

University of São Paulo  
"Luiz de Queiroz" College of Agriculture

Biomass partitioning in Guineagrass: underlying mechanisms and prediction using  
the CROPGRO Perennial Forage Model

**Henrique Bauab Brunetti**

Thesis presented to obtain the degree of Doctor in  
Science. Area: Animal Science and Pastures

Piracicaba  
2020

Henrique Bauab Brunetti  
Agricultural Engineer

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versão revisada de acordo com a resolução CoPGr 6018 de 2011

Advisor:  
Profª. Drª. **PATRÍCIA MENEZES SANTOS**

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2020



**Dados Internacionais de Catalogação na Publicação  
DIVISÃO DE BIBLIOTECA – DIBD/ESALQ/USP**

Brunetti, Henrique Bauab

Biomass partitioning in Guineagrass: underlying mechanisms and prediction using the CROPGRO Perennial Forage Model / Henrique Bauab Brunetti. - - versão revisada de acordo com a resolução CoPGr 6018 de 2011. - - Piracicaba, 2020.

86 p.

Tese (Doutorado) - - USP / Escola Superior de Agricultura "Luiz de Queiroz".

1. *Panicum maximum* 2. Alongamento de colmo 3. Razão V/VD 4. Estágio de desenvolvimento 5. Comprimento do pseudocolmo 6. Plataforma DSSAT 7. Pastagem 8. Gramíneas tropicais 9. Partição de fotoassimilados I. Título

*To my parents Taís and Iguatemy, and my brother Hugo for all the unconditional love and support. This thesis is dedicated to you.*

## ACKNOWLEDGMENTS

First, I would like to thank God for the temperance that allowed me to complete this task. My sincere gratitude to my family who has been with me no matter what: Taís, Iguatemy, and Hugo. You are an essential part of my life and certainly part of this thesis. I appreciate all the moments together from the bottom of my heart.

I also deeply appreciate all the love, patience and affection of my girlfriend Luísa Consentino de Araújo. You are also part of it for being with me in all the happy and not so happy moments! Thank you a lot!

I would like to thank Dr. Patricia Menezes Santos for advising me, for believing in my work and for the friendship. You are an example of a great researcher and leader, and you truly aided on my improvement as a researcher and as a person. Thank you!

My sincere gratitude to Dr. Ken J. Boote for receiving me at the University of Florida. I really appreciate all the taught you gave me about modeling, and all the time we spent together. This thesis certainly would not be the same without your help. Thank you!

I also would like to thank Dr. Gerrit Hoogenboom, for receiving me in his lab and for the taught about DSSAT.

This thesis would not have been possible without the spectrometer, which I borrowed from Prof. Dr. Ricardo Ferraz de Oliveira. Thank you for trusting me with this instrument! I also appreciate all the help, either for lending me field instruments or ideas for the experiment, from Dr. José R.M. Pezzopane. I express my gratitude to some Professors for the comments about this study and for aiding on my professional growth during important steps of my doctorate: Dr. Carlos G. S. Pedreira, Dr. Fabio Marin, Dr. Felipe G. Pilau, Dr. Ricardo F. de Oliveira, Dr. José R. M. Pezzopane, and Dr. Bruno C. Pedreira.

To my lab colleagues and friends, for all the help with my research (hope we can work together again in the future): Lucas Balcão, Mariely Santos, Tíberio Souza, and Everton Lemos. Also, to important people who aided me on the field experiment, the interns: Natália, Renata, Walter, Iza; and the EMBRAPA staff: Luiz and Mineiro. Also, to Guilherme Portes for some valuable comments and conversations about grasses' ontogeny, thank you!

To some friends I made in the U.S., whose I enjoyed spending some valuable time with, and also helped me during my stay there, my sincere gratitude to Luc, Anju, Quardmia, Oscar Monsalve, Oscar Castillo, Tania, Cody, K-teto, Rogério, Pino. Also to all the guys of the agricultural modeling lab, and to the guys of the lab next door for the coffee time.

To the Department of Animal Science and ESALQ for the training I have received during all these years. I am proud of being part of it. Also, to EMBRAPA for allowing me to carry out my field

experiment and for the technical support. To the University of Florida for receiving me as a visitant scholar

To the library staff for helping with the formatting of this document and to the graduate program staff for the patience

To all my friends for the relaxation time, which helped me on focusing during the work time: Flávio, Longo, Lado B, Max, Otávio, Fer, Japa, all the members of 'República Aroeira' and all the members of 'La Moradita del Sol'

I would also like to thank CAPES for the scholarship provided during my doctorate program

Also, to everybody else who cooperated with this work somehow and I did not mention.

*“Thus, the task is not so much to see what no one yet has seen, but to think what nobody yet has thought about that which everybody sees” – Arthur Schopenhauer*

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## RESUMO

**Partição de biomassa em *Panicum maximum*: mecanismos fundamentais e predição utilizando o modelo CROPGRO Perennial Forage Model**

Em sistemas de produção animal baseados em pastagens, a partição de biomassa afeta a qualidade da forragem oferecida aos animais e os ciclos subsequentes de rebrota da pastagem. Os objetivos deste estudo foram (i) investigar os efeitos da razão V/VD e do estágio de desenvolvimento no alongamento de colmo de perfilhos de *Panicum maximum*, (ii) investigar os efeitos do alongamento de colmo no aparecimento e alongamento de folha dos perfilhos e (iii) investigar e melhorar a capacidade do modelo CROPGRO Perennial Forage Model para simular o crescimento e a partição de biomassa de *Panicum maximum*. Para os objetivos (i) e (ii), dados de perfilhos de *Panicum maximum* cv. Mombaça foram coletados em um experimento irrigado avaliado durante dois ciclos vegetativos (verões 1 e 2) e um ciclo reprodutivo (outono). Os dados da razão V/VD foram medidos com o auxílio de um espectrômetro Ocean Optics USB2000+. Em cada ciclo de rebrota, de duas a cinco vezes por semana, das 10 às 11h, foram registradas cinco a dez medidas abaixo do dossel para cada amostra. Para a medição dos comprimentos do colmo verdadeiro e do pseudocolmo, 10-25 perfilhos representativos foram coletados semanalmente e cortados na direção longitudinal. O estágio de desenvolvimento foi observado visualmente com o auxílio de um microscópio estereoscópio Coleman XTB. Dez perfilhos/ ciclo de rebrota foram marcados para as medidas de aparecimento e alongamento de folhas. As variáveis foram plotadas em relação aos graus-dia acumulados (gdd) e modelos foram ajustados usando o procedimento NLIN do SAS 9.2. Durante os ciclos vegetativos, o alongamento de colmo verdadeiro foi ajustado em modelos segmentados (constante - aumento linear) ( $R^2$ -ajustado = 0,95 e 0,99 para os verões 1 e 2, respectivamente). O alongamento não foi primariamente relacionado à razão V/VD abaixo do dossel, mas foi explicado satisfatoriamente pelos gdd (com uma diferença de apenas 35 gdd entre os *breakpoints* dos verões 1 e 2). O alongamento de colmo verdadeiro não encurtou o pseudocolmo. Durante o ciclo reprodutivo, o alongamento de colmo verdadeiro ocorreu concomitantemente com o aparecimento dos primórdios florais (11,7h de fotoperíodo) e encurtou o pseudocolmo. Nos perfilhos vegetativos, ao contrário do que ocorreu com os perfilhos reprodutivos, o alongamento de colmo verdadeiro não encurtou o comprimento final das folhas, nem aumentou a taxa de aparecimento de folhas. Para o objetivo (iii), dados de acúmulo de matéria seca de dois experimentos, um com cultivar Tanzânia e outro com Mombaça, foram utilizados. Os experimentos apresentavam manejos da desfolha e condições de campo contrastantes. A parametrização foi feita manualmente, visando a melhoria do parâmetro estatístico d-Wilmott e da raiz do erro quadrado médio (RMSE), considerando a média dos dois experimentos para o acúmulo de biomassa da parte aérea, massa seca de folhas, massa seca de colmos, índice de área foliar (IAF) e porcentagem de folhas na biomassa da parte aérea. A principal melhoria no desempenho do modelo foi alcançada modificando os parâmetros de partição de fotoassimilados na fase vegetativa entre folha e colmo (aumentando para as folhas durante o início da rebrota e para o colmo em estágios avançados da rebrota). A produtividade durante meses de dias curtos e frios foi diminuída, tornando a fotossíntese e a expansão da área foliar mais sensíveis à baixa temperatura e aumentando a partição para órgãos de reserva durante dias curtos. Durante condições apropriadas de crescimento, a produtividade foi aumentada diminuindo a senescência de folhas e colmo e reduzindo o efeito do estresse de nitrogênio na expansão da área foliar. O d-Wilmott geral médio entre os dois cultivares aumentou de 0,86 para 0,93 e os valores de RMSE médio entre os dois cultivares diminuíram de 2261 para 1768 kg ha<sup>-1</sup> para biomassa da parte aérea, de 1620 para 874 kg ha<sup>-1</sup> para massa seca de colmos, de 11,41 para 7,27% para porcentagem de folhas, de 1,91 para 1,68 para IAF, mas aumentou ligeiramente de 1114 para 1172 kg ha<sup>-1</sup> para massa seca de folhas. O desempenho aprimorado do modelo para ciclos curtos e longos facilitará seu uso para diversas estratégias de manejo de pastagens com esses capins.

Palavras-chave: *Panicum maximum*, Alongamento de colmo, Razão V/ VD, Estágio de desenvolvimento, Comprimento do pseudocolmo, Plataforma DSSAT, Pastagem, Gramíneas tropicais, Partição de fotoassimilados

## ABSTRACT

**Biomass partitioning in Guineagrass: underlying mechanisms and prediction using the CROPGRO Perennial Forage Model**

In pasture-based livestock systems, biomass partitioning affects the quality of forage offered to animals and the subsequent regrowth cycles. The objectives of this study were (i) to investigate the effects of the R/ FR ratio and of the developmental stage on stem elongation of guineagrass tillers, (ii) to investigate the effects of stem elongation on the tillers' leaf appearance and elongation and (iii) to investigate and improve the ability of the CROPGRO Perennial Forage Model to simulate growth and biomass partitioning of guineagrass. For the objectives (i) and (ii), tiller-level data were collected in an irrigated *Panicum maximum* cv. Mombaça field evaluated during two vegetative cycles (summers 1 and 2) and one reproductive cycle (autumn). The R/FR ratio data was acquired with the aid of an Ocean Optics USB2000+ spectrometer. For each regrowth cycle, two to five times per week from 10 to 11h, five to ten measurements beneath the sward were recorded for each sample. For measurement of the true stem and pseudostem lengths, 10-25 representative tillers were weekly clipped and cut longitudinally. The developmental stage was visually observed with the aid of a Coleman XTB Stereoscope Microscope. Ten tillers/regrowth cycle were tagged for leaf appearance and elongation measurements. The variables were plotted against the accumulated growing degree-days (gdd) and models were fitted using the NLIN procedure of SAS 9.2. The true stem data were fitted in segmented (constant - linear increase) curves (adj-R<sup>2</sup>=0.95 and 0.99 for the summers 1 and 2, respectively). The elongation was not primarily related to R/FR ratio beneath the sward, but was satisfactorily explained by gdd (with a difference of only 35 gdd between the breakpoints of the summers 1 and 2). The true stem elongation did not shorten the pseudostem. During the reproductive cycle, the true stem elongation occurred concurrently with the appearance of flowers primordia (11.7h of daylength) and shortened the pseudostem. In the vegetative tillers, as opposed to the reproductive tillers, the true stem elongation did not shorten the final leaf length nor increased the leaf appearance rate. For the objective (iii), data from two experiments were used. One experiment was conducted with cultivar Tanzânia and the other with Mombaça, and they had contrasting harvest management and field conditions. Parameterization was done manually, targeting improvement in d-statistic and root mean square error (RMSE) averaged over both cultivars for aboveground biomass accumulation, leaf biomass, stem biomass, leaf area index (LAI), and leaf proportion on aboveground biomass. The major improvement in model performance was achieved by modifying the vegetative partitioning parameters between leaf and stem (increasing partitioning to leaf during early regrowth while increasing to stem during late regrowth). Productivity during cool, short daylength months was decreased by making photosynthesis and leaf area expansion more sensitive to lower temperatures and increasing the partitioning to storage organs during short days. Productivity under warm-season conditions was increased by decreasing leaf and stem senescence and reducing the nitrogen stress effect on leaf area expansion. The overall d-statistic averaged over the two cultivars increased from 0.86 to 0.93 and the RMSE values averaged over the two cultivars decreased from 2261 to 1768 kg ha<sup>-1</sup> for aboveground biomass, from 1620 to 874 kg ha<sup>-1</sup> for stem biomass, from 11.41 to 7.27% for leaf percentage, from 1.91 to 1.68 for LAI, but increased slightly from 1114 to 1172 kg ha<sup>-1</sup> for leaf biomass. The improved model performance for both short and long harvest cycles will facilitate further use for evaluating various management strategies for these grasses.

Keywords: *Panicum maximum*, Stem elongation, R/FR ratio, Developmental stage, Pseudostem length, DSSAT system, Grassland, Warm-season grasses, Tropical grasses, Photosynthate partitioning



## 1. INTRODUCTION

Brazil had more than 213 million heads of cattle in 2018, which is the largest commercial herd in the world (FAO, 2020). In Brazil cattle is mostly grass-fed, and *Panicum maximum*, commonly known as guineagrass, is the second most cultivated forage grass species in the country. This grass is usually used as an alternative to *Brachiaria* spp. for more intensive cattle production systems. *Panicum maximum* is recommended for regions where annual rainfall ranges from 800 to 1800 mm and have well-drained soils with a medium to high soil fertility (Muir and Jank, 2004).

Biomass partitioning during pasture growth is important as it affects the quality of forage offered to animals and the composition of stubble, which in turn affects the subsequent regrowth cycles. In warm-season grasses, the increase in herbage mass from a certain point is mainly due to stem and pseudostem growth, even during the vegetative stage (Santos et al., 1999).

Several studies related the increase in stem accumulation with the intraspecific light competition. These studies investigated the use of 95% of light interception (LI) and maximum LI as targets for pasture grazing and showed a considerably higher stem accumulation when defoliation was delayed beyond 95% of LI (Carnevali et al., 2006; Barbosa et al., 2007; Pedreira et al., 2007;; Trindade et al., 2007;). Despite the high correlation registered between LI and changes in biomass partitioning, LI is probably not the signal perceived by the plants to sense the light environment surrounding them.

The  $r$  (660nm)/  $fr$  (730nm) ratio is sensed by the phytochromes of many plants as a signal for light competition (Ballaré et al., 1990). Phytochromes are photochromatic proteins existing as two isomeric photo-interconvertible forms: the inactive red absorbing form (Pr) and the active far-red absorbing form (Pfr) (Hughes and Lamparter, 1999). Absorption of red light converts Pr to Pfr, whereas far red absorption reverts it to the inactive Pr state. The balance between Pr/Pfr, in turn, elicits responses referred to as shade avoidance syndrome or photomorphogenesis (Schmitt et al., 2003). Among these responses, internode (stem) elongation is one of the most important for grazing systems and has been described for many species (Casal et al., 1987; Ballaré et al., 1990; Davies and Simmons, 1994). Despite the central role of the light environment in biomass partitioning of the warm-season grasses used in Brazil, none study has been found relating this variable with R/FR ratio.

The transition from vegetative to the reproductive stage also causes abrupt modifications to physiology, biomass partitioning and morphology of the plant (Poethig, 2003). Floral initiation terminates leaf initiation and stimulates internode (stem) elongation which raises the apical meristem (reproductive apparatus) to appear in a high position in the sward. The relative relevance of light competition and of the onset of the reproductive stage in shifting aerial biomass partitioning in plants is not clear.

Mechanistic simulation models are important tools for predicting growth and biomass partitioning of plants, as they consider the system as a whole, using mathematical equations to integrate soil, genetics and climatic factors (Andrade et al., 2016). Among the mechanistic models, CROPGRO has potential for many applications as understanding physiological processes, assisting breeding programs and evaluating management strategies (Tsuji et al., 1998). The model was improved for simulations of perennial grasses by adding a new storage organ which aided on pasture regrowth, leading up to the development of the CROPGRO-Perennial Forage Model (PFM) (Rymph, 2004). The CROPGRO-PFM has been used for simulating warm-season grass yield with success and was calibrated for *B. brizantha* cv. Xaraés (Pedreira et al., 2011), *P. maximum* cv. Tanzânia (Lara et al., 2012), *B. brizantha* cv. Marandu (Pequeno et al., 2014), *B. brizantha* cv. Mulato II (Pequeno, 2014), *B. brizantha* cv. Piatã (Bosi et al., 2020). Despite the unquestionable relevance of these studies, the data used were mostly from “short-term” regrowth cycles (about 28

days during summer/spring and a maximum of 63 days during winter/autumn), which did not allow for an accurate biomass partitioning modeling and parameterization from very early until very late stages of the grasses regrowth cycles. In this context, a systematic sampling approach would benefit simulation of biomass partitioning, being an important aspect of model improvement when dealing with different grazing strategies (i.e. with herbage removal at different severities and frequencies).

## **2. OBJECTIVES**

### **2.1. General**

Investigate the mechanisms underlying the biomass partitioning of Guineagrass and improve the ability of the CROPGRO Perennial Forage Model to simulate it.

### **2.2. Specific**

a1) Investigate the effects of the R/FR ratio beneath the sward and of the onset of the reproductive stage on stem elongation of Mombaça Guineagrass tillers;

a2) Investigate the effects of stem elongation on leaf appearance and leaf elongation of vegetative and reproductive tillers of Mombaça Guineagrass.

b) Investigate and improve the ability of the CROPGRO Perennial Forage Model to simulate growth and biomass partitioning of Tanzânia and Mombaça Guineagrasses.



### 3. LITERATURE REVIEW

#### 3.1. Mombaça guineagrass and its use for understanding biomass partitioning in a competitive light environment

*Panicum maximum* Jacq., commonly referred to as guineagrass, is ubiquitous throughout the tropics and subtropics (Muir et al., 2001). In Brazil, *Panicum* is the second most cultivated genus after *Brachiaria*, being used in more intensive production systems. Recently, the species has been occasionally referred to as *Megathyrsus maximum* after the study of Simon and Jacobs (2003). *Panicum maximum* cv. Mombaça is a tall bunch-type grass used for grazing, recommended for regions where annual rainfall ranges from 800 to 1800 mm and have well-drained soils with a medium to high soil fertility (Muir and Jank, 2004). The cultivar is one of the most cultivated in Brazil, and the yield during the genetic selection program was reported as 41 Mg DM ha<sup>-1</sup> year<sup>-1</sup> (Jank et al., 1994).

The accession was collected in Tanzania, Africa. It shows a caespitose habit of growth reaching 1,65 meters in height. The leaves are brittle, wax-free, with short hard hair on the adaxial face. The sheaths are glabrous and the stems slightly purplish. The inflorescences are panicles with primary long ramifications, while the secondary ramifications are only long in their bases. The spikelets are glabrous, evenly distributed and purplish (Savidan et al., 1990).

According to Grime (1979), basically, two groups of plants species show responses to shade (i): the "shade avoiders", which invest more biomass to stem elongation at the cost of leaf development, providing to the newer leaves a greater chance to be positioned in lit zones of the sward; or (ii) the "shade-tolerant" plants that show slower growth rates, and structural and biochemical adaptations to enhance the efficiency of photosynthetic energy transmission and reduce respiratory carbon loss, allowing the plant to survive and develop in spite of being in a shaded environment (Grime, 1979). The phenotypic characteristics of Mombaça guineagrass suggest this cultivar as a good model of "shade avoider", with important consequences for pasture-based livestock systems.

#### 3.2. Light environment and pasture growth

Pasture growth can be considered, basically, as the transformation of solar radiation into plant tissue. In this context, Mitchell (1954) suggested that having the minimum of bare soil and intercepting as much as possible of the incoming light is the best way to ensure high yields and effective utilization of the incoming energy. For understanding and relating light interception (LI) with the plant itself, the leaf area index (LAI) concept is useful, and it is described as unit leaf area per unit ground area (Watson, 1947). Brougham tested the influence of LI and LAI in forage growth in a series of experiments (1955, 1956, 1958), introducing the firsts ideas about this issue. Firstly, studying pasture growth under intermittent grazing, the author showed that growth following defoliation can be described by a sigmoid curve when plotted against time (Brougham, 1955). The sigmoid curve has three distinct phases: (i) the exponential phase, when the growth rate is increasing; (ii) the linear phase, when the growth rate is maximum and constant; (iii) and the deceleration phase, when growth rate decelerates until it equals to 0 and forage accumulation is null. The first phase is dependent on soluble and storage carbohydrates as well as on the amount and quality of the remaining LAI after defoliation, and the growth rate tends to increase as LAI increases. In the second phase, there is

enough LAI to intercept a high amount of light and, thus, the maximum growth rate is achieved. Finally, in the third phase, forage accumulation is limited by the senescence of leaves due to their leaf lifespan and high self-shading of the sward on leaves located in the lower layers (Hodgson, 1981). Furthermore, Brougham (1956) suggested the maximum growth rate occurred when almost all light had been intercepted (at 95% or over LI). Additionally, the asymptotic relation between LAI and LI was described. Thereafter, the same author introduced the concept of critical LAI, which is the LAI index necessary to intercept 95% of the incoming light (Brougham, 1957).

After the pioneer studies of Brougham (1955, 1956, 1957, 1958), a series of studies followed attempting to describe the effect of light interception on herbage growth. Defoliation before 95% LI has been reported to reduce annual herbage production (Wilson and McGuire, 1961; Sheard and Winch, 1966), while delaying defoliation after 95% LI has been reported to both increase (Mitamura 1972; Terai 1977) and decrease (Tainton 1974) herbage production. Additionally, Korte et al. (1982), concluded that, during autumn and winter, delaying defoliation 2 weeks after reaching 95% of LI increased significantly green herbage accumulation without significantly reducing tillers density but, during spring, on the other hand, defoliation at 95% of LI is more effective on controlling stems elongation due to the presence of reproductive tillers. Parsons and Penning (1988) suggested another way to decide the best time to interrupt forage regrowth (i.e. defoliate) for the achievement of the highest yield. According to the authors, defoliation should occur when the average growth rate is maximum (considering the whole regrowth period), which does not necessarily coincide with the maximum “instantaneous” growth rate. However, as the average growth rate showed to be relatively insensitive to the duration of regrowth beyond a given minimum duration, the authors suggested that management guidelines could concentrate on controlling or harvesting stems and, therefore, considered the use of 95% of LI as a target to interrupt regrowth as valid.

The reduction in green herbage accumulation after 95% LI by the sward can be explained by the fact that, from this point onward, there is high shading of lower leaves by the upper leaves of the sward. Lack of light on a leaf can decrease its photosynthetic activity turning it into a drain of carbohydrates, instead of a source (Donald, 1961). The high rate of respiration of leaves which does not cooperate as a considerable carbohydrate source may have negative consequences on plant growth rate. When intercepting almost all incoming light (95% or over), increases in growth rate and consequently in green herbage accumulation must be related to one or more of these three factors: (i) more efficient utilization of intercepted light; (ii) the use of another source of energy (i.e. soluble and/or storage carbohydrates) and; (iii) the rearrangement of LAI in space (leaves angle and arrangement throughout the sward; Sheehy and Cooper, 1973), which can allow for even higher values of LAI. Among these three, the last one deserves special attention.

