Tropical Grasslands-Forrajes Tropicales (2025) Vol. 13(1):28–39
doi: 10.17138/TGFT(13)28-39

Research Paper

Thermal limits to stoloniferous leaves and root growth in *Paspalum notatum*, a south American native grass

Límites térmicos para el crecimiento de hojas estoloníferas y raíces en Paspalum notatum*, una gramínea nativa de América del Sur*

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Abstract

In tropical regions the cultivation of African grasses for animal forage is extensive and an ecophysiological alternative is to stimulate the use of native species especially in a scenario of global temperature change. The thermal limits to leaf and root growth in *Paspalum notatum* a South American native grass were evaluated. Stolon fragments with roots and dry parts removed and the same number of nodes were placed in transparent plastic boxes on moistened filter papers and transferred to chambers at constant temperatures of 15, 20, 25, 30, 35 °C and alternating temperatures of 25/15 °C and 30/20 °C, all in a 12 h photoperiod. Leaf production was evaluated daily for 30 days. Stolon fragments showed leaf growth in all temperatures, except at 15 °C. The thermal range limits were 14.3 °C as base temperature and 39.2°C as ceiling temperature. Results showed that 50 degree days were necessary for 50% of leaf growth by the stolons. The largest leaf area occurred at 25 to 30 °C and the largest specific leaf area was at 25 °C. The optimal temperature for growth was 30 °C with higher root growth at 20 °C and in alternating temperatures. Results indicate that *P. notatum* has potential to grow in a wide range of temperatures and that the increase of global average temperature should not affect its distribution in its current habitat, presenting promising traits as an option for pastures in all tropical regions.

Keywords: Climate change, grass propagation, leaf growth, native grass, thermal time model.

Resumen

En regiones tropicales el cultivo de gramíneas africanas para forraje animal es amplio y una alternativa ecofisiológica es estimular el uso de especies nativas especialmente en un escenario de cambio de la temperatura a nivel global. Se evaluaron los límites térmicos para el crecimiento de hojas y raíces en *Paspalum notatum*, una gramínea nativa de América del Sur. En cajas plásticas transparentes, sobre papeles de filtro humedecido, se colocaron fragmentos de estolones sin raíces ni partes secas, y con igual número de nudos y se transfirieron a cámaras a temperaturas constantes de 15, 20, 25, 30, 35 °C y temperaturas alternas de 25/15 °C y 30/20 °C, todo en un fotoperíodo de 12 h. La producción de hojas se evaluó diariamente durante 30 días. Los fragmentos de estolones mostraron crecimiento de hojas en todas las temperaturas, excepto a 15 °C. Los límites del rango térmico estuvieron entre 14.3 y 39.2 ºC. Los resultados mostraron que 50 grados-día fueron necesarios para el 50% del crecimiento de las hojas de los estolones. La mayor área foliar se presentó entre 25 y 30 °C y la mayor área foliar específica se presentó a 25 °C. La temperatura óptima para el crecimiento fue 30 ºC, con un mayor crecimiento de las raíces a 20 °C y en temperaturas alternadas. Los resultados indican que

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P. notatum tiene potencial para crecer en un amplio rango de temperaturas y que el aumento de la temperatura media a nivel global no debería afectar su distribución en su hábitat actual, presentando atributos prometedores como una opción para pasturas en todas las regiones tropicales.

Palabras clave: Cambio climático, crecimiento de hojas, modelo de tiempo térmico, pasto nativo, propagación de pastos.

Introduction

Environmental temperature is an important driver of plant growth and development (Hodges and Evans 1992; Bykova et al. 2012; Yamori et al. 2014). An extrapolation of the thermal range tolerated by a species can induce thermal stress in many plants (Porter 2005; Kotak et al. 2007). Therefore, it is one of the environmental conditions which determines vegetation distribution in an area (Scherrer and Korner 2011).

Grasses are an important plant group widely distributed in different biomes (Kellogg 2001). These plants are the largest group with C4 photosynthetic metabolism, which give them an advantage in water use efficiency and high photosynthetic rates at high temperatures over C3 plants (Sage 2004). C4 grasses present higher growth in warm and wet environments, some survive with water shortage (Yamori et al. 2014), some tolerate shading (Martuscello et al. 2009) and low nutrient availability while some are capable of post fire regeneration (Leite et al. 1998). These traits ensure grasses establish in new environments (Tinoco-Ojanguren et al. 2016). Despite the adaptation of most C4 grass species to environments with high average temperatures, it is necessary to understand how specific grass species will respond to the increase of average temperatures predicted by the intergovernmental panel on climate change (Edenhofer et al. 2014). It has been shown that, although some grasses operate through the C4 metabolic route, they do not present a response pattern to temperature increases (Faria et al. 2015), so these results indicate that responses are species-specific. In Brazil, there is wide use of African grasses for grazing, however, such species can escape their cultivation areas and become invasive competing with and replacing native species due to their vigorous growth and large-scale propagation (Martins et al. 2007; Martuscello et al. 2009). Faria et al. (2015) showed that the increase of average temperatures would not affect alien species development. These species already have invasive ability, occupying a niche of native species, because they are highly competitive for natural resources.

