (white bar). Graphs b and d compare the treatments NH (control, black bars), SH (7 days of heating, white bar), and TH (30 days of heating, gray bar). Capital letters compare species and treatments separately ($p < 0.05$).

TABLE 1 Dry mass of roots, epicotyl, and leaves of *Dimorphandra mollis* and *Dimorphandra exaltata* seedlings under three heating treatments.

Species/traits	Root (g)	Epicotyl (g)	Leaves (g)
Dimorphandra mollis	0.217 B	0.009 B	0.009 B
Dimorphandra exaltata	0.336 A	0.010 A	0.017 A

Note: Due to statistical significance, the data from all heating treatments was merged. Capital letters indicate significant differences among species ($p < 0.05$).

forest than in savanna species. More important is the fact that *D. exaltata* is a species at risk of extinction (Fernandes et al., 2021), occurring in a diverse and highly fragmented biome such as the Atlantic Forest (Myers et al., 2000) and with low genetic diversity and phenotypic plasticity (Costa et al., 2025; Muniz et al., 2019). On the other hand, the higher leaf number in seedlings subjected to heating may be due to the natural ecological growth strategy of the species (Moura et al., 2017; Rossatto et al., 2009), and each leaf could work in a cost-effective way producing more biomass in sunny environments, even after a disturbance, such as a fire event (Clemente et al., 2005).

The plasticity observed in *D. exaltata* seedlings in heating treatments can be justified by the evolutionary origin of the species. Over millions of years, climate changes occurred in the Neotropics, and these changes shaped the dynamics of expansion and contraction of the Amazon, Cerrado, and Atlantic Forest biomes (Behling & Hooghiemstra, 2001; Bueno et al., 2017; Oliveira-Filho & Ratter, 1995). The species residing in these biomes experienced adaptive pressures, resulting in speciation events. Especially within the genus *Dimorphandra*, the expansion of Amazonian species to the nearby Cerrado (during humid periods) and from the Cerrado to the Atlantic Forest (during drier periods) was observed. Molecular evidence indicates *D. exaltata* as a species originally from the Cerrado, which, with the reduction in humidity, ended up establishing itself in the adjacent Atlantic Forest (Rocha et al., 2024).

Finally, we concluded that post-fire temperatures differentially affect the two species studied, with *D. mollis* seedlings presenting low root and epicotyl growth, and *D. exaltata* presenting low epicotyl growth. These changes in seedling allometry may result in a reduction in the ability of the Cerrado species to compete for water and nutrients in open environments and for the forest species to compete for light in the understory environment (Melo et al., 2018; Poorter et al., 2012). Despite more studies about the influence of post-fire temperatures and fire frequency on the germination and early growth being necessary, our results indicate that both species could need longer intervals between fires to keep their normal early growth and establish themselves in natural conditions. It is important to highlight that *D. mollis* occurs in an environment with natural fire events, but *D. exaltata* occurs in environments where fire is less frequent. So, the increase in anthropogenic fire could further harm and limit both species in savannas (Cerrado) and forest formations in both the Cerrado and the Atlantic Forest.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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