The sward architecture interferes with light penetration and distribution throughout the plant community. The culture growth rate is related to sward architecture, which can be expressed by the light extinction coefficient “k” (Sheehy and Cooper, 1973). When analyzing Beer’s equation ( $I = I_0 e^{-LAI \cdot k}$ , where “I” is the incoming radiation below the sward; “I<sub>0</sub>” is the incoming radiation above the sward; “LAI” is the leaf area index; “k” is the light extinction coefficient), adapted to plants by Monsi and Saeki (1953), one can conclude that the decreases in “I” may be achieved either by an increase in LAI or by an increase in “k”. The light extinction coefficient is dependent upon the sun position (zenithal angle) and the leaves insertion angle. This dependency is higher when direct radiation is predominant (blue sky) as opposed to the predominance of diffuse light (cloudy sky), as diffuse radiation travels in diverse directions (Bernardes, 1987).

According to Warren Wilson (1961), swards with more erect leaves have better light penetration than the ones with horizontal leaves. The author, using a virtual sward, demonstrated that when leaves are oriented 81° from

the horizontal plane (9° degrees from zenith) there is six times more illuminated surface than in a horizontal leaf (0° from horizontal or 90° from Zenith). Thus, the net photosynthesis of the inclined-leaves sward was twice higher when compared with the horizontal-leaves sward. Additionally, the disposition of leaves in different layers of the sward provides a better light penetration than leaves placed at the same layer (Warren Wilson, 1961). In this context, different sward architectures provide different ceiling LAIs and net accumulation rates.

Due to (i) the results published about relations between light and temperate forage species; (ii) the importance of understanding herbage accumulation as a dynamic process integrated by many processes (growth, senescence, tillers appearance and death) with consequences to the plant community and sward structure (Hodgson, 1985) and (iii), the effect of sward structure on animal ingestive behavior (Chacon and Stobbs, 1976), a series of studies were carried out considering the light relation with herbage accumulation and defoliation targets for warm-season grasses. In warm-season grasses, the increase in herbage accumulation from a certain point occurs mainly due to stem and pseudostem accumulation, even during the vegetative stage (Santos et al., 1999). Increases in LAI and, consequently, in LI, is responsible for the differentiation of quantity and quality of light throughout the sward and, ultimately, for biomass partitioning and structural changes (i.e. stem elongation) in the sward (Sbrissia and Da Silva, 2001). Thus, for warm-season grasses, LI assumes an important role in biomass partitioning.

Several studies compared the use of 95% of LI and maximum LI as a target for pasture grazing and showed a considerably higher stem accumulation when defoliation was delayed beyond 95% LI (Carnevali et al., 2006; Barbosa et al., 2007; Pedreira et al., 2007; Trindade et al., 2007;). Despite the high correlation registered between LI and changes in biomass partitioning, probably LI is not the signal perceived by the plants to sense the light environment surrounding them.

### 3.3. R/FR ratio and plant development

The red (660nm): far red (730nm) ratio is sensed by the phytochromes of many plants as a signal for light competition (Ballaré et al., 1990). Phytochromes are photochromatic proteins existing as two isomeric photo-interconvertible forms: the inactive red absorbing form (Pr) and the active far-red absorbing form (Pfr) (Hughes and Lamparter, 1999). The biologically active form (Pfr) is the one translocated to the nucleus, triggering (or not) biochemical reactions and, in the long run, modifying gene expression and phenotype. Absorption of red light converts Pr to Pfr, whereas far red absorption reverts it to the inactive Pr state. Additionally, Pfr can spontaneously revert to the inactive Pr state by a slow non-photoinduced reaction (Li et al., 2011). In this context, the amount of one form or another is dependent upon the balance between red and far red wavelengths reaching the protein. The absorbing peaks of Pr and Pfr are, 660nm (red) and 730 nm (far red), respectively (Siegelman and Butler, 1965).

The phytochrome was first discovered in 1959 by Hendricks and Borthwick (1959). Soon, it was found that dense swards transmitted a much higher amount of fr as compared to r, resulting in low r: fr ratio in the lower strata of the sward (Kaspebauer, 1971). Thereafter, internode elongation was found to be inversely related to r: fr ratio (Morgan and Smith, 1978), and many studies followed studying the relation of morphological responses with R/FR ratio.

Key environmental evidence supports the idea that R/FR ratio is involved in stem elongation and other morphological changes related to plants escaping from the shade. As opposed to total irradiance, the R/FR ratio is an unambiguous sign of plant competition, as its decrease is proportional to vegetation on the surrounds but almost

unaffected by atmospheric conditions (Smith, 1982). R/FR during daylight is only slightly affected by atmospheric and cloud conditions, whereas total radiance reaching earth atmosphere can drop about 10-fold during overcast days (Holmes and Smith, 1977; Hughes et al., 1984). Additionally, R/FR is unaffected by zenithal angles up to 80° (10° solar angle), remaining about constant with a value of 1.15 - 1.2 (Holmes and Smith, 1977; Smith, 1982; Hughes et al., 1984; Deregibus et al., 1985; Deregibus et al., 1994). During twilight (solar angle less than 10°), however, R/FR ratio drops to 0.65 to 1.15, and is an important cue to the circadian clock and flowering (Smith, 1982; Hughes et al., 1984). During dawn and dusk, the solar angle diminishes the contribution of the direct beam, relative to diffuse radiation leading to a pronounced peak in blue. Simultaneously, the direct radiation traverses an increasingly long path through the atmosphere, which enhances absorption, scattering and refraction, with a higher magnitude for short wavelengths (depleting  $r$  more than  $fr$ ), leading to a small but measurable drop in R/FR ratio.

Despite the unlikely sensing of LI by the plants, LI is highly correlated with R/FR, and thus can be considered as having an important biological role in escaping from the shade. As light traverses the sward, it is depleted and LI increases (transmittance decreases). In analogous proportions,  $r$  is also depleted during light traversing through the sward, which drops the R/FR ratio. R/FR reduction is firstly due to horizontal  $fr$  radiation reflected from neighbors in sparse swards, a situation which can occur during pasture establishment and beginning of regrowth (Casal et al. 1986; Ballaré et al. 1987; Skálová et al. 1999). This signal allows the plant to anticipate competitors, and change its morphology before drops in photosynthetically active radiation occurs (Casal et al. 1986; Ballaré et al. 1987; Smith et al. 1990). Thereafter, in a dense sward, the drop in R/FR is related to self-shading (vertical light flow) (Whitelam and Smith, 1991). Both flows likely integrate triggering physiological and morphological responses (Sattin et al., 1994).

Internode (stem) elongation is the most common response related to intraspecific competition for light, however, there are other responses mediated by phytochromes also related to plants competition. These responses have an important role in biomass accumulation and distribution and generally occur concurrently, being referred to as shade avoidance syndrome or photomorphogenesis (Schmitt et al., 2003). The term syndrome is used to represent, as in medicine, diverse effects that occur in response to the same cause. The responses characterizing the shade avoidance syndrome are: stem and petioles elongation (Morgan et al., 1980; Casal and Smith, 1989; Whitelam and Smith, 1991), higher growth of foliar sheaths and laminae (Skálová and Krahulec, 1992; Skinner and Simmons, 1993) lower appearance and higher mortality of tillers (Deregibus et al., 1985; Casal et al., 1987; Skinnners and Simmons, 1993), flowering acceleration (Schmitt and Wulff, 1993; Smith and Whitelam, 1997), senescence acceleration (Rousseaux et al., 1996) and negative phototropism response to far red (Maddonni et al., 2002). The shade avoidance syndrome and its consequences for warm-season grasses are not well understood.

The shade avoidance syndrome has been assumed as an adaptive advantage (Casal and Smith, 1989; Ballaré et al. 1990; Schmitt and Wulff, 1993), as it allows the development of the appropriate phenotype for the light environment (Casal and Smith, 1989; Ballaré et al., 1990; Schmitt and Wulff, 1993), which makes sense ecologically. Light-sensing must occur in a representative and adequate site for the success of the strategy. R/FR receptors are supposedly found on the plants' bases where the shade is more pronounced. In this context, old leaves sheaths and lateral buds are the sites where the receptors are found in grasses (; Deregibus et al. 1985 Casal et al., 1987). However, Lecharny and Jacques (1979) and Skinnners and Simmons (1993) suggested that young leaves may also participate in R/FR sensing. Due to the divergence of results about the site of perception of the R/FR ratio for triggering the shade avoidance syndrome, likely there is not a unique site of perception, but rather, the sensing of the light environment occurs on the whole plant in a complex and integrated way. In this context, the R/FR reaching the soil surface has

been used as an indicator of R/FR through the vertical profile of the sward (Deregibus et al., 1985; Skalová and Krahulec, 1992).

Other pieces of evidence of the participation of R/FR ratio on the shade avoidance syndrome are the studies suggesting the participation of phytochromes on triggering downstream reactions responsible for such syndrome. The ratio between Pfr and Pr is connected with complex molecular responses that inhibit (or not) gene transcription resulting (or not) on the syndrome, confirming the central role of R/FR ratio in this type of response (Franklin and Whitelam, 2005). The studies were performed using mutants lacking one or more families of phytochromes and, even in environments with low R/FR ratio, they did not present the responses normally registered (Halliday et al., 1994; Devlin et al., 1996; Devlin et al., 1999). Despite the advances in elucidating the phytochromes families involved in the shade avoidance syndrome, there are still questions about the biochemical pathway responsible for translating these signs into alterations on growth and development patterns (Franklin and Whitelam, 2005). Kraepiel and Miginiac (1997) suggested that the Pfr/Pr modify the auxin production (i.e. high R/FR ratio inhibits auxin production) stimulating or depressing apical dominance. Other studies agreed with this suggestion, using mutants insensitive to auxin which did not present alterations on growth and development patterns, (Cline, 1994; Van Tuinen et al., 1995; Kerckhoffs et al., 1996), despite there are divergences against this statement (Romano et al., 1995). Additionally, in an *in vitro* experiment, it was found that AUX/IAA proteins may be phosphorylated by phytochromes, suggesting a molecular mechanism that integrates light signaling and auxin production (Colon- Carmona et al., 2000).

Studies suggest that photomorphogenesis also depends on the photosynthetically active photons flux density (PPFD) (Ballare et al., 1991; Ballare, 1999) and other wavelengths (e.g. blue) (Pierik et al., 2004). However, the r (660 nm): fr (730 nm) is the most utilized as PPFD and blue are considered as more unreliable indexes, due to their unpredictability fluctuations due to weather. On the other hand, spectral distribution is mostly unchanged by weather conditions, being a more reliable index to important ecological responses (Smith, 1982). Additionally, with the increase in sward density, the R/FR decrease occurs concurrently with the PPFD decrease, corroborating the use of R/FR as a reliable index for photomorphogenesis study (Smith, 1982).

Despite the many studies with several species about photomorphogenesis and the importance of the shade avoidance syndrome to warm-season forage species, there are few studies relating the syndrome with such species. In the existing studies, acetate filters and swards artificially changed or artificial lights were utilized (Deregibus et al., 1985; Monaco and Briske, 2000), poorly representing natural conditions. Additionally, no study was found with warm-season grasses broadly used in Brazil.

The radiation study under natural environments and their consequences to plants certainly would aid in connecting physiology and management concepts, allowing the use of the specific knowledge on the field. The study of variables directly related to the photomorphogenesis in warm-season grasses allows for a better understanding of the effect of the light environment in the biomass partitioning, and for the application of the knowledge in a broader and more generalist way. Thus, distinguished light environments (e.g. silvopastoral systems) could also benefit from this approach.

### **3.4. Flowering of Mombaça guineagrass and consequences for the plant development**

The transition from vegetative to the reproductive stage also causes abrupt modifications in physiology, biomass partitioning and morphology of the plant (Poethig, 2003). Floral initiation terminates leaf initiation and

stimulates internode (stem) elongation which raises the apical meristem (reproductive apparatus) to appear in a high position in the sward. Thus, stem accumulation is markedly increased and the production of new leaves is ceased. Additionally, internode elongation shortens the pseudostem, which in turn shortens the leaves that had been initiated before meristem differentiation (Skinner and Nelson, 1995; Gomide and Gomide, 1999), resulting in decreases in leaf accumulation. Thus, to keep a high percentage of leaf, in situations where tillering allows for adequate perennation of the pasture, this type of reproduction (i.e. asexual or clonal reproduction) must be preferred to sexual reproduction.

*Panicum maximum* are short-day plants (Felippe, 1978; Loch, 1980) with about 11,8h of critical photoperiod (Araújo, 2011). Consequently, in São Paulo state of Brazil, flowering (i.e. the appearance of the panicle) must occur between April to May (Santos et al., 1999). Additional details about flowering (e.g. juvenile period, the period under the critical photoperiod) are unknown.

### **3.5. The use of CROPGRO Forage model for simulating growth and biomass partitioning of warm-season grasses used for grazing**

Mechanistic models consider physical, chemical and biological processes governing the phenomena under study and are based on hundreds or thousands of equations for individual processes, organized in algorithms and user-friendly interfaces (Andrade et al., 2016). These models can be powerful tools to assist decision-makers with understanding the interaction among plant genetics, environment, and pasture management on yield and biomass partitioning of plants used for grazing (Pedreira et al., 2011; Araujo et al., 2013).

CROPGRO was developed as a stand-alone model in the early 1990s (Boote et al., 1998), but is now a part of the Decision Support System for Agrotechnology Transfer (DSSAT; [www.DSSAT.net](http://www.DSSAT.net)) crop modeling ecosystem (Hoogenboom et al., 2019), which is capable of running and integrating many models concurrently (Jones et al., 2003). The Cropping System Model integrates species physiological traits, weather, crop C balance, soil and plant water balance, soil and plant nitrogen balance, soil organic C balance, and damage caused by pests and diseases, which allows for the prediction of yield based on weather and soil conditions and management practices (Boote et al., 1998). The crop models in DSSAT have the potential for many applications as understanding physiological processes, assisting breeding programs and evaluating management strategies (Tsuji et al., 1998). In addition, the model follows a modular approach, which allows introducing a new crop by modifying values in a “read-in” species crop template file without changing any computer source code (Boote et al., 1998; Jones et al., 2003).

When considering simulations for pastures, CROPGRO was first adapted for bahiagrass (*Paspalum notatum* Flugge) (Kelly, 1995) and parameterized for *Brachiaria* (Giraldo et al., 2001). However, this version of the CROPGRO model worked only with an “annual” approach, which was unreliable as it consistently over-predicted dry matter yield for cooler months, in part because code limitations did not allow for winter dormancy or re-growth after 100% foliage harvest or freeze-kill (Rymph, 2004). A new version referred to as CROPGRO- Perennial Forage Model was developed, which included a carbohydrate and nitrogen storage perennial organ, which allowed for regrowth of the plant even with 100% foliage harvest (Rymph, 2004). The new version has a different source code than the standard “annual” CROPGRO, and better represents the patterns of regrowth (Pedreira et al., 2011). In this context, the photosynthates and N acquired for the production of new tissues are partitioned among leaf, stem, root system and storage organ according to the current vegetative stage (V-stage) through a look-up function. Additionally, the simulation of partial dormancy during the winter was added as a new process, which increased the partition to the

storage organ in days with shorter daylengths, allowing for a better representation of growth patterns during the cooler short-daylength months.

Lara et al. (2012) working with *Panicum maximum* cv. Tanzânia, created a new input to improve the harvest condition simulation: the MOW parameter (amount of living stubble left after harvest), RSPLF (the leaf percentage of the living stubble) and the MVS (number of leaves left on the primary axis after harvest). MVS is used to reset partitioning parameters to a more juvenile condition according to the harvest cycle phases. The CROPGRO Perennial Forage model was also calibrated for *B. brizantha* cv. Xaraes (Pedreira et al., 2011), *B. brizantha* cv. Marandu (Pequeno et al., 2014), *B. brizantha* cv. Mulato II (Pequeno, 2014). Despite the unquestionable relevance of these studies, the data used were mostly from “short-term” regrowth cycles (minimum of 28 days during summer/spring and a maximum of 63 days during winter/autumn), which did not allow for an accurate biomass partitioning modeling and parameterization from very early until very late stages of the grasses regrowth cycles.

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## 4. UNDERLYING MECHANISMS OF BIOMASS PARTITIONING IN MOMBAÇA GUINEAGRASS TILLERS: EFFECTS OF R/ FR RATIO AND DEVELOPMENTAL STAGE

### Abstract

Light competition and the onset of flowering are two factors affecting tillers' growth and development. The objectives of this study were to investigate: (i) the effects of the R (660 nm)/ FR (730 nm) ratio and of the developmental stage (vegetative/reproductive) on stem elongation of guineagrass tillers and (ii) the effects of stem elongation on leaf appearance and elongation. The experiment consisted of an irrigated Guineagrass field evaluated during two vegetative cycles (summers 1 and 2) and one reproductive cycle (autumn). For each cycle the R/ FR ratio data were acquired with the aid of an Ocean Optics USB2000+ spectrometer. Two to five times per week from 10 to 11h, five to ten measurements beneath the sward were recorded for each sample. For the measurement of true stem and pseudostem lengths, 10-25 representative tillers were weekly clipped and cut longitudinally. The developmental stage was visually observed with the aid of a Coleman XTB Stereoscope Microscope. Ten tillers were tagged for the measurement of the leaf appearance, elongation, and zenithal angle. The variables were plotted against the accumulated growing degree-days (gdd). Models were fitted to the data whenever they aided in understanding the dynamics of the studied processes. The fitting procedure was done using the NLIN procedure of SAS 9.2. During the vegetative cycles, the true stem length was constant up to a point and, thereafter, increased linearly. The data were fitted in segmented (constant-linear increase) curves (adj-R<sup>2</sup>=0.95 and 0.99 for the summers 1 and 2, respectively). The elongation was not primarily related to R/FR ratio beneath the sward, but was satisfactorily explained by gdd (with a difference of only 35 gdd between the breakpoints of the summers 1 and 2, respectively). The true stem elongation did not shorten the pseudostem. During the reproductive cycle, the true stem elongation occurred concurrently with the appearance of flowers primordia (11.7 h of daylength) and shortened the pseudostem. In the vegetative tillers, as opposed to the reproductive tillers, the true stem elongation did not shorten the final leaf length nor increased the leaf appearance rate. The growth dynamic of guineagrass tillers allows for a high leaf net accumulation in long regrowth cycles, even after the onset of stem elongation in vegetative cycles. Comprehending this dynamic aid in the understanding and modeling of growth and biomass partitioning of the guineagrass' plant community.

**Keywords:** *Panicum maximum*; Stem elongation; R/ FR ratio; Developmental stage; Pseudostem length

### 4.1. Introduction

Brazil had more than 213 million heads of cattle in 2018, which is the largest commercial herd in the world (FAO, 2020). The cattle in Brazil are mostly grass-fed and *Panicum* is the second most cultivated forage grass genus, after *Brachiaria*. *Panicum maximum* Jacq., commonly referred to as Guineagrass, is ubiquitous throughout the tropics and subtropics (Muir et al., 2001). The cultivar Mombaça is a tall bunch-type grass used for grazing, recommended for regions where annual rainfall ranges from 800 to 1800 mm and with well-drained soils with a medium to high soil fertility (Muir and Jank, 2004)

Biomass partitioning in forage grass is crucial for pasture-based livestock systems as it has consequences for plant and animal growth. For high productivity and animal performance, green leaf accumulation must be preferred to stem accumulation due to its high utilization efficiency and nutritive value (Gontijo Neto et al., 2006). Additionally,

the biomass partition affects the leaf area index (LAI) formation, with consequences for pasture growth and perennation. In warm-season grasses, the increase in herbage mass from a certain point is related to the increase in stem and pseudostem growth, even during the vegetative stage (Santos et al., 1999). Increases in LAI and, consequently, in light interception (LI), are responsible for the differentiation of quantity and quality of light throughout the sward and, ultimately, for biomass partitioning and structural changes (i.e. stem elongation) in the sward (Sbrissia and Da Silva, 2001). Several studies compared the use of 95% of LI and maximum LI as targets for pasture grazing and showed a considerably higher stem accumulation when defoliation was delayed beyond 95% LI (Carnevali et al., 2006; Barbosa et al., 2007; Pedreira et al., 2007; Trindade et al., 2007). Despite the high correlation registered between LI and changes in biomass partitioning, probably LI is not the signal perceived by the plants to sense the light environment surrounding them.

The  $r$  (660nm)/  $fr$  (730nm) ratio is sensed by the phytochromes of many plants as a signal for light competition (Ballaré et al., 1990). In dense swards, the lowering of the R/FR ratio is due to the specific absorption of red and transmittance/reflection of far red (Casal et al., 1986). The low R/FR ratio affects the phytochrome balance (Pr: Pfr) eliciting diverse phytochrome mediated responses, referred to as shade avoidance syndrome or photomorphogenesis (Schmitt et al., 2003). In grasses, the main responses registered are the higher internode elongation (Casal et al., 1987a; Davies and Simmons, 1994), higher growth of foliar sheaths and laminae (Skálová and Krahulec, 1992; Skinner and Simmons, 1993), lower appearance and higher mortality of tillers (Deregibus et al., 1985; Casal et al., 1987b; Skinner and Simmons, 1993), and negative phototropism response to far red (Maddonni et al., 2002). Despite the major role of light in determining the quality of warm-season grasses used as pasture, no studies have been found relating the shifts in biomass partitioning of these grasses with a biological significant signal (i.e.  $r$ :  $fr$  ratio).

The shifts in biomass partitioning are a consequence of changes occurring at a tiller-level. In a grass tiller, there is a whorl of mature sheaths covering the apical meristem and the new leaves developing, usually referred to as pseudostem, while the “true” stem is located below the apical meristem and its elongation is a result of internode elongation, which in turn is located below the apical meristem. The studies considering the shifts in biomass partitioning in warm-season grasses usually do not separate the two portions, and, consequently, the effects of developing one or other and its relation with the light environment is unknown.

Several studies related the true stem elongation during the reproductive growth with shortening of pseudostem for temperate (Robson, 1973; Maan et al., 1989; Skinner and Nelson, 1995) and warm-season grasses (Maas et al., 1987; Gomide and Gomide, 2000). According to these studies, internode elongation moves the apical meristem upwards, which shortens the pseudostem. The shortening of pseudostem, in turn, is related with a lower leaf growth duration and, consequently, lower final length (Robson, 1973; Wilson and Laidlaw, 1985; Skinner and Nelson, 1995), but with higher leaf appearance rate (Grant et al., 1981; Wilson and Laidlaw, 1985; Skinner and Nelson, 1995). As the net leaf accumulation rate in the tiller-level is the result of the appearance of new leaves and senescence of old ones, the appearance of progressively smaller leaves results in progressively smaller net leaf accumulation, and, from a certain point, when the leaves senescing are larger than the ones appearing, the net leaf accumulation rate becomes negative (Cruz and Boval, 2000). Despite the important results about true stem elongation during the reproductive growth reported in the literature, there is no study comparing the effects of true stem elongation during vegetative and reproductive stages in long regrowth cycles. The objectives of this study were to investigate: (i) the effects of a significant biological light signal (i.e. R/FR ratio) and of the developmental stage (i.e. vegetative or reproductive) on stem elongation of Mombaça Guineagrass tillers and (ii) the effects of stem elongation on leaf appearance and elongation.