Over time, there was natural variation in global temperatures, with alternation of colder and warmer seasons (Ghil 2002). However, what has been observed since the industrial revolution is an increment of average temperatures at an unprecedented speed due to the exponential increase of greenhouse gas in the atmosphere, resulting from the use of fossil fuels (Edenhofer et al. 2014), as well as other factors associated with deforestation and misuse of land (Buizer et al. 2014). The question related to climate change being widely researched is whether plant species will resist climate change and remain in their habitats, or will suffer redistribution impact. Extreme temperatures exceeding the thermal limit inactivate enzymes such as Rubisco activase and compromise photosynthetic yield (Law and Crafts-Brandner 1999; Sharkey 2005). Changes in long-term average temperatures can exceed the ideal thermal limits for plants, therefore compromising their growth and development, directly impacting their productivity, and changing landscapes as we know them today, due to possible changes in the composition of plant communities (Klanderud and Totland 2005; Dieleman et al. 2015; Shi Zheng et al. 2015).

In recent decades, researchers have highlighted temperature influences in leaf emergence (Moles et al. 2014; Nagelmuller et al. 2016; Egan et al. 2017) and the need to understand the minimum heat requirement for each species (Xue Qingwu et al. 2004; Andrade et al. 2005). The thermal time model is an important tool for physiological studies, and in this study, it is used to predict plant growth under thermal conditions. Equally relevant is the assessment of thermal limits for plant development, using base temperature (T_b) and ceiling temperature (T_c), which are important for determining an optimum range or even an optimum growth temperature (T_o) for the establishment of plant species (Daibes and Cardoso 2018; Duarte et al. 2019). The use of this model will make it possible to estimate the chances of species remaining in their current habitat or if they can be redistributed (Walther et al. 2002; Thomas et al. 2004).

Brazil has many native grasses that present high forage potential (Nabinger et al. 2009), but are not used for pastures due to the superior growth of African grasses (D´Antonio and Vitousek 1992). The *Paspalum* genus has 350 species that consist of both annual and perennial species (Ravikesavan et al. 2023) with potential use for forage throughout the country (Ribeiro et al. 2006; Figure 1). Some species are stoloniferous and both seeds and stolons are used for propagation (Batista and Neto 2000; Aliscioni and Denham 2008; Pimenta et al. 2013). The hypothesis for the study is that since *Paspalum* is widely distributed in South America, this grass presents broad thermal adaptation. In this study the thermal time and cardinal temperatures for leaf emergence were determined and root growth in a thermal gradient was evaluated for *Paspalum notatum* Flugge.

Materials and Methods

Plant material and growth conditions

Stolons of *Paspalum notatum* Flugge were obtained from plants growing on the lawns of the Federal University of Minas Gerais. Immediately after collecting stolons, remaining roots, leaves and dried parts were removed. Stolon fragments were prepared with 4 nodes. Stolons were moistened with nystatin solution (2%) for disinfestation to prevent fungal contamination and placed in transparent plastic boxes (11 × 11 × 3.5 cm) on 3 sheets of filter paper moistened with the same solution to keep papers moist. The experimental design used 42 boxes, each one containing 10 stolons. Six boxes were placed in germination chambers with different temperatures, using 10 stolon fragments from the same plant from 6 individual plants per treatment. Germination chambers were maintained at constant temperatures of 15, 20, 25, 30 and 35 °C and alternating temperatures of 25/15 °C and 30/20 °C with a photoperiod for all treatments of 12 h. The light intensity in the germination chambers was approximately 80 µmol/m^2/s.

Leaf emergence and growth

Leaf emergence (defined as leaves >2 mm) and number of leaves were measured daily for 30 days and final percentage of leaf emergence determined. Considering the initial number of leaves at the end of the experimental period, the relative growth rate (RGR) for leaves during the experimental period was determined according to McGraw and Garbutt (1990), using the equation:

$$RGR=(\ln LN_2 - \ln LN_1)/(t_2 - t_1),$$

where:

LN is total leaf number at each time;

t_1 and t_2 measurements were taken weekly for 30 days (n=6).

To estimate the leaf area (LA), all fully expanded leaves were digitalized while still fresh (HP Scanjet G4050), and the total LA was integrated by using the ImageJ software. In order to obtain the specific leaf area (SLA) the digitalized leaves were, then, placed in paper bags and dried in an oven at 60 °C until constant weight (Fanem Model 320-SE). Dry leaves were weighed on a precision scale (Shimadzu, Model AY220). The SLA was estimated through the ratio between the LA and the leaf dry mass (cm^2/g). For both parameters, we sampled 5 individuals per treatment (n=5). To determine the biomass accumulation over 35 days, leaves and roots were placed in paper bags and dried in an oven until constant weight (Fanem Model 320-SE) at 60 °C. After this period, they were weighed (n=5) on a precision scale (Shimadzu Model AY220).

Cardinal temperatures and thermal time for leaf emergence

The cardinal temperature was established to determine the thermal time of leaf emergence (t_g) of the first leaf of each percent fraction of 10% of the stolon population. Following that, the leaf emergence rate (LER) ($1/t_g$) was determined. Temperatures below the sub-optimal range (T_o) were used to calculate base temperature (T_b). LER was plotted for each treatment linked to temperature for different emergence percentiles for each 10% emergence increase (Covell et al. 1986). The intersection point of this line with the x axis determined the base temperature (T_b) of the tested fraction. The chosen T_b value was obtained from linear regression, from the fraction with the highest R^2. The same procedure was used for the supra optimal portion to determine the ceiling temperature (T_c). The optimal temperature (T_o) was obtained through the intersection of the lines used to obtain T_b and T_c and the value which corresponds to this point in the temperature axis.

Once the linearity relation between LER and the temperature was evident, and T_b showed a general tendency to converge between percentile fractions, the probit model was used to calculate the thermal time for the emergence of the first leaves from stolons in infra-optimal temperatures (below T_o) using the equation Ellis et al. (1986):

$$\theta_{(sub)}=(T - T_b) \cdot t_{(g)},$$

where:

T is the growth temperature;

T_b is base temperature;

t_g is the necessary time for leaf emergence of a given fraction (%) from the stolon population.

Statistical analyses

The design was completely randomized for the 7 temperature treatments. Data were analyzed by Generalized Linear Models (GLM) and the means were compared by contrast test at 5% probability using the software R 3.3.1 (R Core Team 2015). For the parameter percentage of leaf emergence, growth temperatures were used as explanatory variables. Data of relative growth were submitted to a one-way ANOVA and the means compared by Tukey test. For growth analysis, the response variables used were leaf biomass, leaf area and specific leaf area.

Results

Leaf growth

Stolon leaf emergence was observed at all tested temperatures, except for 15 °C where leaf growth was not sufficient to be analyzed (Figure 1 and 2). Emergence of up to the 6th leaf was common in all the other 6 treatments where leaf growth was observed, and no statistical difference was found between them (Figure 2a1, 2a2 and 2a3). The final leaf emergence percentage was above 70% up to the 4th leaf and below 70% for the 5th and 6th leaves (Figure 2a1, 2a2 and 2a3). For the 1st leaf, only at 30 °C, there was a higher speed of leaf emergence, however, for the following leaves there was no difference in leaf emergence (Figure 2b1, 2b2 and 2b3).

The highest relative growth rates (RGR) were observed in plants submitted to constant temperatures of 20, 25, and 30 °C (0.1128 to 0.1219 g/g/day) and alternating temperatures of 25/15 °C and 30/20 °C (0.1219 and 0.1200 g/g/day, respectively) (Figure 3a). Plants growing at 35 °C showed the lowest relative growth rate (0.1127 g/g/day) (Figure 3a). Considering leaf, root and total biomass, there was no difference in production, however, there were differences for root production (Figure 3b). The 20 °C temperature induced higher root growth, with no differences among other temperatures (Figure 3b).