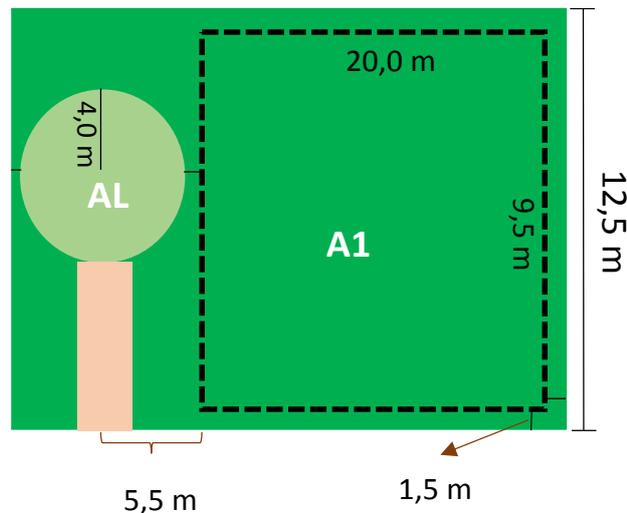
## 4.2. Hypothesis

-The true stem elongation is caused by a low R/FR ratio in the sward during the vegetative growth of Guineagrass and present a similar dynamic to that observed for the reproductive growth;

-The true stem elongation occurs at the expense of leaf elongation during both vegetative and reproductive cycles.

## 4.3. Material and methods

The experiment consisted of an irrigated *Panicum maximum* cv. Mombaça field carried out from December 2017 to January 2019 at Embrapa Southeast Livestock facilities in São Carlos, state of São Paulo, Brazil (21°57'42"S, 47°50'28"W, 860 m asl). The influences of quality of light (R/ FR ratio) and developmental stage (i.e. vegetative or reproductive) on the grass were evaluated on the tiller level in three long regrowth cycles: from December 2017 to February 2018, February 2018 to June 2018, and November 2018 to January 2019, totaling 10, 14 and 12 weeks for the first, second and third regrowth cycles, respectively. At the end of each regrowth cycle, the entire plot was clipped to 30cm height and, between the second and third evaluating cycles, the clipping to 30-cm height was also done every 30-60 days (without any measurements), depending on the pasture growth rate. Mombaça guineagrass was sown on 09/28/2017 and clipped twice for pasture establishment. After the second clip the first evaluating cycle started. The plot was 9.5 by 20 m for analysis on vegetation (A1) +  $\pi 4^2$  m<sup>2</sup> (AL) for analysis on quality of light (Figure 1), established on an Oxisol soil. The AL was separated only for radiation-related measurements to avoid changing in sward structure and, consequently, in the light environment, when performing the tiller-related measurements. Additionally, special care was taken when walking and taking measurements in this area to preserve the light conditions within the sward.



**Figure 1.** Layout of the experimental area. A1 and AL are the areas for measuring tiller-related variables and quality of light, respectively.

The macro and micronutrients content on the top 20cm layer of the soil before the beginning of the experiment are described in Tables 1 and 2, respectively. Nitrogen fertilization during the experimental period (considering establishment period) totaled 370 kg N ha<sup>-1</sup> year<sup>-1</sup>, split into four applications of 80 kg N ha<sup>-1</sup> applied

three times as ammonium nitrate and once as urea and one application of 50 kg N ha<sup>-1</sup> applied as calcium nitrate, and phosphorus fertilization of 200 kg ha<sup>-1</sup> split into five applications of 40 kg P ha<sup>-1</sup> applied as single super phosphate. Potassium fertilization totaled 160 kg K<sub>2</sub>O ha<sup>-1</sup> split into four applications of 40 kg K<sub>2</sub>O ha<sup>-1</sup> applied as potassium chloride. Sprinkler irrigation (4-8mm) was supplied based on the readily available water concept, considering the readily available water as 30% of the total of 60mm soil water holding capacity (SWHC). Whenever the soil water content came close to depleting the readily available water (70% of the SWHC left), irrigation was supplied. Weather data (daily solar radiation, maximum and minimum temperature and rainfall) were collected at a weather station located 1 km from the experimental site. The registered averages of daily solar radiation were 18.99; 18.25; and 22.47 MJ m<sup>-2</sup> d<sup>-1</sup>, for the first, second and third regrowth cycles, respectively. The maximum, average and minimum monthly temperatures and the accumulated monthly precipitation are described in Figure 2.

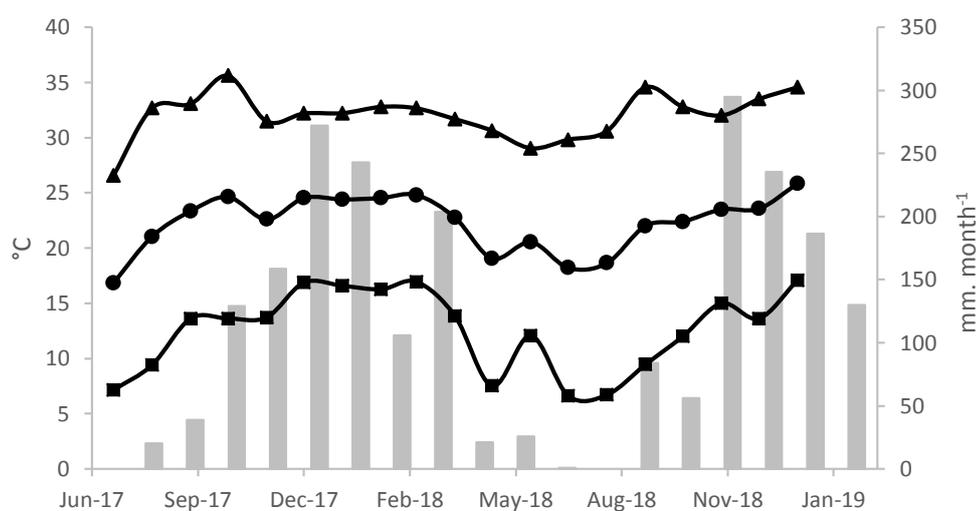
**Table 1.** Macronutrients analysis in the top 0-20 cm of the soil

pH	pH	OM	P	K	Na	Ca	Mg	H+Al	Al	S.SO4	SB	CEC	V	m
H2O	CaCl	g.dm <sup>-3</sup>	mg.dm <sup>-3</sup>	-----mmolc. dm <sup>-3</sup> -----					mg.dm <sup>-3</sup>	--mmolc. dm <sup>-3</sup> --	--%--			
6,1	5,4	37	7	1,8	ns	24	9	27	0	11	35	62	56	0

OM: organic matter; SB: sum of exchangeable bases; CEC: cation exchange capacity; V: base saturation; m: aluminum saturation.

**Table 2.** Micronutrients in the top 0-20 cm of the soil

B	Cu	Fe	Mn	Zn
-----mg dm <sup>-3</sup> -----				
0,35	3,5	35	5	1,9



**Figure 2.** Minimum (■), average (●), and maximum (▲) monthly temperatures, and monthly accumulated precipitation (bars) during the experimental period.

#### 4.3.1. Red/ far red ratio measurements

The red (660±5 nm)/ far red (730±5 nm) ratio data were acquired with the aid of an Ocean Optics USB2000+ spectrometer (Ocean Optics In., Dunedin, Florida) equipped with a remote cosine corrector. For each

sample, the spectrometer was placed underneath the sward on the soil level (the sensor was located 5cm of the soil level due to the instrument height) and 5 to 10 measurements were recorded. The number of measurements depended upon the light environment condition beneath the sward so that more measurements were taken in heterogeneous conditions. Heterogeneous conditions occurred when the ground covered by the sward was medium and there was a considerable amount of both lit and shaded ground. When there was almost no ground cover the conditions were homogeneously lit, while when the ground was almost entirely covered by vegetation, the conditions were homogeneously shaded. During the regrowth period of each evaluation cycle, the samples were taken twice to five days per week, from 10 to 11h (solar time).

### **4.3.2. Measurements on individual tillers**

#### **4.3.2.1. Destructive analysis**

The analysis of the stem development was done separating “true stem” and “pseudostem”, so that the true stem refers to the portion from the base of the plant to the apical meristem, while the pseudostem refers to the portion from the apical meristem to the last visible ligule. For this analysis, 10-25 tillers were weekly clipped and taken to the laboratory, where the true stem and pseudostem lengths were measured. The tillers were clipped in the soil level and the tillers collected were representative of the average tiller height and structure of the sward. Additionally, the tillers were cut in longitudinal direction to visually observe the apical meristem developmental phase (vegetative/reproductive). The observation was done with the aid of a Coleman XTB Stereoscope Microscope and, whenever the flower primordia could be observed, the tiller was considered as reproductive (Araújo, 2011). Tillers with emerged panicles were not sampled in this analysis, as they did not represent the average tiller height and structure. An additional analysis was done at the end of the reproductive cycle (second regrowth, when reproductive tillers were observed) to analyze the portion of tillers in the reproductive and vegetative phase. For that, entire tussocks were clipped and 40 tillers were chosen randomly. To avoid bias on the choosing procedure, all the tillers were numbered and 40 numbers were drawn. The drawn tillers were finally separated into vegetative (vegetative meristem), reproductive (emerged panicle), and aborted (brown meristems; see results and discussion for details).

#### **4.3.2.2. Morphogenetic analysis**

Analysis of the leaf zenithal angle, the final leaf lengths, leaf elongation and leaf appearance were performed in the three regrowth cycles. For that, 10 tillers were tagged at the beginning of each regrowth period using colored plastic coated wires. The evaluations were done twice a week, and the leaf zenithal angle was always analyzed first before the tiller structure was affected by manipulation due to the other measurements. The leaf zenithal angle was measured with the aid of a 180 protractor with a tied weight, and the other variables with the aid of a ruler. After the observation of the first reproductive meristems on the destructive analysis during autumn (see section 4.3.2.1.), the tillers were separated in two categories: (i) tillers in which the panicle emerged until the end of regrowth period, considered as “reproductive” (n=5) and (ii) tillers in which the panicle did not appear until the end of the regrowth period, considered as “vegetative” (n=5).

The tillers that presented developmental problems were replaced, totaling five tillers for each summer evaluation cycles and one tiller for the autumn evaluation cycle. As replacing from one tiller to another may cause miscalculation of the leaf appearance rate (the interval between the appearance of the “first” leaf in the substituting tiller and the preceding leaf is uncertain), and due to the considerable number of tillers replaced during the regrowth cycles, the rate of leaf appearance was estimated by deriving the equation fitted for accumulated number of leaves appeared.

### 4.3.3. Presentation of results and statistical analysis

The presentation of results and the statistical analysis performed were done considering the thermal time course of the variables in growing degree days, due to the dominant effect of temperature on plant development (Gallagher, 1979). The accumulated growing degree-days was estimated according to Moreno et al. (2014):

$$GDD_i = \sum\{(tmax_i + tmin_i/2 - tb)\} - C \quad \text{when } tmax_i + tmin_i/2 > tb \quad (1.1)$$

$$GDD_i = \sum\{(tmax_i - tb)^2/2(tmax_i - tmin_i)\} - C \quad \text{when } tmax_i + tmin_i/2 \leq tb \quad (1.2)$$

$$C = (tmax_i - 40)^2/2(tmax_i - tmin_i) \quad \text{when } tmax_i + tmin_i/2 > 40 \quad (1.3)$$

$$C=0 \quad \text{when } tmax_i + tmin_i/2 \leq tb \quad (1.4)$$

Where GDD is the growing degree-days (C°d),  $tmax_i$  is the maximum temperature at the day  $i$ ;  $tmin_i$  is the minimum temperature at the day  $i$ ;  $tb$  is the base temperature of the cultivar; and  $C$  is the correction coefficient. The  $C$  values along the experimental period were always equal to 0 and the base temperature was 11° C (Moreno et al., 2014). The statistical analysis was descriptive, and, thus, the averages with their respective standard deviations over thermal time are presented in graphs. Models were fitted to the data whenever they brought about morphological/physiological insights and aided in understanding the dynamics of the studied processes. The fitting procedure was done using the NLIN procedure of SAS 9.2. (SAS Institute, Cary, NC, USA).

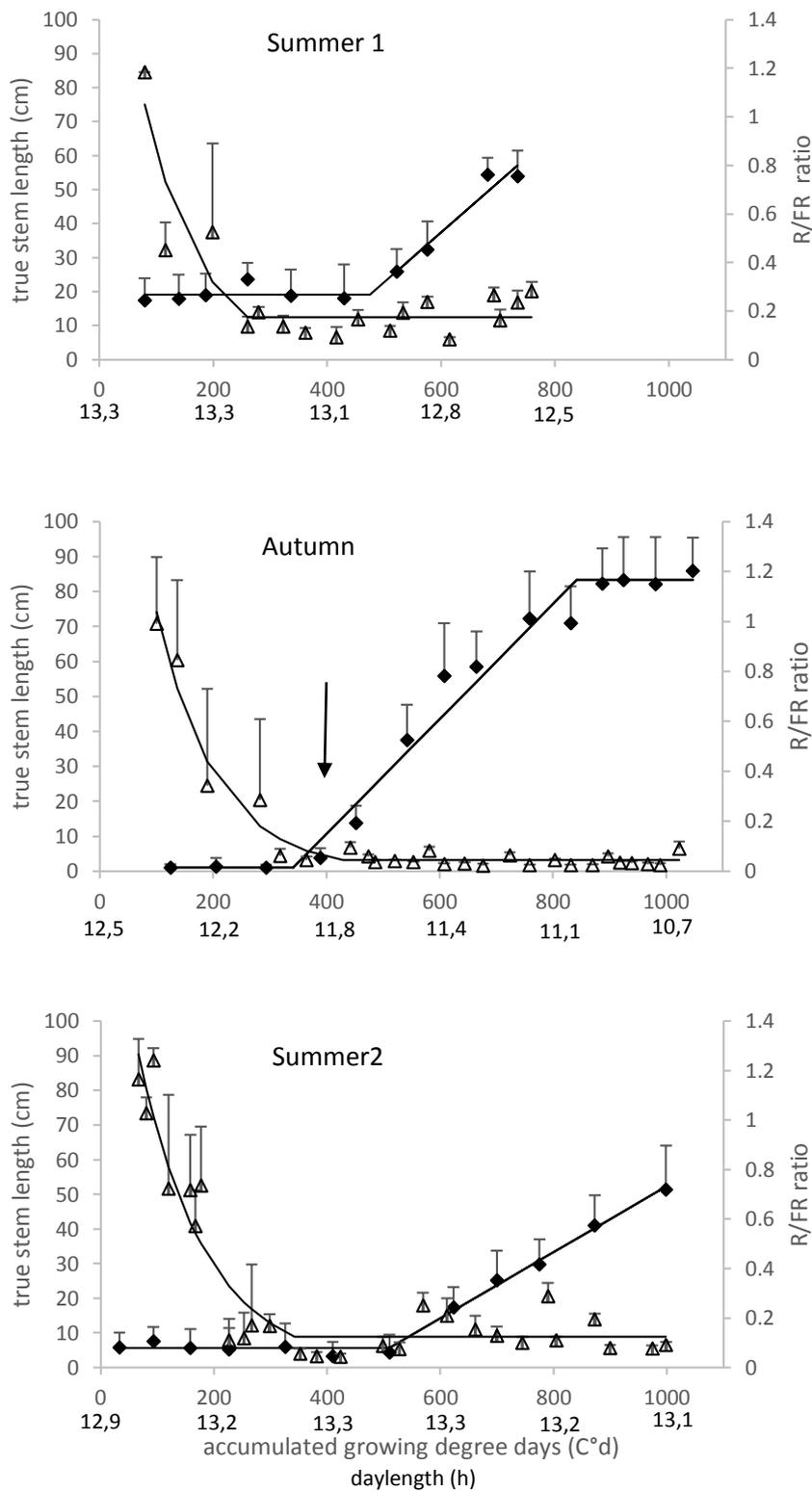
## 4.4. Results

### 4.4.1. Shade avoidance syndrome and flowering stimulus effects on tillers development

Segmented (exponential decline-constant value) regressions were fitted in the three seasons for R/ FR.ratio (Figure 2). The exponential decline in R/ FR values when plotted against gdd is explained by an increase in LAI and, consequently, LI by the sward (Evers et al., 2006). Subsequently, after reaching high values of LAI and LI, the R/ FR ratio tends to fluctuate around a constant value. These fluctuations are probably explained by the interaction between leaf architecture and atmospheric conditions, which alter light penetration through the sward. Due to the random and slight nature of the fluctuation, fitting the data in a constant minimum value after the exponential decrease was considered appropriate. The gdd values in which the curve turns from an exponential decline to a constant value were

260.2, 429.3 and 342.4 for the summer 1, autumn and summer 2, respectively (Table 1). The higher gdd value registered for autumn is probably due to the inferior growth conditions during this season when compared to the summers. The constant minimum R/FR estimated values were 0.17, 0.04 and 0.12, for the summer 1, autumn and summer 2, respectively.

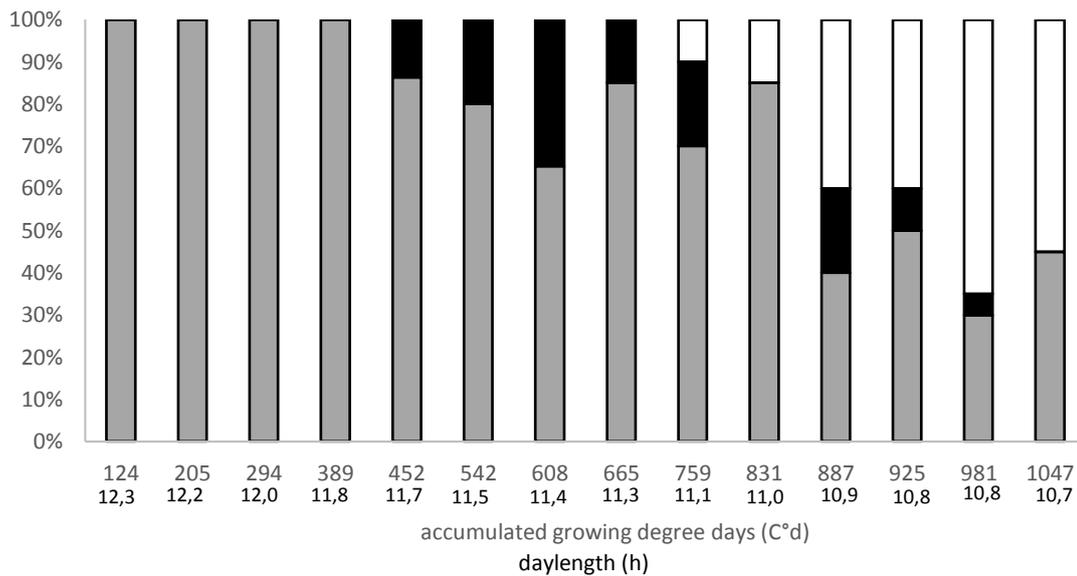
The true stem length followed the same pattern for the summers 1 and 2 but had a different pattern during autumn (Figure 3). During summers 1 and 2, the true stem length was nearly constant up to a point and, from this point onward, there was a linear increment until the end of the regrowth cycle. In this context, both data could be fitted in segmented (constant-linear increase) models, presenting estimated breakpoints of 475.4 and 509.4 gdd, for summers 1 and 2, respectively (Table 3). The estimated breakpoints represent the moment when the stem shifted from a nearly constant value to a linear increase. In both cases, the breakpoint of the curve occurred distant from the minimum value of R/FR, which shows that R/FR was not able to explain true stem elongation solely. During Autumn, on the other hand, the true stem length was fitted in a segmented (constant-linear increase-constant) model (Table 3). The increment on true stem length coincided with the minimum value of R/FR, but was also slightly before the observation of the firsts reproductive meristems (Figure 3). In this context, the increments on true stem length during autumn were attributed to the onset of the reproductive phase, rather than to low values of R/FR ratio.



**Figure 3.** True stem length (◆) and red/ far red ratio (Δ) as a function of accumulated growing degree days (C°d) and daylength in summer 1, autumn, and summer 2. Solid lines are fits of the data. The arrow indicates when the first flowers primordia were observed (only in the autumn). Bars indicate standard deviation.

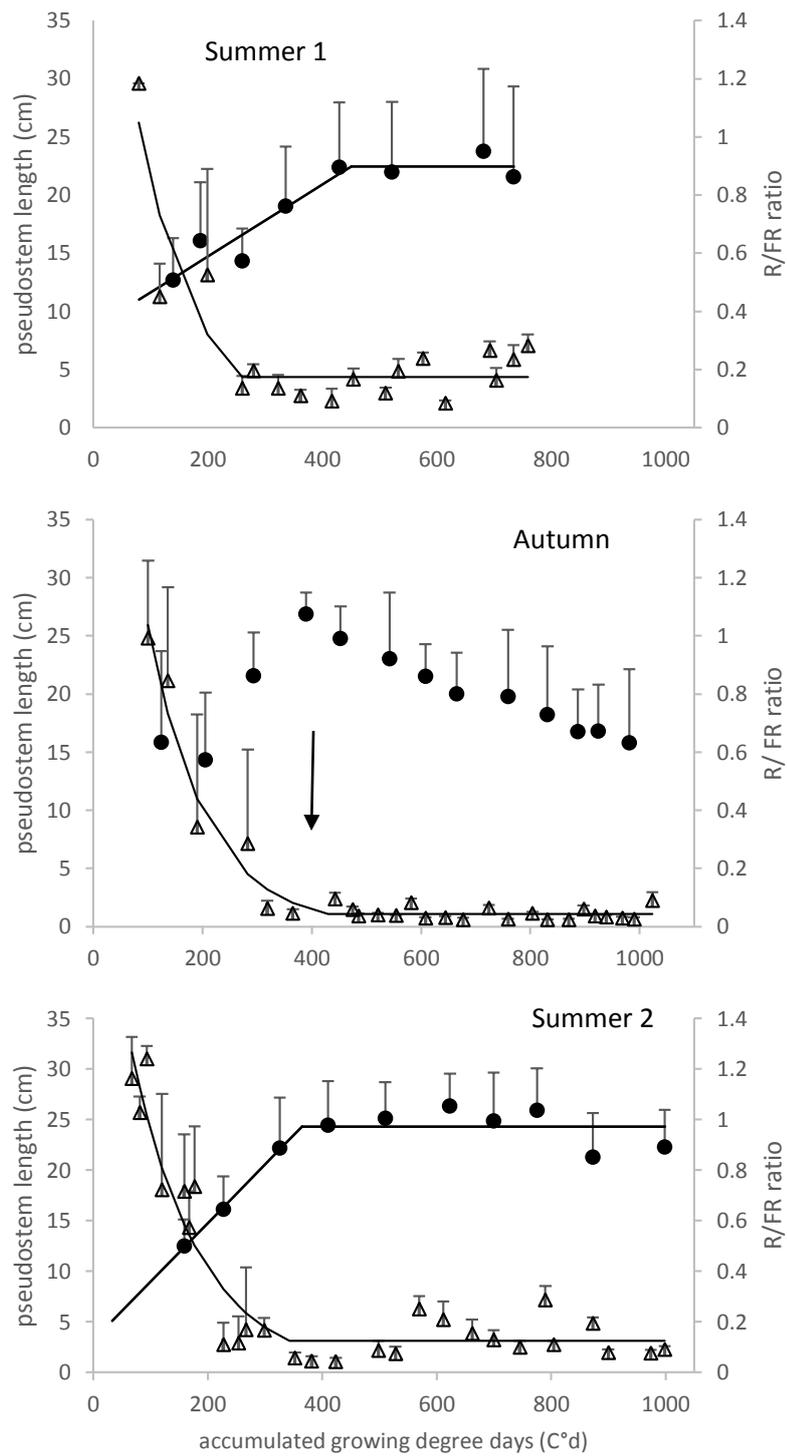
The observation of the firsts flowers primordia occurred during autumn at daylength of 11.7 h (Figure 4), similar to the 11.6 h of daylength registered by Araujo (2011). Additionally, senesced (brown) meristems were observed during autumn, after flower primordia initiation. The proportion of senesced meristems increased progressively up to

the end of the regrowth period. As only the meristems senesced, while the rest of the plant remained green, these meristems were assumed as aborted (this observation was also done with the aid of the stereoscope). It is worth noting that, tillers with visible panicles were avoided for the observation of meristems. Thus, this measurement estimated the appearance of flower primordia over the regrowth period and not the total amount of reproductive tillers (which would include tillers with visible panicle). To consider the total amount of reproductive tillers, at the end of regrowth period (04/06/2018 or 1023 gdd), when the panicles of reproductive tillers had already emerged, 40 tillers were randomly collected and divided into flowered (visible panicle), vegetative (vegetative meristem) and aborted (brown meristem). It was found 37.5% vegetative, 42.5% aborted, and 20% flowered tillers. During summers 1 and 2, when the daylength was higher than 11.7h during the entire regrowth period, none reproductive or senesced meristem was observed.