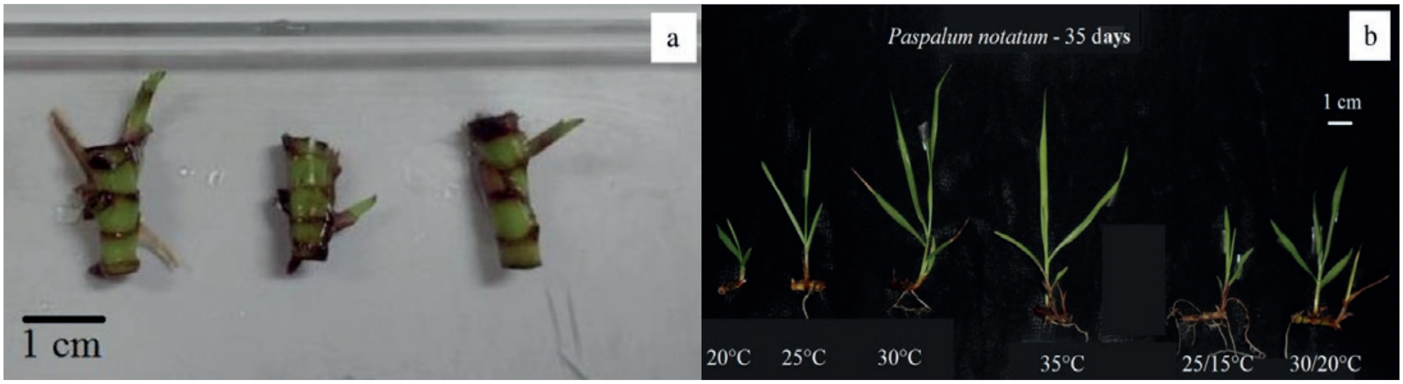

Figure 1. *Paspalum notatum* stolons (a) 4 days after moistening and (b) seedlings at 35 days of growth at different temperatures.

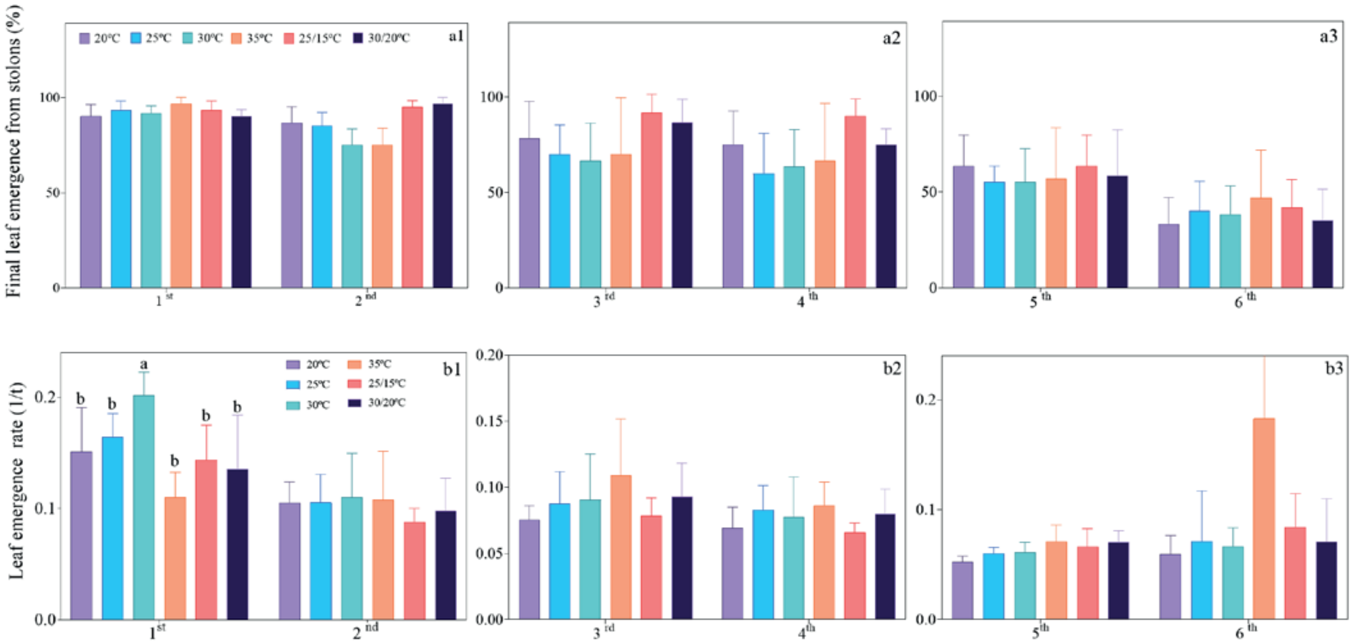

Figure 2. Final leaf emergence from *Paspalum notatum* stolons growing at different temperatures. (a1) stolons leaves 1 and 2; (a2) leaves 3 and 4; (a3) leaves 5 and 6; (b1) leaf emergence rate of leaves 1 and 2; (b2) leaves 3 and 4; (b3) leaves 5 and 6. Same letters in (b1) indicate no difference between growth and temperatures (n=10; P≤0.05). Bars show the average ± standard deviation.