**Figure 4.** Proportion of meristems in the vegetative stage (grey), reproductive stage (black) and aborted (white) in tillers without visible panicle as a function of accumulated growing degree days (C°d) and daylength during autumn.

The pseudostem elongation had a similar pattern for summers 1 and 2, but a different pattern for autumn (Figure 5). During the summers, the pseudostem increased linearly until reaching a maximum constant value and were fitted to segmented (linear increase-constant) models (Table 3). According to the fitted curves, the maximum values were 22.4 and 24.3 cm, for the summers 1 and 2, respectively. The increase in pseudostem occurred concurrently with the decreasing R/FR, indicating a possible interference of R/FR on pseudostem growth at the beginning of the regrowth periods, although an interference of plant development in pseudostem length is not discarded. Differently from what was registered for the summers, during autumn the pseudostem length increased at the beginning of the regrowth but decreased after about 400 gdd. The decrease in pseudostem length occurred concurrently with the observation of the first reproductive meristem (Figure 4), indicating the influence of the onset of flowering and apical meristem rising on pseudostem reduction for this season.



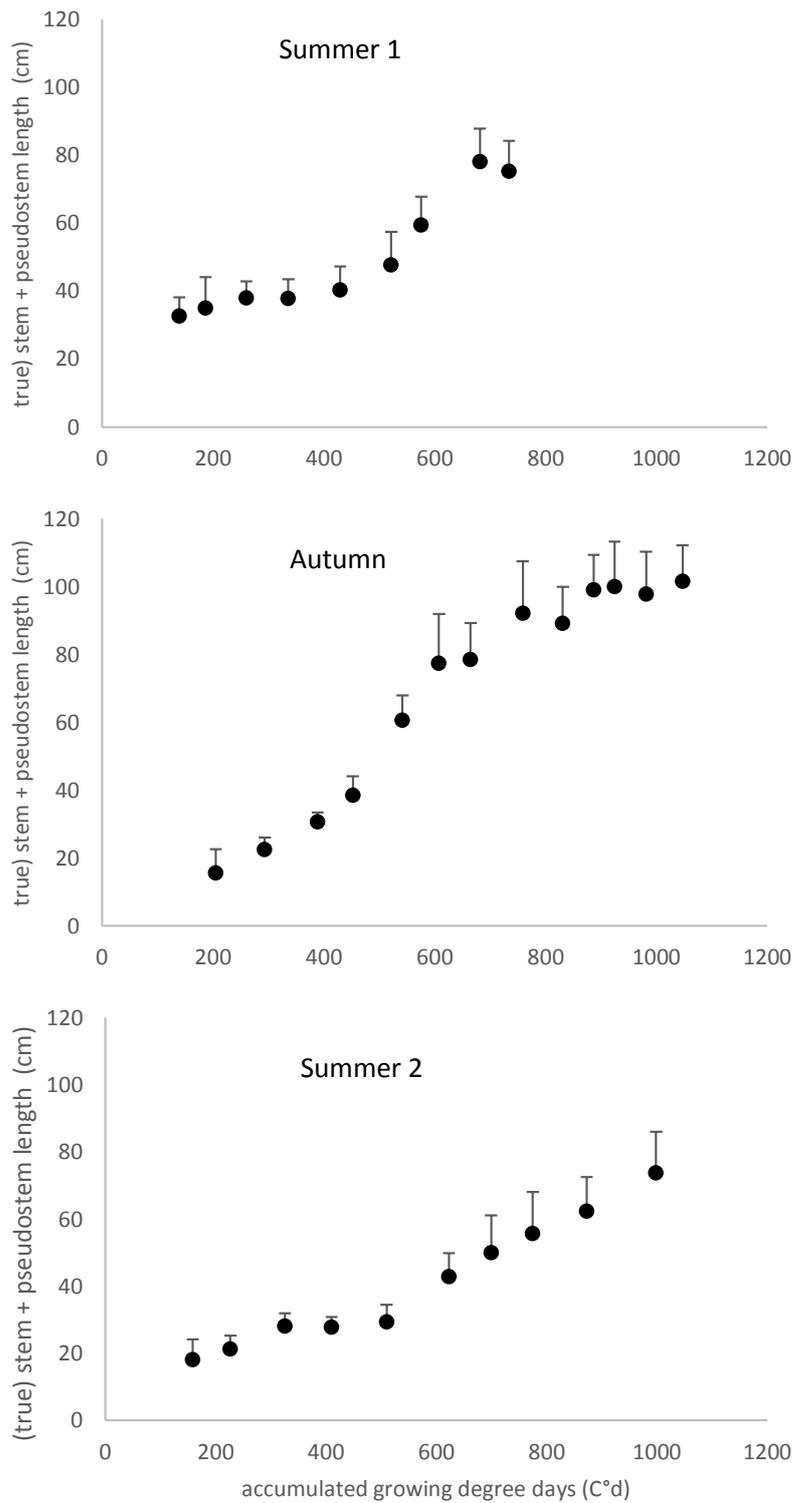
**Figure 5.** Pseudostem length (●) and red/ far red ratio (Δ) as a function of accumulated growing degree days (C°d) in summer 1, autumn, and summer 2. Solid lines are fits of the data. The arrow indicates when the first flowers primordia were observed (only in the autumn). Bars indicate standard deviation.

**Table 3.** Functions, estimated parameters and adjusted coefficients of determination for R/FR ratio beneath the sward, and true stem length, and pseudostem length of Mombaça tillers

variable - season	function type	estimated parameters	adjusted R <sup>2</sup>
R/ FR ratio – summer 1	segmented (negative logarithmic-constant)	c=2.3184; d=0.0095; gdd**=260.2; k=0.17	0.79
R/ FR ratio – autumn	segmented (negative logarithmic-constant)	c=2.7165; d=0.0096; gdd**=429.3; k=0.04	0.96
R/ FR ratio – summer 2	segmented (negative logarithmic-constant)	c=2.2269; d=0.0084; gdd**=342.4; k=0.12	0.89
true stem length - summer 1	segmented (constant-linear increase)	b1= 19.135; a2= 0.147; gdd* = 475.4	0.95
true stem length - autumn	segmented (constant-linear increase-constant)	a=0.1642; b=1.0867 gdd0=341.6; gdd00=842.2	0.97
true stem length - summer 2	segmented (constant-linear increase)	b1= 5.5622; a2= 0.0953; gdd*= 509.4	0.99
pseudostem length - summer 1	segmented (linear increase-constant)	a1= 0.0308; b1= 8.5698; gdd*=450.5	0.83
pseudostem length - summer 2	segmented (linear increase-constant)	a1= 0.0581; b1= 3.1416; gdd*=364.2	0.83

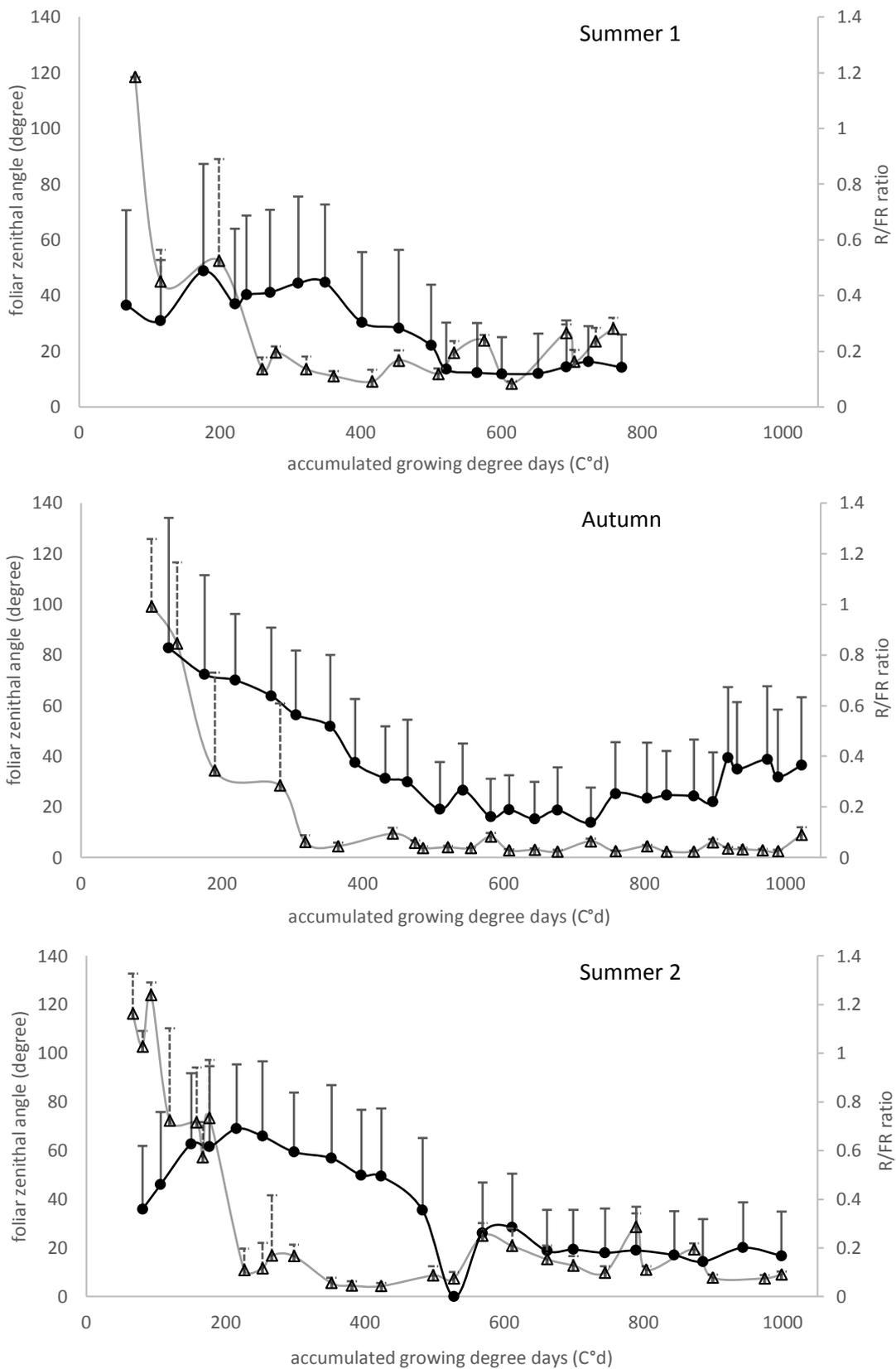
For the segmented (negative logarithmic-constant) functions: c is the coefficient multiplying the log function and d is coefficient multiplying (-)\*argument of the first segment; k is the value of the second segment; and gdd\*\* is the breakpoint. For the segmented (constant-linear increase) functions: b1 is the value of the first segment; a2 is the angular coefficient of the second segment; and gdd\* is the breakpoint. For the segmented (constant-linear increase-constant) function: a and b are the angular and linear coefficients of the second segment, respectively; gdd0 and gdd00 are the first and second breakpoints, respectively. For the segmented (linear increase-constant) functions: a1 and b1 are the angular and linear coefficients of the first segment, respectively; and gdd\* is the breakpoint.

The elongation of true + pseudostem over thermal time occurred in two distinct phases in summers 1 and 2. The first phase is characterized by the elongation of the pseudostem and null elongation of the true stem and, consequently, the increase in true + pseudostem length has the same shape of that observed in pseudostem length (Figure 6). Thereafter, the pseudostem length reaches its maximum value and the pseudostem + true stem elongation is due to the linear increase in true stem length. During autumn, due to the high elongation of the true stem and the decrease in pseudostem length which occurs after the flowering stimulus, most of the elongation of true stem + pseudostem is explained by the elongation on true stem solely. Consequently, the length of true stem + pseudostem over thermal time presents a similar shape from what observed for the true stem during this season. When comparing the true + pseudostem length at the same thermal time for the three seasons, the values were 75, 90, and 55 cm, at 730 gdd (end of summer 1), for summer 1, autumn and summer 2, respectively.

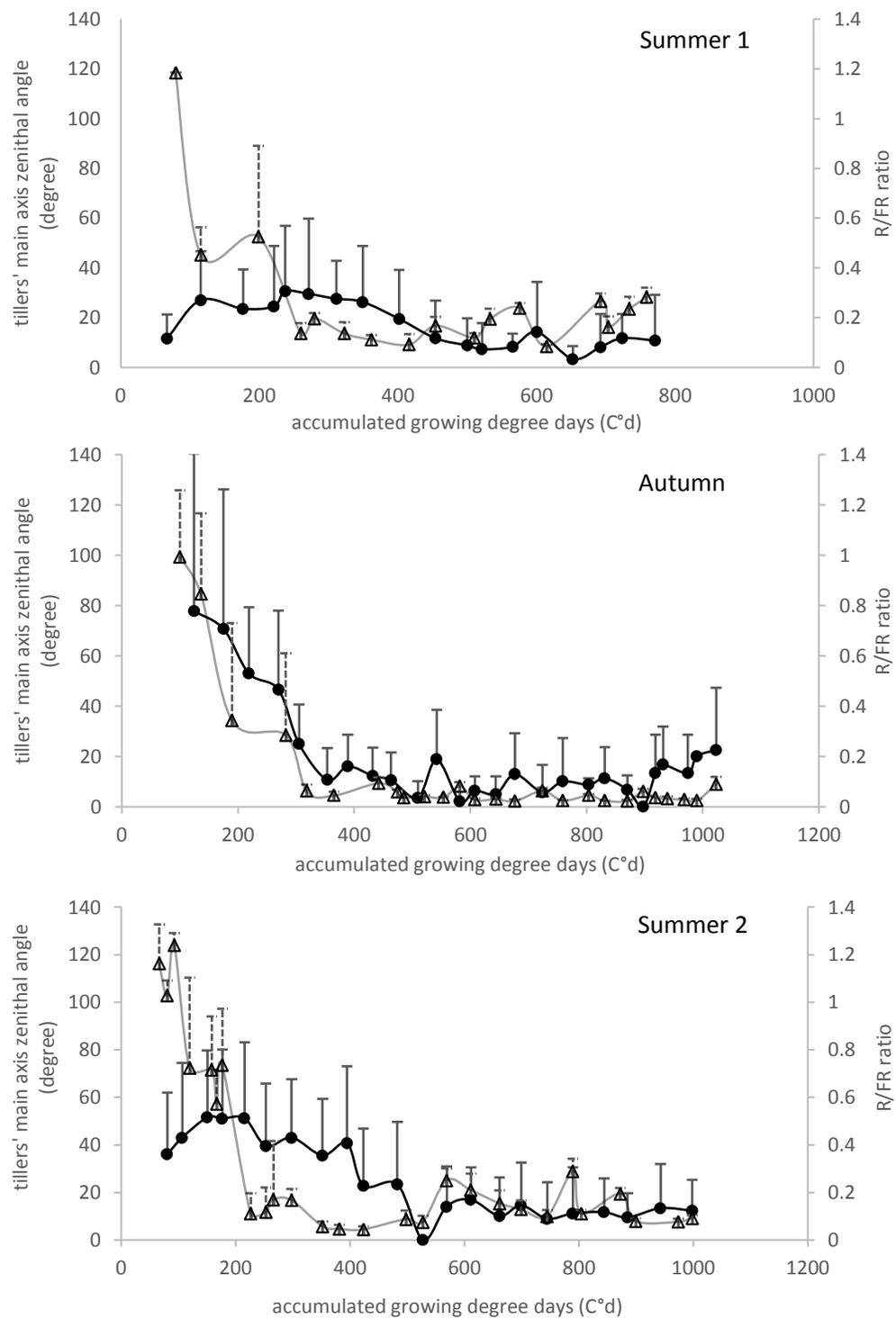


**Figure 6.** True stem + pseudostem length (●) as a function of accumulated growing degree days (C°d) in summer 1, autumn, and summer 2. Bars indicate standard deviation.

The zenithal angle of insertion of fully expanded green leaves + leaves in expansion and the R/FR ratio decreased concurrently over gdd during the three regrowth periods (Figure 7). At the beginning of the regrowth, the green leaves zenithal angles were about 40° and 60°, for summer 1 and summer 2, respectively, and it progressively decreased to about 20° for both regrowth periods. During autumn, the initial value was 80° and it decreased progressively up to 720 gdd reaching 20°. From this moment onward, there was a slight increase in zenithal green leaf angle to about 35°, caused by the expansion of leaves in more horizontal position of those tillers in which the panicle emerged during the regrowth period. The leaves expanding in reproductive tillers are located at higher strata of the sward and have a higher zenithal angle. Likewise, the tillers' main axis zenithal angle decreased concurrently with the decrease in R/FR, over the accumulated gdd (Figure 8). The initial values were about 25°, 80° and 50° for summer 1, autumn and summer 2, respectively and in the three regrowth periods the final values floated around 10°.



**Figure 7.** Fully expanded green leaves + leaves in expansion zenithal angle (●) and R/FR ratio (Δ) as a function of accumulated growing degree days (C°d) in summer 1, autumn, and summer 2. Zenithal angle was measured at leaves' insertion. Bars indicate standard deviation.

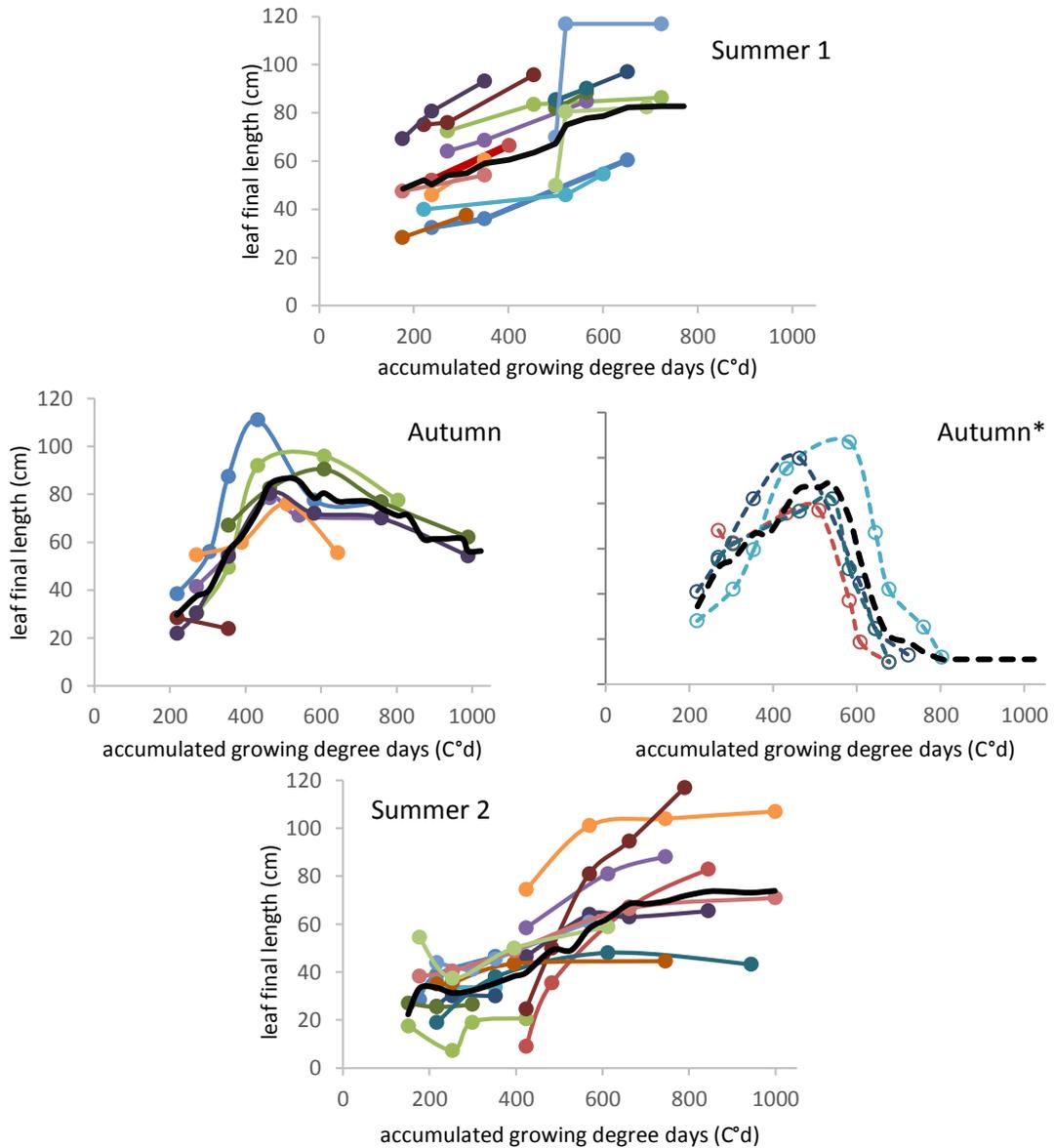


**Figure 8.** Tillers' main axis zenithal angle (●) and R/FR ratio (△) as a function of accumulated growing degree days (C°d) in summer 1, autumn, and summer 2. The tillers' main axis zenithal angle was estimated by measuring the zenithal angle of insertion of the youngest expanding leaf (the leaf emerging from the whorl of sheaths). Bars indicate standard deviation.

#### 4.4.2. Consequences for leaf appearance and elongation

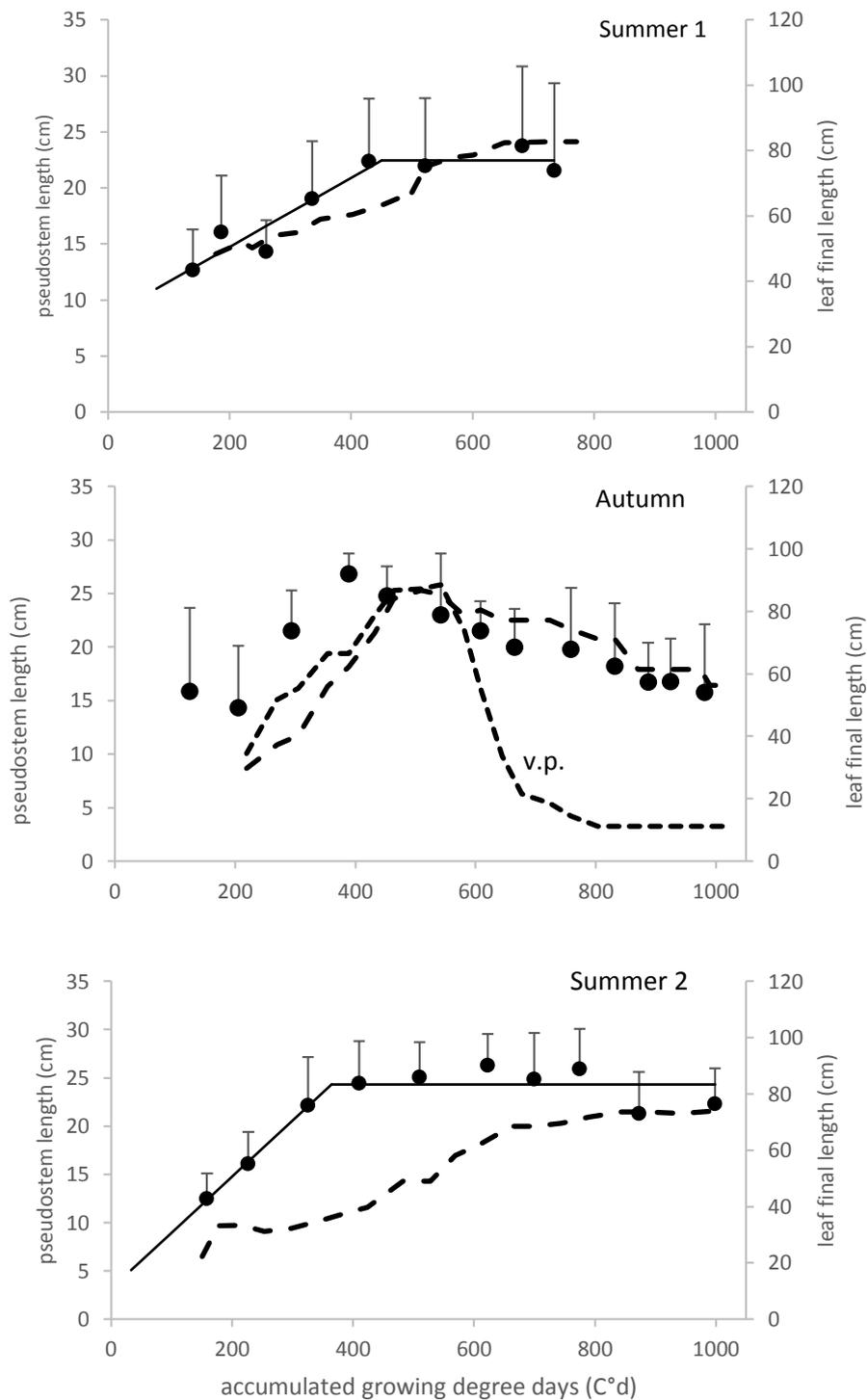
The final length of the youngest expanded leaves in individual tillers increased over summer 1 and summer 2 until the end of the regrowth periods (Figure 9). The increase was sharp for summer 1, and the beginning and middle of the regrowth period in summer 2. However, from the middle to the end of summer 2, the increase in the final leaf lengths decelerated resulting in lower differences in length of successive leaves. When considering the average final length of the youngest expanded leaves during the summer seasons, a sharp increase in length is followed by a deceleration until reaching a nearly constant value. It is worth noting, however, that this average value is, not only influenced by the final length of the new leaves in individual tillers, but also by the time taken to full expansion of new leaves. As at the end of the regrowth periods the leaves take more time to expand (see colored lines), the average value also takes more time to increase.

During autumn, the final leaf lengths increased sharply until reaching a maximum and then decreased progressively until the end of the regrowth. The decrease occurred for tillers with and without visible panicle at the end of the regrowth period, however, it was sharper for those which the panicle emerged. The inflection point where the decrease in leaf length begins, coincides with the observation of the first reproductive meristem (Figure 4), indicating the influence of this event in this variable.



**Figure 9.** Final length of the youngest expanded leaf on individual tillers (colored) and averaged among the tillers (black) as a function of accumulated growing degree days ( $C^{\circ}d$ ) in summer 1, autumn, and summer 2. Solid lines and closed symbols are for tillers in which the panicle did not emerge up to the end of the regrowth, while dashed lines and open symbols are for tillers in which the panicle emerged during the regrowth. The circles for individual tillers represent the length of the last expanded leaf at the moment it fully expanded.

When plotting the thermal time course of pseudostem length and the average final leaf length on the same figure, it is possible to see the dependence of the latter on the former (Figure 10). The increase in pseudostem at the beginning of the regrowth period is accompanied by the increase in the final length of the last expanded leaf in both summers. Thereafter, the approaching of the pseudostem length to the maximum value is accompanied by the reaching of a nearly constant value of averaged final leaf length. Likewise, during autumn, the initial increase in pseudostem length occurs concurrently with the increase in average final leaf length and, subsequently, the abrupt and progressive decrease occurs for both variables (Figure 10) by the time of observation of the first reproductive meristem (Figure 4).

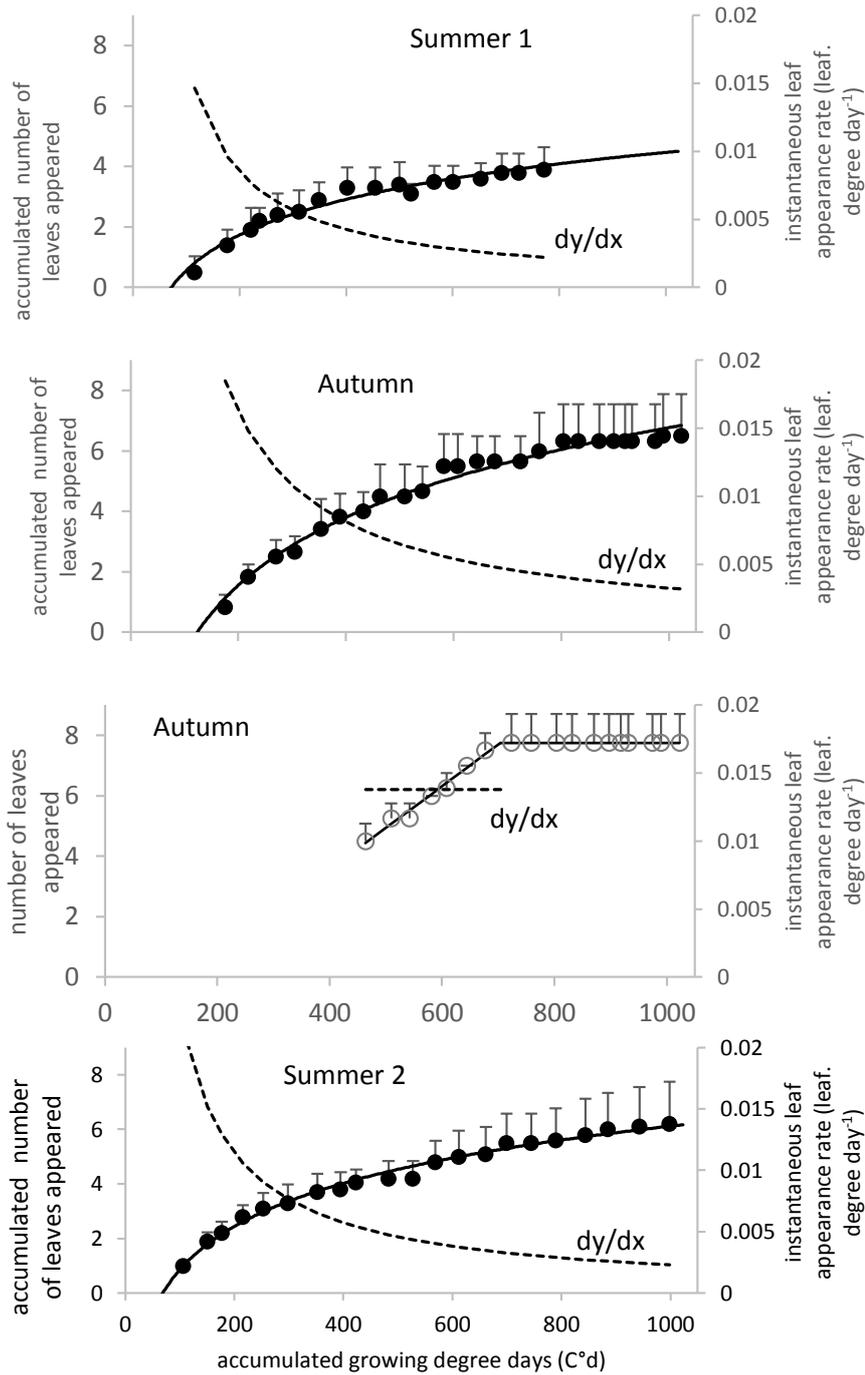


**Figure 10.** Pseudostem length (●) and the final length of youngest expanded leaf (dashed lines) as a function of accumulated growing degree days (C°d) in summer 1, autumn, and summer 2. “v.p.” (visible panicle) curve represents tillers in which the panicle emerged during the regrowth. Solid lines are fits of the data. Bars indicate standard deviation.

For tillers of summers 1 and 2 and for those tillers in which the panicle did not emerge during autumn, the accumulated number of appeared leaves increased rapidly at the beginning of the regrowth but decelerated progressively over gdd (Figure 11). The data was described by a natural logarithm function (Table 4), while the

derivatives of the curves obtained describe the leaf appearance rate. The leaf appearance rate decreases over gdd since the beginning of the regrowth until approaching a nearly constant value. For the tillers in which the panicle emerged in the autumn, the accumulated number of appeared leaves was described by a segmented (linear increase-constant) function (Figure 11; Table 4). The curve is described by two lines, being the first the appearance of successive leaves at a constant rate and the second the cessation of leaf appearance. Therefore, the derivative describes a constant rate of leaf appearance followed by a null rate of leaf appearance. The leaf appearance rate for tillers which the panicle did not emerge was the highest for autumn, followed summer 2 and, finally, summer 1 (Figure 12). For those tillers in which the panicle emerged, the rate of leaf appearance was the highest when compared to other tillers in the three regrowth periods.

The decrease registered in the leaf appearance rate follows an inverse pattern from that observed for pseudostem length (Figure 13). The decrease in the leaf appearance rate is proportional to the increase in pseudostem length during summers 1 and 2, and both variables tend to stabilize around a nearly constant value. During autumn, the onset of decay on pseudostem length is accompanied by the rapid leaf appearance rate of the tillers which the panicle emerged during the autumn season.

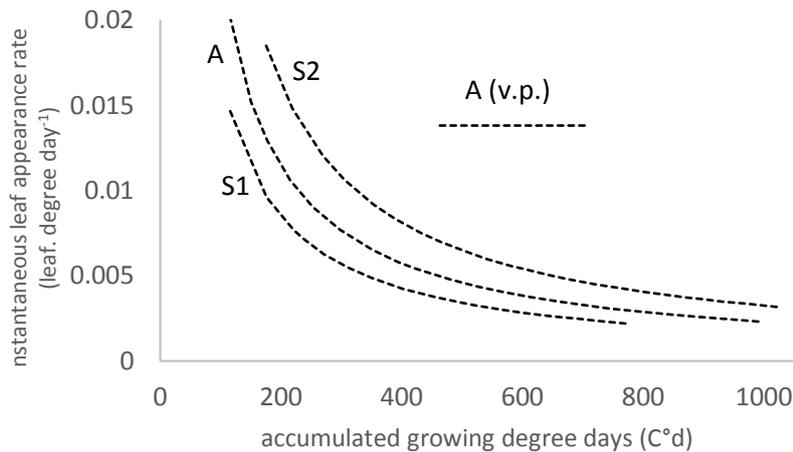


**Figure 11.** Accumulated number of appeared leaves (●/○) and instantaneous leaf appearance rate (dotted lines) as a function of accumulated growing degree days ( $C^{\circ}d$ ) in summer 1, autumn, and summer 2. The closed symbols are for tillers which the panicle did not emerge up to the end of the regrowth, while open symbols are for tillers in which the panicle emerged during the regrowth. The leaf appearance rate is given by the derivative of the accumulated number of appeared leaves over thermal time ( $dx/dy$ ). Solid lines are fits of the data (see Table 4 for details). The derivative was calculated from the fits of the data. Bars indicate standard deviation.

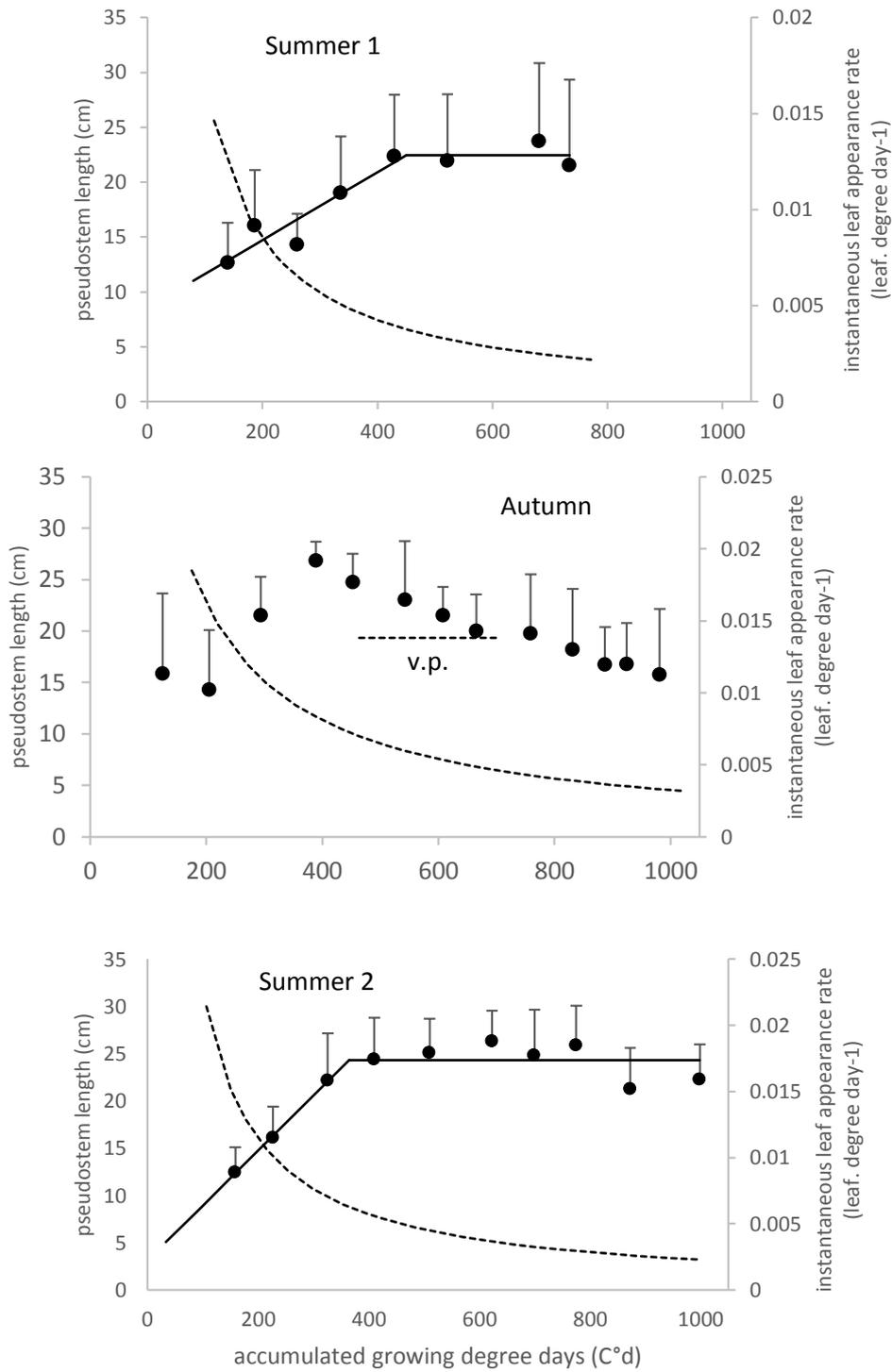
**Table 4.** Table 4– Functions, estimated parameters and adjusted coefficients of determination for accumulated number of leaves appeared on Mombaça tillers

season	function type	estimated parameters	adjusted R <sup>2</sup>
summer 1	natural logarithmic	a= 1.6982; b= -7.2648	0.96
autumn (tillers which did not emerge panicles)	natural logarithmic	a= 3.2426; b= -15.63	0.98
autumn (tillers which in which the panicles emerged)	segmented (linear increase-constant)	a1=0.0138; b2= 7.75; gdd0= 704.2	0.99
summer 2	natural logarithmic	a= 2.2875; b= -9.683	0.99

For the natural logarithmic models: a is the parameter multiplying  $\ln(\text{gdd})$ ; and b is the coefficient summing to  $a \cdot \ln(\text{gdd})$ . For the segmented (linear increase-constant) function: a1 is the angular coefficient of the first segment; b2 is the value of the second segment; and gdd0 is the breakpoint.



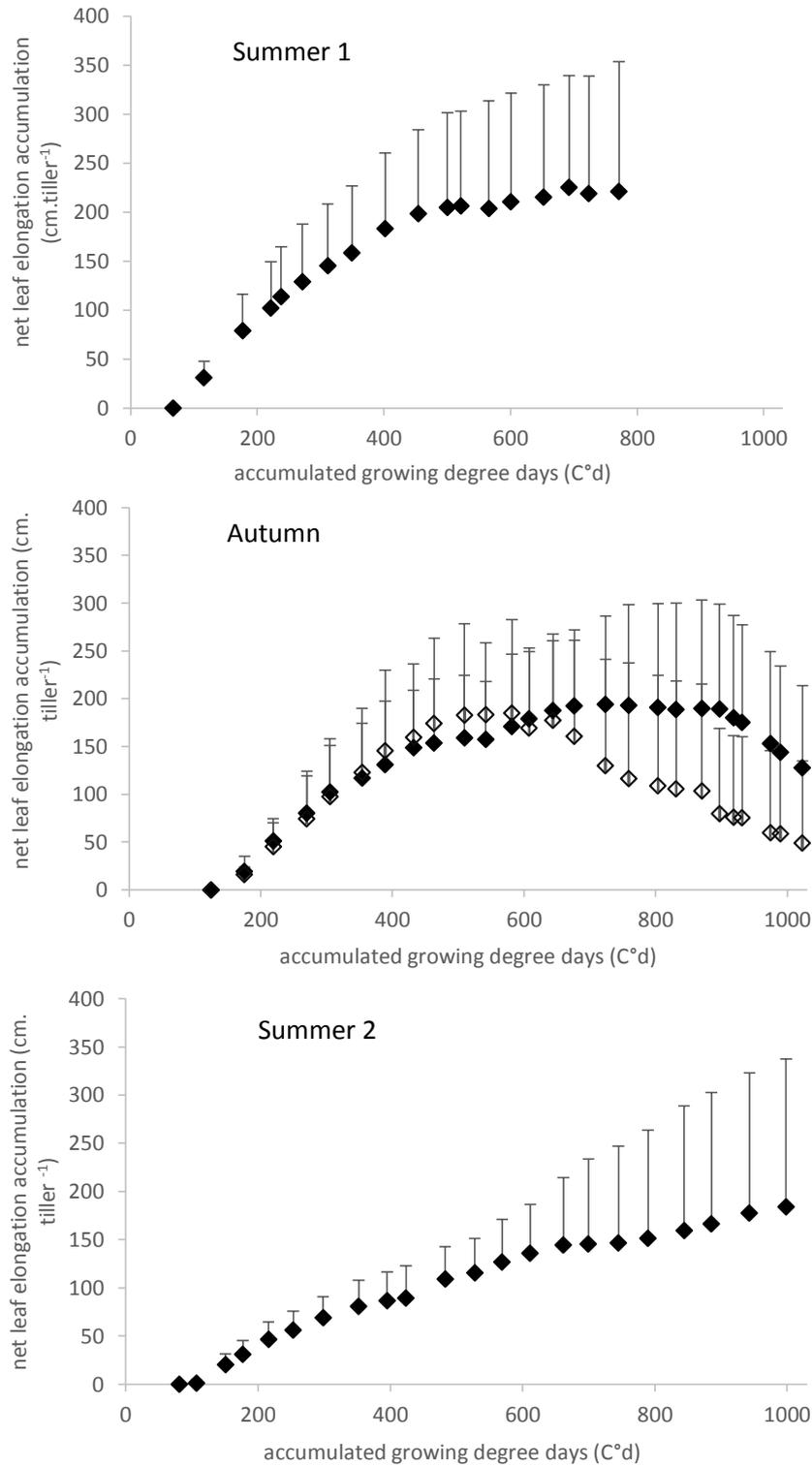
**Figure 12.** Estimated instantaneous rate of leaf appearance as a function of accumulated growing degree days (C°d) in summer 1, autumn, and summer 2. The “v.p.” indicates tillers in which the panicle emerged during the regrowth.



**Figure 13.** Pseudostem length (●) and estimated instantaneous rate of leaf appearance (dotted lines) as a function of accumulated growing degree days (C°d) in summer 1, autumn, and summer 2 (C). “v.p.” (visible panicle) curve represents tillers in which the panicle emerged during the regrowth. Solid lines are fits of the data (see Tables 3 and 4 for details). Bars indicate standard deviation.

The leaf elongation net accumulation over thermal time increased up to 500 gdd during summer 1, when it reached a plateau of about 200 cm. tiller<sup>-1</sup>, which persisted until the end of the season (Figure 14). The reaching of the plateau means the elongation equaled the senescence during this period. For summer 2, the leaf elongation net

accumulation continued to increase until the end of the regrowth period reaching an accumulated 180 cm leaf. tiller<sup>-1</sup>. In the latter, leaf elongation was higher than leaf senescence during the whole period, despite the long period analyzed. In autumn, for those tillers in which the panicle did not emerge, the leaf elongation net accumulation increased up to 680 gdd, when it reached a plateau of 190 cm leaf. tiller<sup>-1</sup>. The value remained nearly constant up to 900 gdd and then decreased progressively until the end of the regrowth period, reaching 125 cm leaf. tiller<sup>-1</sup>. In the same season, for those tillers in which the panicle emerged, the accumulated value of net leaf elongation increased up to 510 gdd, reaching 180 cm leaf. tiller<sup>-1</sup>. This value remained nearly constant until 580 gdd and then decreased progressively until the end of the regrowth period, reaching only 50 cm leaf. tiller<sup>-1</sup>. The decrease in the net leaf elongation accumulated value for these tillers was steeper than for tillers in which the panicle did not appear.



**Figure 14.** Leaf elongation net accumulation as a function of accumulated growing degree days (C°d) in summer 1, autumn, and summer 2. Closed symbols are for tillers in which the panicle did not emerge during the regrowth, while open symbols are for tillers in which the panicle emerged during the regrowth period. Bars indicate standard deviation.