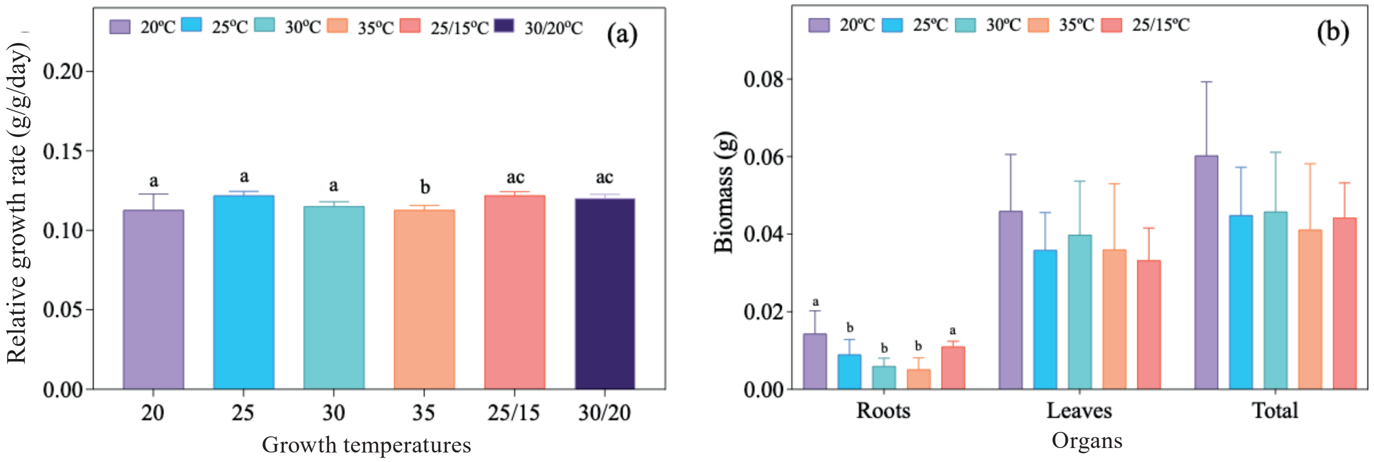

Figure 3. Leaf relative growth rate (a) and (b) root, leaf and total biomass accumulation of *Paspalum notatum* stolons after growth at different temperatures. Different letters in (a) and (b) indicate differences between growth temperatures and same letters indicate no difference between growth temperatures (n=6; P≤0.05). Bars show the average ± standard deviation.

Leaf area and specific leaf area

Leaf area and specific leaf area presented differences among thermal treatments (Figure 4). Larger leaf area was observed in plants grown in temperatures from 25, 30 and 35 °C ($P \leq 0.05$), surpassing 10 cm^2, and the most extreme temperatures tested resulted in smaller leaf area, varying from 4.6 to 10 cm^2 (Figure 4a). The specific leaf area was only larger at 25 °C ($P \leq 0.001$), with average values of 121 cm^2/g (Figure 4b). The plants from the other thermal treatments presented equivalent values, not surpassing 101 cm^2/g (Figure 4b).

Thermal time for leaf emergence

Cardinal temperatures determined for the 1st leaf emergence were 14.3 °C (T_b) 39.2 °C (T_c) and T_0 was 29.9 °C (Figure 5a). The necessary thermal time for 50% (θ_{50}) of the stolons to form the 1st leaf was determined in 50 degree days and 110 and 180 degree days to form the 2nd and 3rd leaves, respectively (Figure 5b).