#### 4.5. Discussion

It was not found a clear correlation between the true stem length and the R/FR ratio for summer 1 and summer 2, as the onset of the true stem elongation occurred 215 and 170 gdd after R/FR reached its minimum value, for summer 1 and summer 2, respectively (Figure 3). However, the onset of true stem elongation occurred with a difference of only 35 gdd between summer 1 and summer 2, indicating that gdd may be a good indicator for the onset of the internode elongation. Probably, there is a primary biological switch rather than R/FR ratio which controls internode elongation, such as the vegetative stage (number of phytomers developed; V-stage). Silva et al. (2019), working with isolated plants (i.e. no light competition) being monitored since the seedling phase to overly mature, found that the true stem elongation in elephantgrass occurred after the appearance of the 13<sup>th</sup> leaf in two growth cycles. Gomide et al. (2007), working with a Mombaça grass sward, found that the true stem elongation occurred after the appearance of 3.5 leaves after clipping. In the present study, the true stem elongation occurred at the appearance of 3.3 and 4.2 leaves, for summer 1 and summer 2, respectively (see accumulated number of leaves appeared at 480 gdd, Figure 11). The considerable differences found between the elephantgrass and the Mombaça experiments, besides working with different species, may be attributed to different conditions of growth and monitoring of the V-stage. In the elephantgrass study with isolated plants, it was considered the real V-stage from the seedling phase onward, while in the studies done in swards periodically clipped, it was considered the appearance of leaves after clipping, not considering the leaves that appeared before the clipping event and its effects on plant development. In fact, the effect of clipping on V-stage is not clear. Moreover, in the elephantgrass study, as opposed to the Mombaça studies, there was no light competition. In this context, it is not possible to state that R/FR does not play a role in internode elongation. Probably, after the primary biological trigger, it is likely that the quality of light plays a major role in the magnitude of the true stem elongation. However, there is not enough data to confirm this hypothesis.

During Autumn, internode elongation occurred concurrently with the observation of the first flowering primordia (Figure 4), corroborating that flowering is the reason of apical meristem raise for this season. The steeper meristem erection of this season when compared to summers 1 and 2, indicates a higher internode elongation and, thus, a higher partitioning of photoassimilates to stem in the reproductive phase than in the vegetative phase. Additionally, differently from both summers, the true stem elongation data were fitted in segmented (constant-linear increase-constant) curve, as it reached the maximum length before the end of the regrowth period. Differently from the vegetative phase, the apical meristems turn into the floral apparatus and emerge above the top layer of the sward for spreading the seeds, and consequently, stop being raised by the internode elongation. The “brown” meristems observed in the present study could not be differentiated into vegetative or reproductive. However, there is a possibility that those meristems were reproductive, as the abortion of reproductive meristems or flowering apparatus during the reproductive phase is common in several species, but not well understood (Kinet, 2018). The lack of resources for full development of all flower apparatus (i.e. from the differentiation of the meristem until the emerging of the panicle) in a plant community is usually considered as one of the major reasons for abortion (Kinet, 2018). In this context, tillers with aborted meristems would be committed to flowering and, thus, presented the characteristics of a reproductive tiller.

The increases in the pseudostem length occurred concurrently with the decreases in R/FR ratio for summers 1 and 2, at the beginning of the regrowth, indicating a possible relation between R/FR ratio and pseudostem elongation (Figure 5). Decreasing R/FR ratio has been shown to increase sheath elongation in different grasses as *Lolium multiflorum*, *Sfiorobolus indicus*, *Paspalum dilatatum* (Casal et al., 1987a), and *Hordeum vulgare* L (Skinner and Nelson,

1993). This response makes sense ecologically as high R/FR ratio may serve as a sign to stop sheath development when leaf laminae are located in lit zones of the sward. However, due to the observational nature of this study, the effects of other variables such as V-stage and accumulated growing degree days could not be separated from the light quality effect.

The increase in pseudostem length at the beginning of the regrowth period was followed by the reaching of a constant maximum value, irrespective of the low values of R/FR ratio registered (Figure 5). In a growing sward, there is a constant need for placing new leaves at successively increasing heights above ground, so the green sward moves upwards. During the vegetative cycles (summers 1 and 2), the increase in pseudostem occurred first, positioning the new leaves in lit zones of the sward. Thereafter, the pseudostem reaches a constant length, but the true stem length increases linearly until the end of the cycles, ensuring the positioning of new leaves at appropriate lit zones of the sward (Figure 6). The onset of the true stem elongation also occurred right after the stabilization of pseudostem length in elephantgrass, as found by Silva (2018). On the other hand, several studies related shortening of pseudostem with internode elongation (true stem elongation) for temperate (Skinner and Nelson, 1995; Maan et al., 1989; Robson, 1973) grasses in the reproductive stage. Differently from what observed for temperate species, the true stem elongation during the vegetative cycles did not shorten the pseudostem in this study. In this context, the positioning of new leaves in lit zones of the sward occurred coordinately in two distinct phases: (i) the elongation of the pseudostem and null elongation of the true stem and, (ii) the stabilization of pseudostem length and true stem linear elongation (Figure 6).

It is worth noting that true stem elongation also plays a role in the effective use of carbohydrates. In tillers of a hypothetical grass sward which internode elongation does not occur, the apical meristem, which is the origin of the development of new leaves, is always positioned in the low strata of the sward and enclosed in progressively lengthier sheath tubes. Thus, for placing leaves at successively higher heights, the tiller has to spend increasing amounts of carbohydrates to overcome the sheath whorl. In this context, rising the meristem seems to be a good strategy to avoid the increasing use of carbohydrates for emerging new leaves, ensuring the perennation of the plant even in the vegetative stage.

In autumn, when the rising of the apical meristem is due to flowering, the pseudostem length decreases progressively after the onset of the true stem elongation (Figure 6), as is observed for temperate grasses (Skinner and Nelson, 1995; Maan et al., 1989; Robson, 1973). In this context, the true stem elongation plays a major role in placing new leaves in progressively higher heights and ensures that the leaves are subjected to high irradiation regimes for making photosynthates to feed the floral apparatus.

Another mechanism of the shade avoidance syndrome is the adjustment of leaf angle to position leaves in optimally lit zones of a sward (de Wit et al., 2012). Many plants reorient their leaves through reversible changes in the volume of cells within a pulvinus, a process referred to as hyponasty (Mullen et al., 2006). Other plants, orient their organs irreversibly away from low R/FR signals, in a process caused by differential growth of cells, referred to as negative phototropic response to far red (Maddonni et al., 2002). Mombaça guineagrass does not show short-term reversible movements of leaves or stems. However, during the three regrowths of this study, it was registered development of leaves with successively lower zenithal angle as well as more erect tillers' main axis (Figures 7 and 8). This response may be attributed to negative phototropic response to far red (low R/FR ratio) as registered for *Lolium multiflorum* tillers (Casal et al., 1990). This response also could not be separated from a possible effect of V-stage or gdd in this study, thus these effects are not discarded. As new leaves develop with a more erectophile position, the average of the zenithal angle of insertion of green leaves slowly decreases, which could explain the lag between the decreases

on the leaves zenithal angle and R/FR ratio. Additionally, the differential growth of stem cells causes the stem, and consequently the sheath tube, to slowly position itself vertically.

At the beginning of regrowth, when there is a considerable area of bare soil, horizontal disposal of leaves and tillers aids in site filling and overcoming of interspecific competition. However, as the sward grows, intraspecific competition increases considerably and the vertical disposal of leaves and tillers turns into an important feature for light competition (van Zanten et al., 2010). Thus, the adaptive and plastic response of *Mombaça* demonstrates its ability to grow and survive in different environmental conditions. Leaves placed in horizontal positions (planophiles) result in constant light extinction coefficients ( $k=1$ , irrespective of solar zenithal angle). Thus, in situations where the solar zenithal angle is higher than  $60^\circ$ , planophile leaves have a higher light interception. However, in crowded swards, leaves placed horizontally difficult light penetration, while in swards with erectophile leaves, not only there is a higher amount of light transmission, but also there is ricocheting of reflected light throughout the sward, which guarantees reuse of the reflected radiation (Gillet, 1984). In this context, erectophile leaves allow for higher leaf area indexes than planophiles leaves, and thus continuous grow in leaf for longer periods. Warren Wilson (1961), studying a virtual sward, confirmed that a leaf placed with  $9^\circ$  zenithal angle yielded more than a leaf placed with  $90^\circ$  zenithal angle (horizontal). It is important to highlight, however, that light extinction is not only dependent upon the leaf zenithal angle but also in the solar zenithal angle, which in turn is dependent upon local, day of the year and horary, resulting in an infinity of combinations for light extinction.

During the development of a new leaf inside the sheath tube, when its tip reaches the top of the sward, the formation of the ligule begins, and the leaf is divided into laminae and sheath, and cell division of leaf laminae stops (Skinner and Nelson, 1994). In this context, the final length of the leaves is proportional to the sheath tube (pseudostem) length as shown in several studies (Wilson and Laidlaw, 1985; Begg and Wright, 1962; Gomide and Gomide, 2000; Robson, 1973). Additionally, several studies found that the internode elongation moves the apical meristem upwards, which shortens the pseudostem (Skinner and Nelson, 1995; Maan et al., 1989; Robson, 1973). Due to the shortening of the pseudostem, the new leaves formed have a shorter final length, and, thus, the lengthiest leaves are located in the intermediary insertion of the tillers' main axis (Gomide, 2000; Maas et., 1987; Maan., 1989). However, during both summers in this study, the pseudostem stabilized after reaching a constant maximum value, and the average of the final length of the last expanded leaf followed a similar pattern (Figure 10).

The average final length of the last expanded leaves is influenced by the length of the leaves expanded and the time taken for their expansion. In this context, analyzing the final length of the last expanded leaf for each tiller individually is also important. The final length of the last expanded leaf on individual tillers during summers 1 and 2 continued to increase slightly until the end of the regrowth period (Figure 9), even with the stabilization of pseudostem length (Figure 10). The final leaf length is a function of the phyllochron, the number of leaves expanding concurrently and the leaf elongation rate (Lemaire and Agnusdei, 2000). Silva (2018), working with isolated elephantgrass, suggested the higher final length of the leaves occurring with constant pseudostem length, may be attributed to a higher number of leaves expanding simultaneously. However, variations among tillers' development also must be considered in the present study, as there was no absolute control of the V-stage of the tillers selected for measuring the pseudostem length.

The onset of stem elongation occurred concurrently with a progressively shortening of the pseudostem during the autumn regrowth cycle. Thus, differently from what observed for the summer seasons, the final length of the leaves decreased concurrently with the decreasing on pseudostem length (Figure 10). The decrease was steeper for those tillers that the panicle emerged, as the apical meristems were raised all the way through the pseudostem until

emerging. The decrease in the final length of the leaves of those tillers in which the panicle did not emerge may be explained by the commitment to flowering by those tillers until a certain point, which may have been interrupted at the abortion of meristems or by the worse growing conditions of this seasons when compared to the summers.

Several studies have shown that longer pseudostems lead to a decrease in leaf appearance rate (Grant et al., 1981; Wilson and Laidlaw, 1985; Skinner and Nelson, 1995; Duru et al., 1999). As leaf elongation occurs inside the whorl of mature sheaths (pseudostem; Skinner and Nelson, 1995), leaves developing in lengthier pseudostems present higher elongation duration, but lower appearance rates. Thus, as the tiller develops, there is a decrease in leaf appearance rate, which is compensated by a longer final leaf length (Duru and Ducroq, 2000). However, when the true stem elongation occurs, the situation is inverted, and the leaf appearance rate increases as a consequence of the shortening of the pseudostem (Warrington and Kanemasu, 1983). In the present study, a similar pattern of inverse proportions between pseudostem length and leaf appearance rate was registered. For summers 1 and 2, at the beginning of the regrowth, the pseudostem length increases rapidly and concurrently with a proportional decrease in leaf appearance rate (Figure 13). The following stabilization of pseudostem length is also accompanied by a decelerated decrease in leaf appearance rate. However, differently from what registered in other studies (Warrington and Kanemasu, 1983), as the true stem elongation did not shorten the pseudostem during the summers in the present study, the leaf appearance rate remained low until the end of the regrowth period of these seasons.

During autumn, on the other hand, the flowering stimulus accelerated the leaf appearance rate in those tillers in which the panicle appeared, as a consequence of the true stem elongation. In this context, the dynamics of leaf appearance rate is different when comparing reproductive and vegetative tillers in warm-season grasses. The leaf appearance rate during autumn of those tillers in which the panicle did not emerge was higher when compared with both summers 1 and 2, despite following a similar pattern (Figure 12). The hypothesis that some of the tillers were committed to flowering until a certain point, but they were not able to emerge the panicle is also valid for this variable (Figure 4).

The leaf net accumulation is the result of the development of new leaves and the senescence of older leaves (Cruz and Boval, 2000). When analyzing long cycles like the ones of the present study, it is expected that, from a certain point, the new leaves appearing are smaller than the older leaves senescing and, therefore, the net accumulation rate on the tiller level becomes negative (Cruz and Boval, 2000). However, this pattern only occurred during autumn (Figure 14), when the successive leaves became smaller than the precedent ones, decreasing the net leaf accumulation mainly for those tiller in which the panicle emerged during the regrowth period. During the summers 1 and 2, on the other hand, the net accumulation rate was never negative, reaching nearly 0 for summer 1 (see the part where net accumulation approximates to a plateau, from 500 gdd to the end of regrowth, Figure 14) or being always positive in case of summer 2.

Several attributes during the vegetative cycles allowed for a continuous net accumulation of leaf during the whole regrowth cycles. The elongation of the true stem allowed for positioning of new leaves at increasingly higher heights of the plant community, without spending increasingly amounts of photosynthates with increasingly higher sheaths (pseudostems), which certainly would not be sustainable from some point onward. Additionally, as the pseudostem did not shorten after the true stem elongation, the new leaves continued to expand with high lengths, as opposed to what is observed during the reproductive stage of temperate grasses (e.g. ryegrass) and warm-season grasses (e.g. maize). Thus, during the vegetative cycle, the partitioning of photosynthates to true stem elongation occurs concurrently with a considerable amount destined to leaves. It appears that, for vegetative tillers, differently from what occurs for the reproductive ones, the ecological significance of true stem elongation is to ensure the continued increase

in leaf area with appropriate positioning in the sward. Moreover, the plastic response of leaf insertion also contributes to the positioning of tillers' new leaves at lit zones with lower self-shading, which also aids on a high net accumulation of leaf tissue.

#### 4.6. Conclusions

-True stem elongation during vegetative cycles is primarily triggered by another biological switch rather than R/FR ratio, however, a secondary influence of R/FR ratio is not discarded. The accumulated growing degree days explained satisfactorily the onset of true stem elongation during the vegetative stage, occurring with a difference of 35 Cd° between the summers 1 and 2. Further studies are needed to confirm the use of gdd as a good indicator of true stem elongation in a diverse range of conditions. Additionally, further investigations relating the V-stage with accumulated growing degree days and the clipping effect on the tillers are also desired. During the reproductive cycles, the elongation of the true stem is explained by the flowering stimulus, and the true stem elongation occurs more rapidly than during the vegetative cycles, indicating a higher use of photosynthates by the stem in the reproductive tillers.

-The effect of R/FR ratio on pseudostem elongation, could not be separated from the V-stage effect in this study. During the vegetative cycles, the pseudostem elongation occurred at the beginning of the regrowth, and, when it stabilized at a maximum value, there was a linear increase in true stem length. This coordination ensures the positioning of new leaves at lit zones of the sward. During the reproductive cycle, on the other hand, the true stem elongation shortened the pseudostem, and the true stem elongation ensured the positioning of new leaves in lit zones of the sward solely.

-As for pseudostem elongation, the effect of the R/FR ratio could not be separated from the effect of the V-stage for leaf insertion and tiller's main axis zenithal angle. The angles decreased with the diminishment of R/FR ratio and with the increase in growing degree days concurrently. The plasticity of angle insertion of leaves and tillers' main axis allows for a better site filling in the beginning of the regrowth (horizontal leaves) and better utilization of incoming energy in dense swards (erectophile leaves).

-True stem elongation has different effects on the vegetative and reproductive tillers. For the vegetative tillers, the true stem elongation does not shorten the pseudostem nor the new leaves final length and does not increase the leaf appearance rate. For the reproductive tillers, the true stem elongation shortens the pseudostem and the new leaves final length, but increases the leaf appearance rate, until the panicle finally emerges into the top of the sward. The growth dynamic of vegetative tillers of *Mombaça guineagrass* (i.e. stem x leaf elongation) is different from what is registered in the literature for temperate and warm grasses during the reproductive cycles. This dynamic allied with the plasticity of leaf insertion angle allows for a high leaf net accumulation of vegetative tillers in long regrowth cycles, even after the onset of the true stem elongation. Comprehending tillers' growth and dynamic aids on the understanding and modeling of growth and biomass partitioning of the *Guineagrass*' plant community.

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## 5. PARAMETERIZING AND EVALUATING THE CROPGRO PERENNIAL FORAGE MODEL FOR SIMULATING GROWTH AND BIOMASS PARTITIONING OF PANICUM MAXIMUM CULTIVARS TANZÂNIA AND MOMBAÇA

### Abstract

Mechanistic simulation models can be powerful tools to assist in decision making for pasture-based livestock systems. The objective of this research was to improve and evaluate the ability of the Cropping System Model-CROPGRO-Perennial Forage model (CSM-CROPGRO-PFM) to simulate growth and biomass partitioning of two guineagrass (*Panicum maximum* Jacq. Syn. *Megathyrsus maximus* (Jacq.) BK Simon & SWL Jacobs) cultivars, Tanzânia and Mombaça. Data from two experiments with contrasting harvest management and field conditions were used. Parameterization was done manually, targeting improvement in d-statistic and root mean square error (RMSE) averaged over both cultivars for aboveground biomass accumulation, leaf biomass, stem biomass, leaf area index (LAI), and leaf proportion on aboveground biomass. The major improvement in model performance was achieved by modifying the vegetative partitioning parameters between leaf and stem (increasing partitioning to leaf during early regrowth while increasing to stem during late regrowth). Productivity during cool, short daylength months was decreased by making photosynthesis and leaf area expansion more sensitive to lower temperatures and increasing the partitioning to storage organs during short days. Productivity under warm-season conditions was increased by decreasing leaf and stem senescence and reducing the nitrogen stress effect on leaf area expansion. The overall d-statistic averaged over the two cultivars increased from 0.86 to 0.93 and the RMSE values averaged over the two cultivars decreased from 2261 to 1768 kg ha<sup>-1</sup> for aboveground biomass, from 1620 to 874 kg ha<sup>-1</sup> for stem biomass, from 11.41 to 7.27% for leaf percentage, from 1.91 to 1.68 for LAI, but increased slightly from 1114 to 1172 kg ha<sup>-1</sup> for leaf biomass. The improved model performance for both short and long harvest cycles will facilitate further use for evaluating various management strategies for these grasses.

**Keywords:** DSSAT system; Grassland; Warm-season grasses; Tropical grasses; Photosynthate partitioning

### 5.1. Introduction

*Panicum maximum* (Jacq.) (syn. *Megathyrsus maximus* (Jacq.) BK Simon & SWL Jacobs) is a forage grass native to Africa and widely naturalized in the tropics. In Brazil, the species is commonly known as guineagrass and is the second most cultivated forage grass, with growing importance in intensively managed pasture-based systems. It is recommended for regions where annual rainfall ranges from 800 to 1800 mm and the soils are well-drained with a medium to high soil fertility (Muir and Jank, 2004). Tanzânia and Mombaça are the most planted guineagrass cultivars in Brazil, and both are tropical tall, bunch-type grasses used mainly for grazing. Yields during the genetic selection and breeding program of guineagrass have been largely improved and reported as 33 and 41 Mg DM ha<sup>-1</sup> year<sup>-1</sup> for Tanzânia and Mombaça, respectively (Jank et al., 1994).

Forage growth and biomass partitioning are two major processes on determining productivity in pasture-based livestock systems, as these factors are related to the quality of forage offered to animals and plant regrowth after grazing. Thus, understanding these dynamic processes is essential for the success of pasture-based livestock systems under different grazing strategies and pasture management. Mechanistic crop simulation models aid in the understanding of the interaction between plant genetics, environment, and pasture management (Araujo et al., 2013, Pedreira et al., 2011) and can be powerful tools to assist decision-makers and for ensuring high productivity.

The CROPGRO model was developed in the early 1990s (Boote et al., 1998), and is part of the Decision Support System for Agrotechnology Transfer (DSSAT; [www.DSSAT.net](http://www.DSSAT.net)) crop modeling ecosystem (Hoogenboom et al., 2019a, 2019b), which is capable of running and integrating many models (Jones et al., 2003). The Cropping System Model (CSM) integrates species physiological traits, weather, crop C balance, soil and plant water balance, soil and plant nitrogen balance, soil organic C balance, and damage caused by pests and diseases, which allows for the simulation of yield based on weather and soil conditions and management practices (Boote et al., 1998; Jones et al., 2003). The crop models in DSSAT may be used for understanding physiological processes, assisting breeding programs and evaluating management strategies (Tsuji et al., 1998). In addition, the model follows a modular approach, which allows introducing a new crop by modifying values in a “read-in” species crop template file without changing any computer source code (Boote et al., 1998; Jones et al., 2003; Hoogenboom et al., 2019b).

CROPGRO was initially developed for annual grain crops, and was adapted and parameterized for forage grasses including bahiagrass (*Paspalum notatum* Flugge) (Kelly, 1995) and brachiariagrass (*Brachiaria spp*) (Giraldo et al., 2001). However, that version of the CROPGRO model worked only with an “annual” approach, which consistently over-predicted dry matter yield for cooler months, in part because it required a minimum residual LAI to prevent failure and because code limitations did not allow for winter dormancy or regrowth after 100% foliage harvest or freeze-kill (Rymph, 2004). The model was improved for simulations of perennial grasses by adding a new storage organ, which aided on pasture regrowth, leading to the development of the CROPGRO-Perennial Forage Model (PFM) (Rymph, 2004). The CROPGRO-PFM has been used for simulating warm-season grass yield with success and has been calibrated for major tropical forage grasses including palisadegrass (*Brachiaria brizantha* syn. *Urochloa brizantha* cv. Xaraés) (Pedreira et al., 2011), guineagrass cv. Tanzânia (Lara et al., 2012), palisadegrass cv. Marandu (Pequeno et al., 2014), brachiariagrass hybrid cv. Mulato II (Pequeno, 2014), and palisadegrass cv. Piatã (Bosi et al., 2020). Despite the unquestionable relevance of these studies, the data used were mostly from “short” regrowth cycles (about 28 days during summer/spring and a maximum of 63 days during winter/autumn), which did not allow for an accurate parameterization of biomass partitioning and growth during very early all the way to very late stages of the grass regrowth cycles. Improving the biomass partitioning simulation accuracy would be an important aspect of model improvement when dealing with different grazing strategies (i.e. with herbage removal at different severities and frequencies), mainly for tall, bunch-type grasses – such as *Panicum maximum* – which tend to accumulate stems late in the regrowth cycle.

Although the previous version was calibrated for *P. maximum* cv. Tanzânia by Lara et al. (2012), the species parameterizations were never released in an official version of DSSAT and, since that time, several improvements have been made in the CROPGRO-PFM, including N effects on leaf area expansion and new options for initializing the soil carbon pools. Therefore, the objective of this research was to improve and evaluate the ability of the CROPGRO-PFM to simulate the growth and biomass partitioning of the *Panicum maximum* cultivars Tanzânia and Mombaça using a single common species file for parameterization of both cultivars, and to be included in the next DSSAT software version.

## 5.2. Materials and Methods

### 5.2.1. Field experiment data

Two field experiments (a separate site experiment for each cultivar) were used for model adaptation. The experiments differed in harvesting management (cycle duration), sampling frequency, seasons evaluated, and N status, bringing complementing datasets. The Tanzânia cultivar experiment was conducted at the University of São Paulo “Luiz de Queiroz” College of Agriculture (USP-ESALQ), in Piracicaba, state of São Paulo, Brazil (22°42'S, 47°30'W, 546m elevation). The Tanzânia guineagrass plots were periodically clipped from December 2002 to April 2004. From December 2002 through March 2003 and from November 2003 through April 2004 it was clipped at 35-d intervals, while during the cooler months (from April to October 2003) it was cut at 63-d intervals. The plots measured 10 by 4 m, with four replications, and established on a highly fertile Kandiualfic Eutrudox. Plots were fertilized immediately after each harvest with approximately 250 kg N ha<sup>-1</sup> yr<sup>-1</sup> and 210 kg K<sub>2</sub>O ha<sup>-1</sup> yr<sup>-1</sup> applied as (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> and KCL, respectively. To avoid water stress, sprinkler irrigation was supplied whenever the soil water potential reached -30 kPa. Weather data (daily solar radiation, maximum and minimum temperature and rainfall) were collected at a station located 2 km from the experimental site and entered into the model's weather file.

To quantify forage accumulation, forage mass above 35-cm stubble height was clipped at the end of each regrowth period within three 0.5- by 2 m quadrats. Additionally, the aboveground stubble mass below the stubble height was determined three times during the year (first spring-summer cycle, autumn-winter cycle and second spring-summer cycle) to characterize the stubble and facilitate the modeling. On these three occasions, the forage mass collected both above and below stubble height was hand-separated into live leaf and stem, and dead material fractions (but for modeling purposes, only the living leaf and stem were considered as stubble). The LAI was determined weekly using a model LAI 2000 plant canopy analyzer (Li-Cor, Lincoln, Nebraska, USA) (Welles and Norman, 1991). For more details about the field sampling the reader is referred to Moreno et al. (2014).

The data on Mombaça guineagrass were collected in a field experiment carried out from December 2017 to January 2019 at Embrapa Southeast Livestock, in São Carlos, state of São Paulo, Brazil (21°57'42"S, 47°50'28"W, 860 m elevation). The experiment consisted of an irrigated field sampled weekly in three long evaluating cycles (hereafter referred to as “evaluating cycles”) from December 2017 to February 2018, February 2018 to June 2018, and November 2018 to January 2019, totaling 10, 14, and 12 weeks for the first, second, and third evaluating cycles, respectively. The plots were not harvested during the cycle, although cumulative biomass samples were collected weekly. At the end of each evaluating cycle the entire plot was clipped to 30-cm height. Between the second and third evaluating cycles, clipping to 30-cm height was also done every 30-60 days (without any measurements), depending on the pasture growth rate. Mombaça guineagrass was sown on 09/28/2017 on a Typic Hapludox soil and clipped twice for pasture establishment and, thereafter, the evaluating cycles started on 12/18/2017. The plot area was 12.5 by 23 m. During the experiment a total of 370 kg N ha<sup>-1</sup> was applied, split over time as three applications of 80 kg N ha<sup>-1</sup> as ammonium nitrate, one application of 80 kg N ha<sup>-1</sup> as urea, and one application of 50 kg N ha<sup>-1</sup> as calcium nitrate. In addition, plots were fertilized with 200 kg ha<sup>-1</sup> of phosphorous split into five applications of 40 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> applied as single super phosphate and 160 kg ha<sup>-1</sup> of potassium split into four applications of 40 kg K<sub>2</sub>O ha<sup>-1</sup> applied as potassium chloride. Sprinkler irrigation (4-8 mm) was supplied based on the readily available water concept, assuming that readily available water amounts to 30% of the total of 60 mm soil water holding capacity (SWHC). Whenever the soil water content came close to depleting the readily available water (70% of the SWHC left), irrigation was supplied.

Weather data (daily solar radiation, maximum and minimum temperature and rainfall) were collected at a weather station located 1 km from the experimental site area and entered into the model's weather file.

To quantify forage accumulation during regrowth, forage mass was sampled weekly by clipping the biomass above and below the 30-cm stubble within two 0.5- by 1.0 meter quadrats. The forage mass harvested above and below stubble height was subsampled and then hand separated into living leaf, living stem and dead material fractions. Whenever a leaf had 50% or more of its tissue senesced (visual assessment), it was considered as dead material. Subsequently, the living leaf subsample fraction was scanned on a model LI-3100 leaf area meter (Li-Cor, Lincoln, Nebraska, USA). Additionally, the growth stage (i.e. vegetative or reproductive) of ten to twenty tillers was recorded weekly by cutting tillers longitudinally and visually observing the presence or absence of floral buds in the apical meristems. The observation was done with the aid of a Coleman XTB Stereoscope Microscope.

### 5.2.2. Approach for model adaptation and model inputs

For parameterization, model simulation outputs were compared to the observed data of the field experiments. The simulated output variables were aboveground live biomass accumulation, leaf biomass, stem biomass, leaf area index, specific leaf area, and % leaf of aboveground live biomass. The parameter setting was done manually, considering the statistical improvement over both cultivars concurrently, aiming for an improved version with good performance for both cultivars. Statistics were computed and averaged over the two cultivars to determine whether to retain a given calibration set of parameters or not. The statistical tools used were the root mean square error (RMSE) and the Willmott agreement index (*d-statistic*) (Willmott et al., 1985). We attempted to follow a general logical sequence; nevertheless parameter modification was somewhat iterative in the pathway of model improvement.

The DSSAT-PFM version 4.7 was used for this study (Hoogenboom et al., 2019b). The genetic coefficients from Lara et al. (2012) for guineagrass (parameterized using data from the same Tanzânia trial) were used as a starting point to define the species, ecotype, and cultivar for this study. The original Tanzânia species parameter file was updated with addition of two parameters (N effect on specific leaf area and reallocation of photosynthates from shoot to root due to N stress), new to the latest DSSAT V4.7 version that were not in the version used by Lara et al. (2012).

### 5.2.3. Tanzânia guineagrass experiment inputs

Initial simulations based on the Lara et al. (2012) parameterization resulted in over-prediction of nitrogen stress due to differences in the way DSSAT versions V4.0 (used by Lara et al., 2012) and the present V 4.7 deal with soil organic carbon pools. The CENTURY model requires three soil organic matter (SOM) fractions to describe organic matter in the soil: the active (microbial) soil organic matter existing in both the surface mulch layer and in the soil (SOM1), the intermediate soil organic matter (SOM2), and the passive or stable soil organic matter (SOM3) (Gijsman et al., 2002). In DSSAT V4.7 version, those SOM fractions are specified in the soil analysis section of the File X, in which the variable SASC is the stable organic carbon "SOM3", the fraction with the slowest mineralization rate. However, these were missing in File X taken from Lara et al. (2012), and thus model "default" values were used resulting in over prediction of N stress. In the DSSAT V4.0 used by Lara et al. (2012), the fractions were set in an external read-in SOM file, which is no longer used. Therefore, the SOM3 previously estimated by Lara et al. (2012) of 0.57 of total soil organic carbon for each layer was inserted into the SASC column of soil analysis section (Table 1). In effect, we made no change in SOM3 setting from Lara et al. (2012) (as there was just a different way to read in the value). Correct entry of SASC addressed the over prediction of nitrogen stress. Initial conditions were taken from Lara

et al. (2012): ammonium and nitrate was assumed to be 0.1 and 0.8 g N kg soil<sup>-1</sup> (Table 1), the residue of the previous crop was assumed as 2000 kg DM ha<sup>-1</sup> with 1% of nitrogen, incorporated to 20-cm depth by tillage. The MOW input file is specific to the PFM and defines the harvest conditions for regrowth: (i) dates of harvests, (ii) the amount of living stubble left after harvest (MOW), (iii) the percentage of live leaves in the stubble (RSPLF), and a “re-staged” leaf number (MVS) used to define the vegetative stage (V-stage) for regrowth after harvest. The MOW file was set with the same values as those of Lara et al. (2012), based on field data.

The CENTURY model (Gijsman et al., 2012) is used for all CROPGRO-PFM simulations as it simulates better the decomposition of plant tissue that falls to the soil surface as well as sloughed roots within the soil, as occurs for perennial forage species. The actual management, soil, and weather (entered daily in the model and collected at the field weather station) were used for running the model.

#### **5.2.4. Mombaça guineagrass experiment inputs**

The stable organic carbon fraction (SOM3) was assumed as 0.6 of total soil organic carbon (SOC) for each layer (Table 1) similar to that of Pequeno et al. (2014), which SOC was measured to 1 m depth. The residue of the previous crop was assumed as 4000 kg DM ha<sup>-1</sup> of shoot and 4000 kg DM ha<sup>-1</sup> of roots, both with 1% nitrogen, incorporated to 20-cm depth by tillage. The assumed values of stable organic carbon and residue of the previous crop were those of Pequeno et al. (2014), as the experiment was conducted in a tropical environment that had pasture as previous crop. Ammonium and nitrate in the soil for initial conditions section were measured next to the experimental site (Table 1). The MOW file was set with observed data whenever it was available (the beginning and the end of each evaluating cycle). The clipping, which occurred at the end of the second evaluating cycle, resulted in stubble with 3% of leaf. When the model was run with this low percent leaf, the crop died between the second and third evaluating cycles (when data was not collected) as a result of lack of assimilate for maintenance and growth immediately after the clipping. For regrowth after harvest, the model relies on small residual LAI along with mobilized carbohydrates from the storage pool, stem, and root tissues. Apparently, the simulated mobile carbohydrates were not enough to ensure plant regrowth during this period. In this context, RSPLF, initially set as 3%, was increased to 6% for the clipping event at the end of the second evaluating cycle. This additional LAI allowed the plants to regrow and recover sufficiently to grow through the winter and the subsequent regrowths.

The CENTURY model (Gijsman et al., 2012) was used for the same reasons as for Tanzânia simulations. The actual management, soil, and weather (entered daily in the model and collected on the field weather station) were used for running the model.

**Table 1.** Total and stable organic carbon, ammonium and nitrate, and properties of soil-water relations used in the soil analysis and initial conditions sections of File X for the sites where cultivars Tanzânia and Mombaça were grown.

Soil analysis			Initial conditions		Properties of soil-water relations		
Tanzânia							
Layer	Soil organic carbon	C (SOM3)	SNH <sub>4</sub> <sup>+</sup>	SNO <sub>3</sub> <sup>-</sup>	LL	DUL	SSAT
cm	%		g N Mg soil <sup>-1</sup>		cm <sup>3</sup> H <sub>2</sub> O cm <sup>-3</sup> soil		
5	1.74	0.99	0.1	0.8	0.242	0.366	0.48
15	1.74	0.99	0.1	0.8	0.242	0.366	0.48
25	1.1	0.63	0.1	0.8	0.242	0.366	0.48
40	0.7	0.4	0.1	0.8	0.242	0.366	0.48
55	0.4	0.23	0.1	0.8	0.24	0.34	0.48
75	0.4	0.23	0.1	0.8	0.24	0.34	0.49
85	0.36	0.21	0.1	0.8	0.24	0.34	0.49
200	0.36	0.21	0.1	0.8	0.25	0.35	0.49
450	0.1	0.06	0.1	0.8	0.25	0.35	0.49
Mombaça							
10	2.82	1.692	63.6	63.6	0.269	0.423	0.497
20	2.82	1.692	32.5	45.4	0.269	0.423	0.497
40	2.04	1.224	52	72.4	0.279	0.405	0.469
60	1.59	0.954	56.6	75.6	0.268	0.382	0.454
80	1.45	0.87	47.8	79.7	0.269	0.378	0.448
100	1.09	0.654	54.3	77.7	0.257	0.36	0.436
200	0.36	0.216	1	1	0.257	0.36	0.436
450	0.36	0.216	1	1	0.257	0.36	0.436

LL, DUL and SSAT are the lower limit of plant extractable soil moisture, drained upper limit and saturated soil water content, respectively

### 5.2.5. Statistical analysis for model parameterization and evaluation

The statistical tools used were the root mean square error (RMSE) and the Willmott agreement index (*d*-*statistic*) (Willmott et al., 1985).

The equation for RMSE is:

$$RMSE = \sqrt{\frac{1}{N} \sum_{i=1}^N (Y_i - \hat{Y}_i)^2} \quad [1]$$

Where N is the number of observed data points for comparison,  $Y_i$  is a given observed value and  $\hat{Y}_i$  is the corresponding value predicted by the model. The RMSE is low when the model gives a good prediction. The equation for Willmott agreement *d*-statistics is:

$$d = \frac{\sum_{i=1}^N (Y_i - \hat{Y}_i)^2}{\sum_{i=1}^N (|Y_i - \bar{Y}| + |\hat{Y}_i - \bar{Y}|)^2} \quad [2]$$

Where  $N$  is the number of observed data points for comparison,  $Y_i$  is a given observed value,  $\hat{Y}_i$  is the corresponding value predicted by the model, and  $\bar{Y}$  is the mean of observed data. The  $d$ -statistic ranges from 0 to 1, and values near 1 indicate good model prediction near to observed values while values near 0 indicate model prediction far from the observed values.

Specific leaf area (SLA) was not considered in either statistic because SLA of Mombaça showed unusual patterns of thin leaves early in cycles with subsequent thickening, whereas that did not show up with Tanzânia data (there are questions of whether code change is needed to improve SLA simulations for the Mombaça case). However, simulation outputs of this variable were compared to observed data to try to maintain a good proportion between leaf biomass and LAI.

### 5.3. Results

The two sites had different conditions and attributes that were beneficial to parameterization of different aspects of *Panicum maximum* growth. The Tanzânia dataset had data for the entire calendar year, resulting in the need for evaluation of cooler conditions with short daylength months, as well as evaluating nitrogen stress, aspects that not present on the Mombaça data set. On the other hand, the Mombaça data set had long growth cycles with weekly sampling that allowed the evaluation of partitioning to leaf and stem during later maturation phases that approached stem elongation/reproductive onset.

First, we present simulation outcomes of the parameterization with the final parameterized version compared to simulations with the original parameter values. It is important to recognize that our goal was to use a single common parameterization to simulate both cultivars, and not to distinguish among cultivars. Then we show the relative importance of the main steps (and parameter settings) of model improvement by presenting step-by-step improvements in  $d$ -statistic and RMSE throughout parameterization.

The overall  $d$ -statistic of model performance improved from 0.86 to 0.93 going from the original to final parameterization. The RMSE values were reduced from 2261 to 1768 kg ha<sup>-1</sup> for aboveground live biomass, and from 1620 to 874 kg ha<sup>-1</sup> for stem biomass, but slightly increased from 1114 to 1172 kg ha<sup>-1</sup> for leaf biomass. The RMSE values were reduced from 11.41 to 7.27% for percent leaf and from 1.91 to 1.68 for LAI. The small RMSE increase for leaf biomass was considered a minor effect when compared with the much larger RMSE decreases for aboveground live biomass, stem biomass, percent leaf and LAI.

#### 5.3.1. Parameterization and model improvement

The original and final values of each modified parameter are presented along with indication of major parameters and steps modified (Table 2). Some parameters were changed more than once (iteration, more than one step) until being set as the final value, but intermediate values are not given. In total, there were 34 steps until the final parameterized version.

Water balance simulated by DSSAT did not show any moisture stress for either cultivar (data not shown) when irrigation and rain data were input in the model, so no parameters related to water stress were modified.

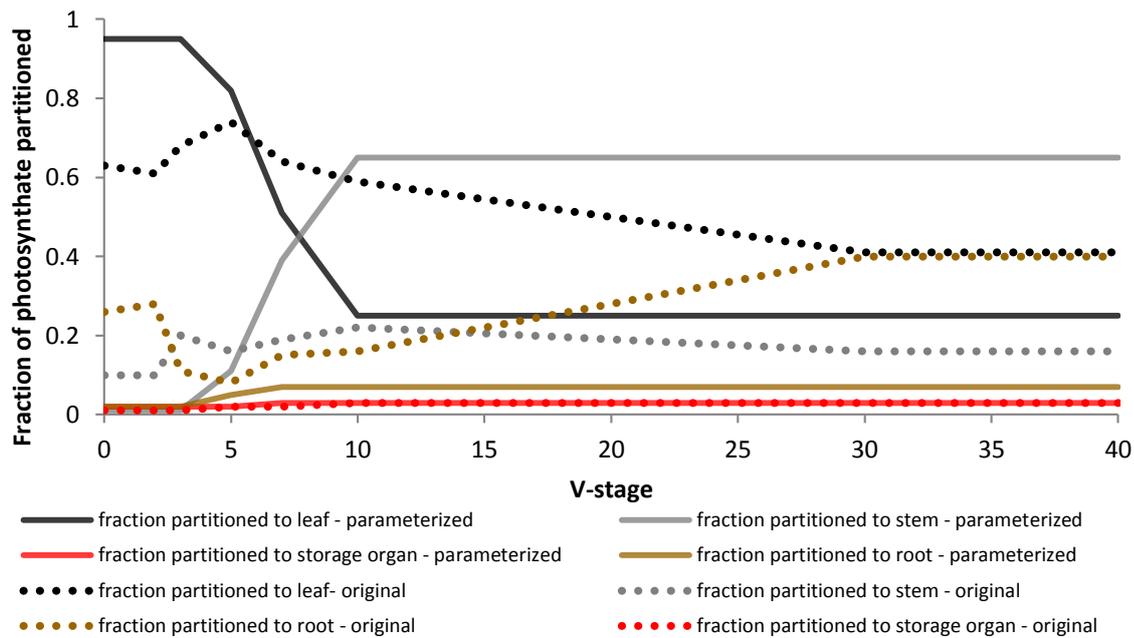
**Table 2.** Initial and final values of important parameters modified in SPE, ECO, and CUL files of *Panicum maximum* for simulation of Tanzânia and Mombaça cultivars and steps at which the parameters were modified throughout parameterization.

parameter (and step)	description ( and parameter's file)	initial value	final value
<b>Effects on specific leaf area</b>			
SLAVR (4, 29)	specific leaf area of cultivar under standard growth conditions, cm <sup>2</sup> g <sup>-1</sup> (CUL)	175	180
SLAREF (2, 29)	Specific leaf area of standard cultivar, cm <sup>2</sup> g <sup>-1</sup> (SPE)	166	180
SLAMIN (3, 29)	The thickest leaves under high light, cm <sup>2</sup> g <sup>-1</sup> (SPE)	137	180
SLAMAX (28, 29)	The thinnest leaves under low light, cm <sup>2</sup> g <sup>-1</sup> (SPE)	356	320
XSLATM (5, 25)	Relative effect of temperature on specific leaf area of newly formed leaves, C (X vs. Y pair) (SPE)	11.8 26.6	12.7 26.6
YSLATM (6)	Relative effect of temperature on specific leaf area of newly formed leaves, fraction reduction (X vs. Y pair) (SPE)	0.39 1.00	0.30 1.00
NSLA (28)	N effect on specific leaf area (SPE)	1.00	0.75
<b>Partitioning during perennial phase (established pasture phase)</b>			
XLFEEST (not changed)	Leaf number or vegetative stage at which the partitioning is defined (SPE)	0.0 2.0 3.0 5.0 7.0 10.0 30.0 40.0	0.0 2.0 3.0 5.0 7.0 10.0 30.0 40.0
YLFEST (7, 15, 19)	Dry matter partitioning to leaf as a function of V-stage, fraction (SPE)	0.63 0.61 0.68 0.74 0.64 0.59 0.41 0.41	0.95 0.95 0.95 0.82 0.51 0.25 0.25 0.25
YSTEST (7, 15, 19)	Dry matter partitioning to stem as a function of V-stage, fraction (SPE)	0.10 0.10 0.20 0.16 0.19 0.22 0.16 0.16	0.01 0.01 0.01 0.11 0.39 0.65 0.65 0.65
YSREST (7, 15, 19)	Dry matter partitioning to storage as a function of V-stage, fraction (SPE)	0.01 0.01 0.01 0.02 0.02 0.03 0.03 0.03	0.02 0.02 0.02 0.02 0.03 0.03 0.03 0.03
SDLEST (22)	Photothermal days from sowing to established pasture, C (SPE)	Coded as 60	30
NSTFAC (30)	Reallocation of photosynthates from shoot to root due to N stress (0-1) (SPE)	0.7	0.8
<b>Senescence/Abscission</b>			
ICMP (9)	Light compensation point (mol PPFD m <sup>-2</sup> d <sup>-1</sup> ) for abscission of lower leaves	1.17	0.8

	due to excessive self-shading by crop canopy (SPE)		
TCMP (10)	Time constant (days) for abscission of lower leaves due to excessive self-shading by crop canopy (SPE)	13.1	20
LFSEN (8, 14)	Natural leaf abscission rate/photothermal day (0.015 means 66.67 d of life span) (SPE)	0.02	0.015
PORPT (11, 13)	Stem abscission as a function of the abscised leaf mass (gram stem per gram leaf abscised) (SPE)	0.27	0.15
<b>Photosynthesis</b>			
LFMAX (12, 33)	Maximum photosynthetic rate at 30 C, 350 $\mu\text{L L}^{-1} \text{CO}_2$ , and saturating light, mg $\text{CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (CUL)	1.91	1.91 (changed in step 12 but reverted to original in step 33)
XLMAX (17, 20, 27)	Relative rate of photosynthetic electron transport in response to temperature; linear shape, first values defines base (0.0) and second value defines maximum (1.0), C (SPE)	8.7 33.4	8.0 40.0
FNPGL (21, 23, 34)	Relative effect of minimum night temperature on next day's leaf light-saturated photosynthesis rate; quadratic shape, first value defines base (0.0) and second defines maximum (1.0), C (SPE)	5.9 17.4	7.8 18.0
<b>Dormancy/Partition to Storage</b>			
FNPTD (16, 24, 31)	Daylength effect on partitioning to storage (and away from shoot), first value defines maximum to storage, second is minimum to storage, h (SPE)	9.1 13.5	10.8 13.7
RDRMT (26, 32)	Relative partitioning/dormancy sensitivity, daylength effect on partitioning (ECO)	0.299	0.350
<b>MOW file</b>			
MOW inputs, Mombaça (not parameters; 18)	DATE (D) is the harvest date in day of year; MOW (MW) is kg/ha dry matter of living leaf and stem in the stubble; RSPLF (R) is the % of leaf in living stubble; MVS (M) is the number of main axis nodes left after harvest (MOW)	D MW R M D MW R M	
		17327 2757 06 3	17327 2230 08 3
		17352 2757 06 3	17352 2230 08 3
		18058 2136 04 3	18058 1237 07 3