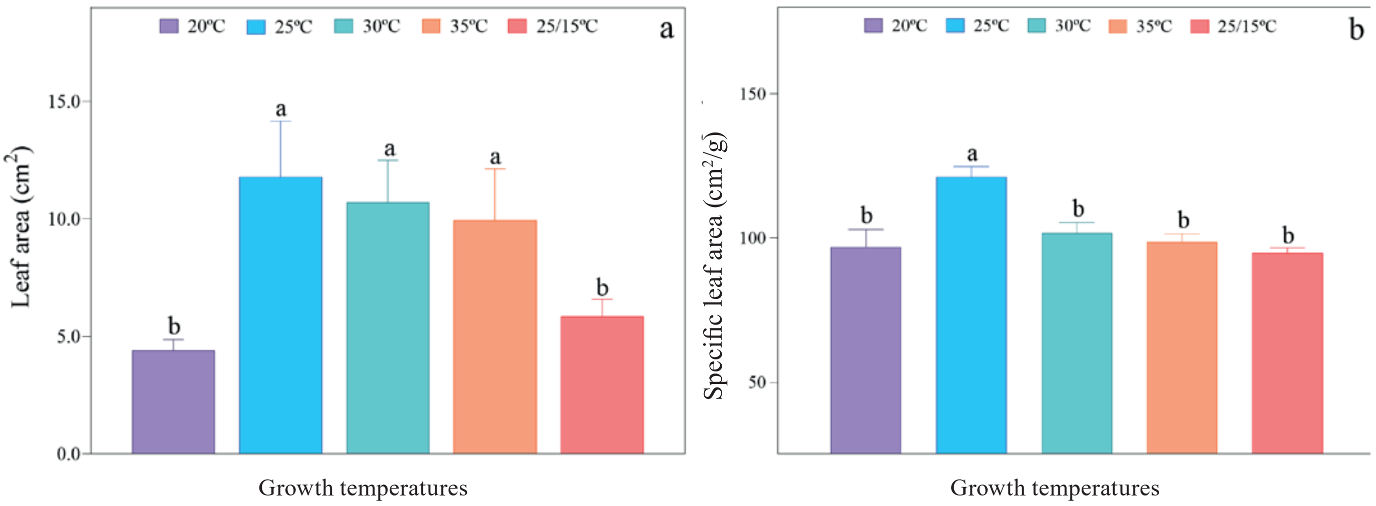

Figure 4. Leaf area (a) and specific leaf area (b) of *Paspalum notatum* stolons at 30 days of growth. Different letters in (a) and (b) indicate differences between growth temperatures and same letters indicate no difference between growth temperatures (n=5; $P \leq 0.05$). Bars show the average ± standard deviation.

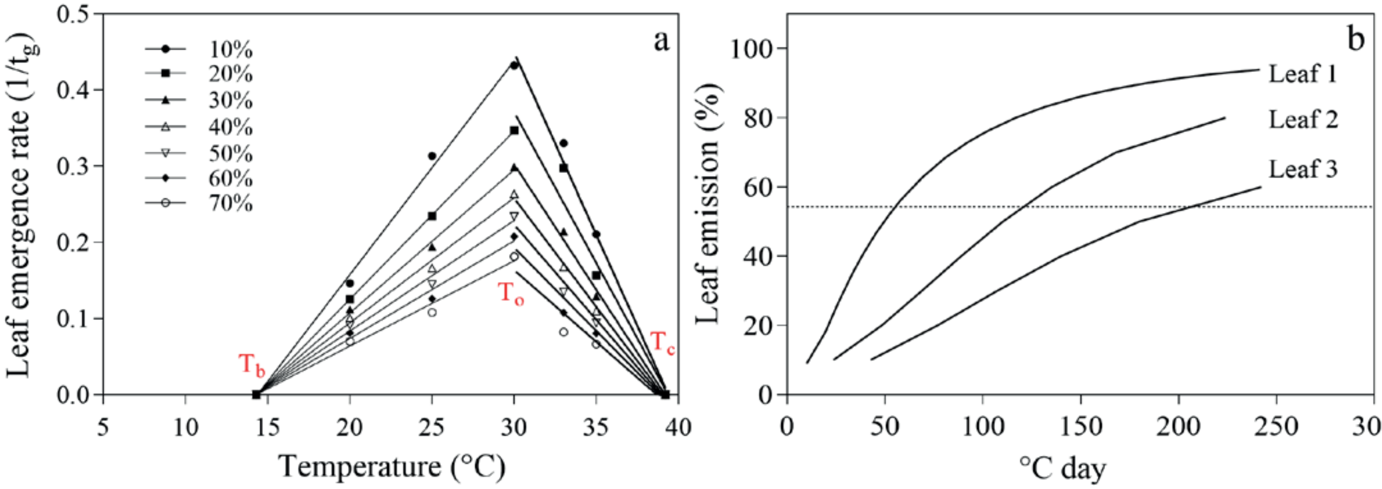

Figure 5. Necessary cardinal temperatures for leaf emergence from *Paspalum notatum* stolons. (a) Leaf emergence rate of first leaf at isothermal temperatures, were T_b=14.3 °C, T_0=29.9 °C and T_c=39.2 °C and (b) Leaf emission of the first leaves of P*aspalum notatum* whose stolons were submitted to different temperature requirements in degree days (°C). Values show the average ± standard deviation (n=6; $P \leq 0.05$).

Discussion

Leaf growth

The stolon is a reserve organ used for vegetative propagation in grasses (Donaghy and Fulkerson 1998), because it provides the ability to re-sprout through the mobilization of reserves until the sprout reaches its photosynthetic autotrophy (Fulkerson and Donaghy 2001). It was observed that the percentage of leaf emergence decreased from the 7th leaf (data not shown) as stolon reserves were depleted with possible rooting incapacity. In this study, there was neither substrate nor nutrient solution or soil to obtain nutrients, sustain newly formed roots and favor plant growth. In a natural environment, this pause would probably not have occurred due to the availability of soil for the roots to take hold and for the plant to continue its development.

Leaf emergence is associated with leaf expansion, and directly related to significant capacity for light interception, photosynthesis and, consequently, early growth (Streck et al. 2002; Streck 2002). Cardinal temperatures vary within the same species, according to the development phase of the plant (Bykova et al. 2012; Sanchez et al. 2014). When temperature reaches a value beyond this optimal range, leaf emergence and elongation become stagnated due to the discontinuance of cell division and elongation, as shown for wheat, corn and rice (Sanchez et al. 2014). Considering all stages of plant development, the extrapolation of T_0 in the field can favor other physiological phases, such as reproduction, for example. According to Sanchez et al. (2014), the T_0 for the reproductive phase is higher than the T_0 for the vegetative development phase for wheat, corn and rice, therefore, it is feasible that the T_0 for *P. notatum* grain filling to be higher than 30 °C.

Although the aim of this study was to assess the influence of temperature on the thermal time for leaf emergence, root growth is also essential for plant establishment. The study showed that the optimum temperature for root growth was different from the optimum temperature for leaf growth. The highest accumulation of root biomass at 20 °C can be related to the need for lower temperatures for its development, once the soil temperature is generally lower than air (Kaspar and Bland 1992). Different temperatures cause different responses in biomass accumulation in plants (Gunn and Farrar 1999; Moles et al. 2014), however, in *P. notatum* different responses were observed only in the roots and not for the leaves in the tested temperatures. Under low average temperatures, metabolism becomes slower and therefore it is expected that plants grown in these conditions accumulate less biomass than plants grown in higher temperatures. This was observed during the experiment through leaf area increases, however, during the period when the dry mass quantification was performed, time was only standardized in calendar days and the number of degree days accumulated were not the same for all treatments, which might have influenced the response (Gunn and Farrar 1999). Plants which grew faster may have had their growth stabilized due to the lack of resources to continue development and those which had a slower growth reached values equivalent to biomass accumulation (Gunn and Farrar 1999).

Such results reaffirm that this grass adapts to higher temperature averages. Exotic African grass species are attractive forages due to the higher germination rate of seeds, fast growth (D′Antonio and Vitousek 1992; Pivello et al. 1999) and commercial seed supply. *P. notatum* can also be attractive due to its forage potential, ability to grow in environments with high average temperatures and, as a native species, it poses no threat to other populations in natural areas.

Leaf area and specific leaf area

A larger leaf area confers a greater photosynthetic activity, production and photoassimilate accumulation in the culms. This carbon reserve is mobilized for initial leaf growth (Corre et al. 1996). SLA is an appropriate parameter to verify the effect of environmental factors such as temperature because the SLA value is proportional to plant growth (Poorter et al. 2010). Considering that stolons growing under temperatures of 25, 30 and 35 °C had larger LA, this can confer advantages in producing photoassimilate and ensure a higher carbohydrate reserve for the re-sprout. Such responses may be similar to those observed in the field where water availability is not limiting, because leaf expansion is extremely sensitive to water deficit (Liu Mengzhou et al. 2017). Kikuyu grass, a tropical species, presented shorter leaves at lower temperature than its T_b, and there was an increase in leaf thickness to compensate for the smaller size indicating that there is not an interruption in metabolism but a change in growth (Acero-Camelo et al. 2021).

Specific leaf area is a very efficient parameter to measure plant growth (Liu Mengzhou et al. 2017), but its relation to temperature has not been studied. A study to evaluate the best method of SLA analysis found that tropical species showed greater plasticity when growing in areas with temperature variation than plants growing in areas with mild weather (Poorter et al. 2010). In the present study, the SLA results might indicate plasticity. In agreement with Poorter et al. (2010) cold temperatures may have induced less cell production resulting in a lower SLA. This can explain values obtained at low temperatures but does not explain results from the treatments at high temperatures. Results show that, although this grass is able to grow in a wide temperature range, the growth in either colder or extremely hot environments will result in a reduced SLA.

Determining thermal time for leaf emergence

The thermal limit found for the leaf growth of *P. notatum* (average values between 14.5 to 39.5 °C) explains why the species grows in several vegetation types and altitudinal gradients on the American continent (Batista and Neto 2000). Based on information from SpeciesLink (2021) system it also indicates its adaptation in regions with mild temperatures. Although a low leaf emergence rate was observed in a 15 °C constant temperature, it is important to highlight temperatures vary during the day and seasons of the year (Fogliatto et al. 2020) and stolons subjected to alternating temperatures of 25/15 °C showed higher leaf emergence, similar to higher temperatures, evidencing the ability of *P. notatum* to establish in regions with this thermal range. The values determined for T_b and T_c indicated the influence of temperature on leaf emergence, as highlighted by Martins et al. (2007). Responses to the thermal gradient can be attributed to the phenotypic plasticity of the species related to the natural environment thermal variation.

High phenotypic plasticity related to temperature was observed in the C4 grass *Urochloa brizantha*, highlighting that this grass suffers more under low temperatures (Nakao and Cardoso 2016). Considering the leaf emergence percentage and leaf emergence speed did not present differences between growth temperatures, this high plasticity for leaf emergence can be considered as a positive attribute of *P. notatum* conferring advantages in environments with milder temperatures when compared to invasive species. However, the T_0 of 30 °C indicates that *P. notatum* presents faster growth in spring/summer periods, when there is more water and nutrient availability and higher average air temperature.

The thermal requirement for 50% (θ_{50}) of the population to produce first leaves was 50 degree days, indicating a low thermal requirement for half of the stolon population to emit the first leaves compared to other grasses. Higher values of θ_{50} were found for *Pennisetum purpureum* (Andrade et al. 2005) with the thermal requirement estimated as 84 degree days. In a study with *Panicum virgatum*, there was a strong relation between the necessary thermal requirement to produce leaves and the beginning of the reproductive phase (van Esbroeck et al. 1997). According to these authors, higher or lower thermal requirements matched with the late or early start of the reproductive phase, respectively. Therefore, it is possible to predict that *P. notatum* plants which present low thermal requirements, grown in average temperatures around 30 °C could be early flowering compared to plants grown in other temperature ranges. This can represent a growth strategy of the species at the beginning of the rainy season.

Determining the T_b indicated that *P. notatum* stolons have potential to sprout and grow even in colder months, which may represent a competitive advantage for the species when compared to others that have higher thermal requirement and a narrower thermal niche (Bykova et al. 2012). It suggests that this plant is able to remain green and keep an active metabolism throughout the entire year, if the only limiting resource is temperature.

In most Brazilian states, higher temperature averages occur in the summer when rainfall is more abundant and therefore it is the most favorable period for fast growth. The highest averages of air temperatures occur in the period from January to March and in November and December (INMET 2021). In 2020, the region that presented the lowest temperature average was the South, with 13 °C in July and rainfall of 262 mm and total annual rainfall of 1,425.2 mm. In this region, there are many records of *P. notatum* (Figure 1) in the SpeciesLink (2021) system, indicating that the species grows better in milder temperatures. The Midwest presented the highest averages the same year with 32.4 °C in September and only 10.2 mm rainfall with fewer records of the species compared to the South. Despite the low volume of rainfall, stolons ensure the persistence of the grass until conditions become more favorable.

Using the average monthly and daily temperatures, it is possible to estimate the periods when stoloniferous leaf emergence of *P. notatum* will take place. It is also possible to predict the time for this in a future scenario of climate change, considering the forecast of temperature averages increase, where there is a possibility of an increase up to 6 °C in the worst scenario (Edenhofer et al. 2014). Considering such increase (scenario A), it is probable there will be a reduction of approximately 35% of the time taken by *P. notatum* stolons to emit leaves. With the increase of 4 °C in temperature averages (scenario B), this time can be reduced by approximately 30% compared to present. Colder temperatures in winter may compromise growth, which becomes slower or stops, especially in low rainfall seasons in its native environment. Some authors highlighted that progressive increase in averages of air temperatures may benefit some species (Gunn and Farrar 1999; Faria et al. 2015). However, regardless of an increase of 4 °C or 6 °C, the forecast of maximum average temperatures will still remain within the thermal gradient suitable for *P. notatum*, which indicates that the species has potential to grow in environments with thermal averages around 30 °C.

Besides the capacity to grow in a wide thermal range, the stolon remaining in the soil is important to ensure *P. notatum* regrowth because their stolons are not dormant and present low thermal requirements compared to other grasses (Andrade et al. 2005). Different to stolons, seeds from this species, show some traits which make propagation difficult, such as physiological maturity, low viability and physical dormancy (Gates et al. 2004), requiring higher average temperatures (around 30 °C) to germinate, which is a disadvantage compared to the species with easily germinated seeds.

Conclusions

P. notatum demonstrated the potential to develop stolon leaves in environments with a wide thermal range from around 15 °C lower average up to around 39.5 °C higher average. *P. notatum* can grow in environments with a high thermal gradient throughout tropical regions outside of its native distribution showing potential as a forage alternative to exotic African grasses. Results show that within the current temperature averages in Brazil and the forecast of increased averages of 6 °C, establishment and development of *P. notatum* will not be affected by climate change.

Acknowledgments

This study was supported by CNPq and Programa de Pós-graduação em Biologia Vegetal (PPGBV) of the Universidade Federal de Minas Gerais (UFMG). The authors thank CAPES and FAPEMIG from “Rede Mineira de Fisiologia de Plantas em Condições de Estresses”. The authors also thank Tereza Vale for her English language support.

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(Note of the editors: All hyperlinks were verified 22 January 2025).

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(Received for publication 27 March 2024; accepted 15 January 2025; published 31 January 2025)