### 5.3.1.1. Parameters affecting partitioning and changes in the MOW input file

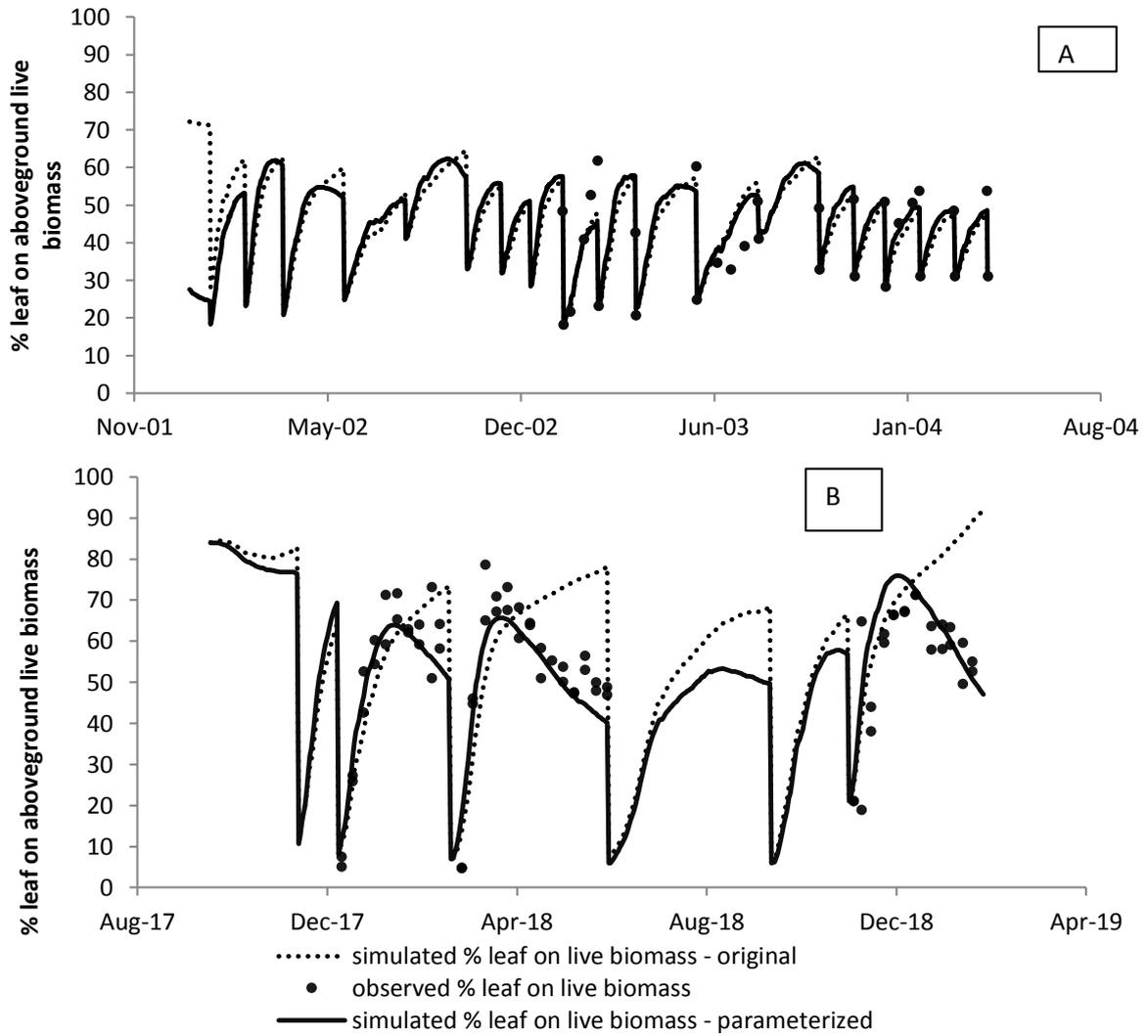
The partitioning function in the model describes instantaneous fractional allocation of today's assimilate to leaf, stem, root, and storage as a function of V-stage (node number on the main axis). Parameters were modified to increase photosynthate partitioning to leaf early in the cycle and shifting to stem late in the cycle. XLFFEST defines the V-stage at which partitioning to each organ is defined, while YLFEST, YSTEST and YSREST describe the fraction of photosynthate partitioned to leaf, stem and storage organ at a given V-stage (Table 2). The amount of photosynthate partitioned to roots is calculated by difference (i.e. the percentage of photosynthate to root is the remainder of the total after subtracting the sum of fractions partitioned to leaf, stem and storage organ; Figure 1).



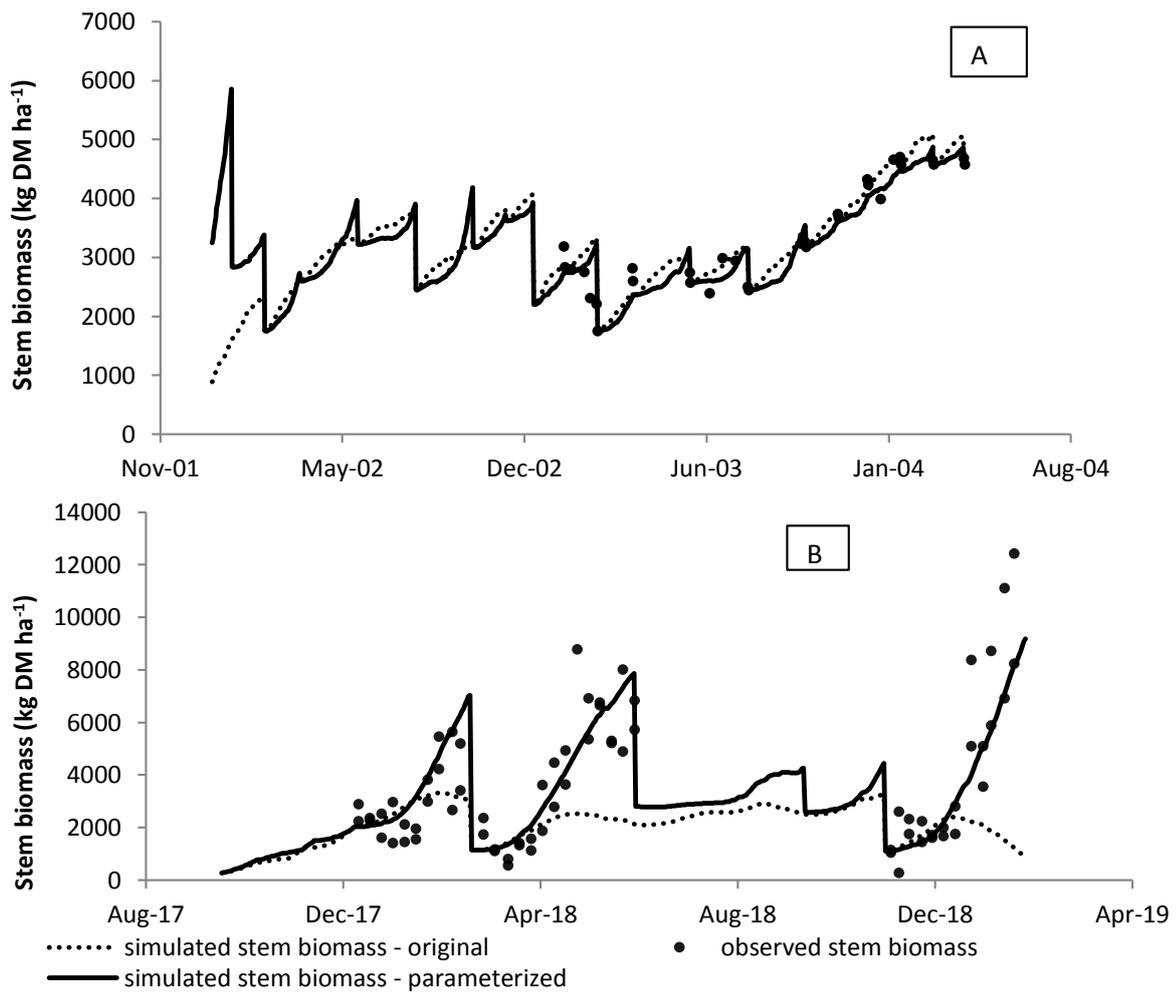
**Figure 1.** Original (dashed) and parameterized (solid) fraction of photosynthate partitioned to leaf, stem, roots and storage organ as a function of vegetative stage (V-stage) during the established perennial phase for *Panicum maximum*, set in the species file.

Changing the partitioning in the species file (Table 2 and Figure 1) allowed for a much better simulation of percent leaf for Mombaça and maintained an already good prediction for Tanzânia (Figure 2). The parameterized simulation also showed a much better fit of stem mass accumulation by the end of three cycles for Mombaça (Figure 3b). Additionally, stem accumulation in late phases of regrowth also contributed to a good simulation of aboveground live biomass accumulation in the later regrowth cycles (Figure 4).

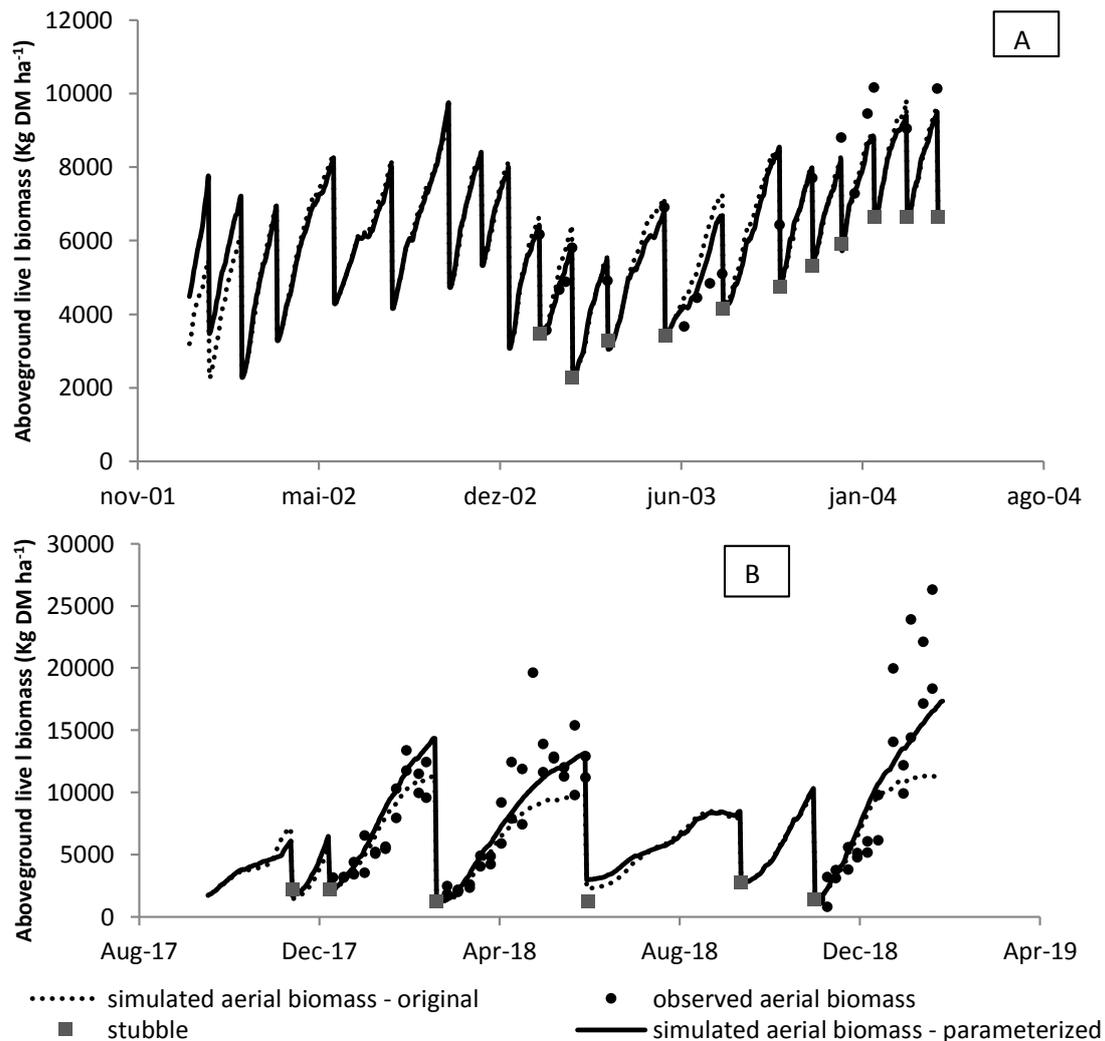
The total amount of stem left after harvest for the Mombaça experiment was reduced to the values measured at ~15 d after cutting, for the first two evaluating cycles (Table 2). This was done to account for stems that seemed to be alive right after cutting, but senesced after about 15 days. These changes were made to the MOW file (Table 2) and reduced the total amount of live biomass left after harvest (MOW) and, consequently, increased the percentage of leaf left in the stubble (RSLPF). Beginning with an appropriate amount of stem as compared to an overestimated value resulted in a better fit over the entire regrowth cycle (Figure 3b).



**Figure 2.** Original and parameterized simulated % leaf of aboveground live biomass as a function of date for (A) Tanzânia in Piracicaba, SP, Brazil and (B) Mombaça in São Carlos, SP, Brazil.

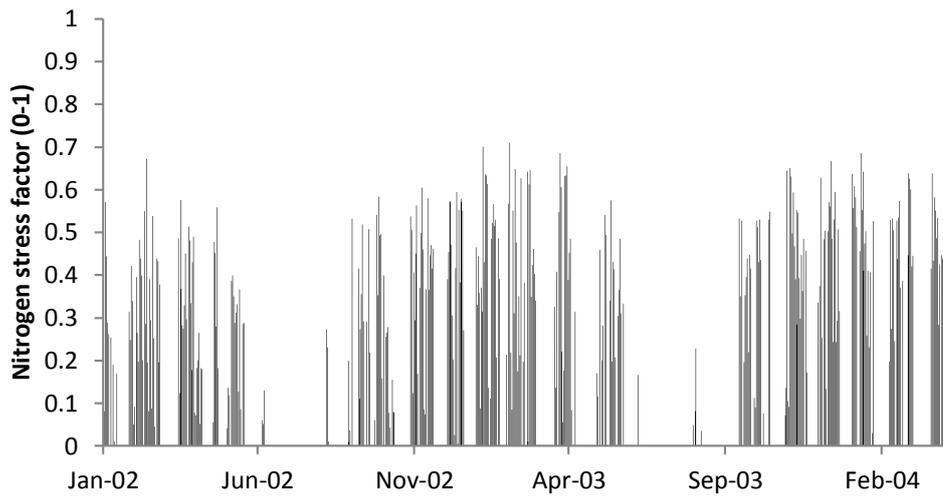


**Figure 3.** Original and parameterized simulated stem biomass as a function of date for (A) Tanzânia in Piracicaba, SP, Brazil and (B) Mombaça in São Carlos, SP, Brazil.

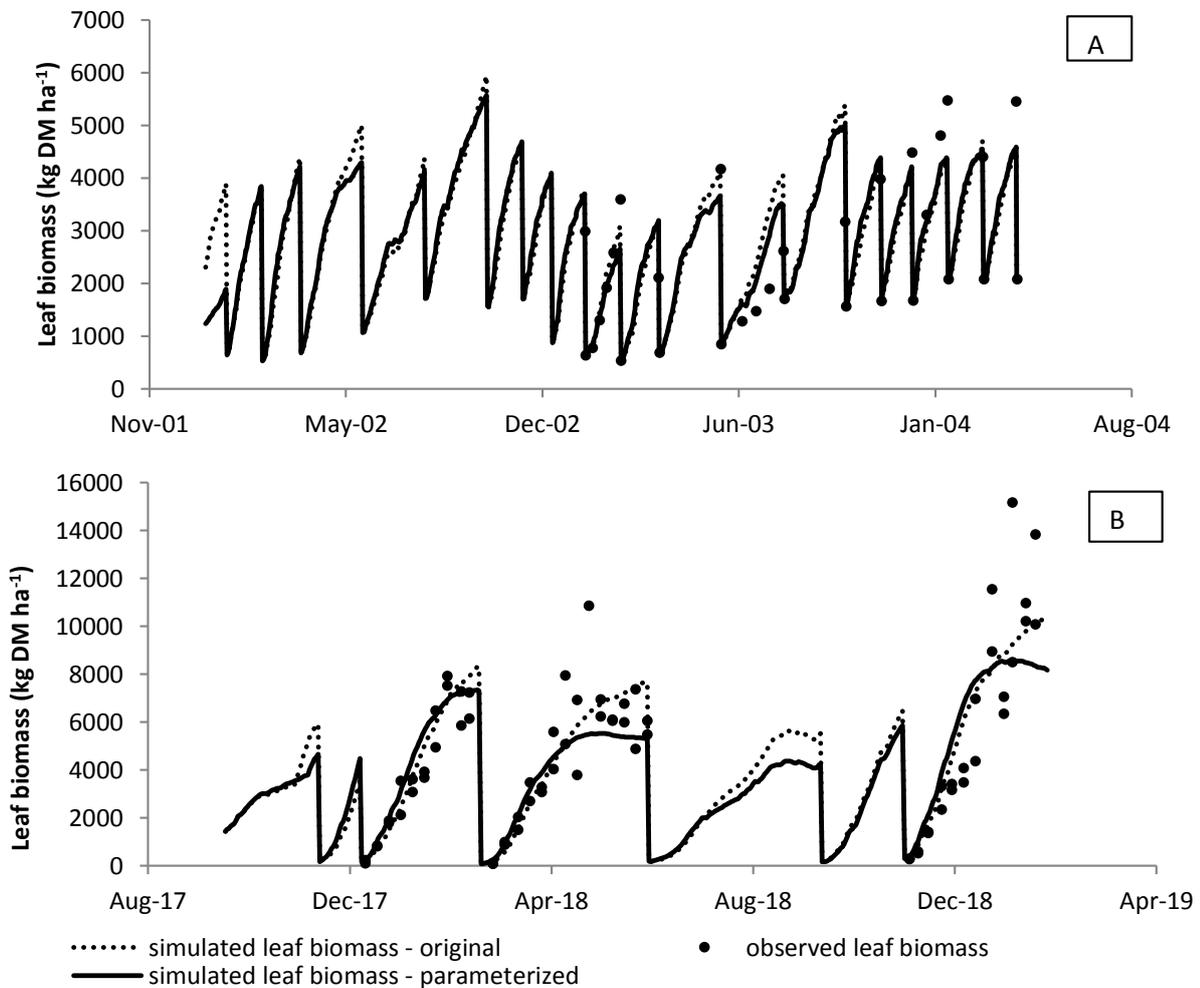


**Figure 4.** Original and parameterized simulated aboveground live biomass as a function of date for (A) Tanzânia in Piracicaba, SP, Brazil and (B) Mombaça in Sao Carlos, SP, Brazil.

Simulated nitrogen stress was relatively severe (Figure 5) for Tanzânia, whereas it was null for Mombaça (data not shown). The daily N stress within the model ranges from 0 (no N stress) to 1 (maximum N stress) and is computed as the ratio of actual daily N uptake divided by the N necessary for growth of new tissues (and N refill of older existing tissues). The effect of nitrogen stress on shifting the partitioning from shoot to roots (NSTFAC) was changed from 0.7 to 0.8, which had the effect of increasing the partitioning to roots whenever N stress occurred on the Tanzânia trial, and this resulted in a better fit of Tanzânia aboveground live biomass simulation (Figure 4a). The leaf biomass simulation during the whole cycle for both cultivars was also well predicted after parameterization (Figure 6).



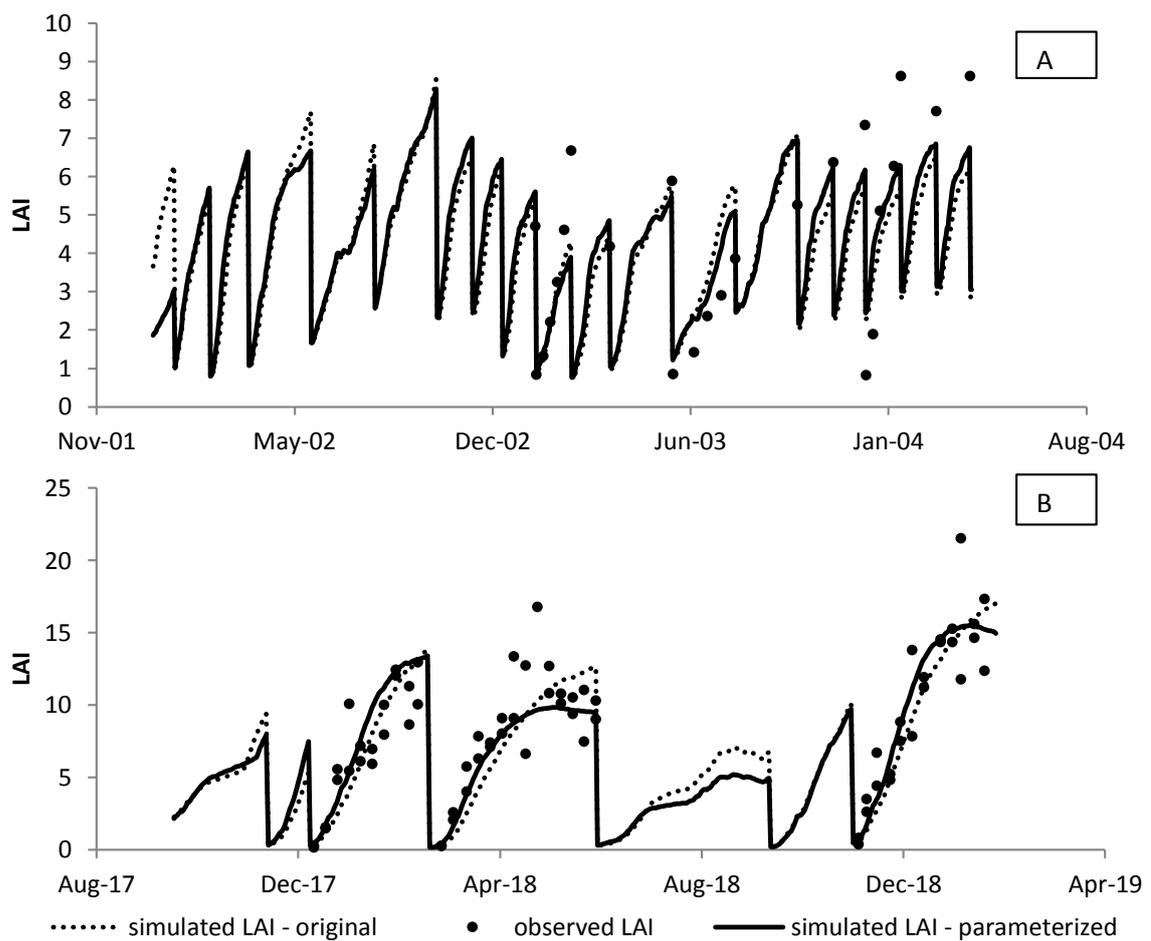
**Figure 5.** Nitrogen stress factor simulated with the parameterized version as a function of date for Tanzânia in Piracicaba, SP, Brazil.



**Figure 6.** Original and parameterized simulated leaf biomass as a function of date for (A) Tanzânia in Piracicaba, SP, Brazil and (B) Mombaça in São Carlos, SP, Brazil.

### 5.3.1.2. Parameters affecting senescence

Senescence due to excessive self-shading by the canopy was decreased by lowering the leaf light compensation point (ICMP; Table 2) for lower leaf abscission from 1.15 to 0.8  $\text{mmol m}^{-2} \text{d}^{-1}$  and increasing the half-time constant in which leaves under the light compensation point abscise (TCMP) from 13.1 to 20 days. These changes allowed the plants to carry more leaves even with large LAI, allowing for greater aboveground live biomass, leaf accumulation, and LAI, especially for Mombaça (Figures 4, 6 and 7, respectively). In addition, natural heat-unit related senescence of leaves (LFSEN) was also decreased from 0.02 to 0.015 fraction per day, which means that the leaf life span is about 67 days. Similarly, Silveira et al. (2010) found that the leaf life span of four cultivars of guineagrass under free growth was 70 to 80 d.



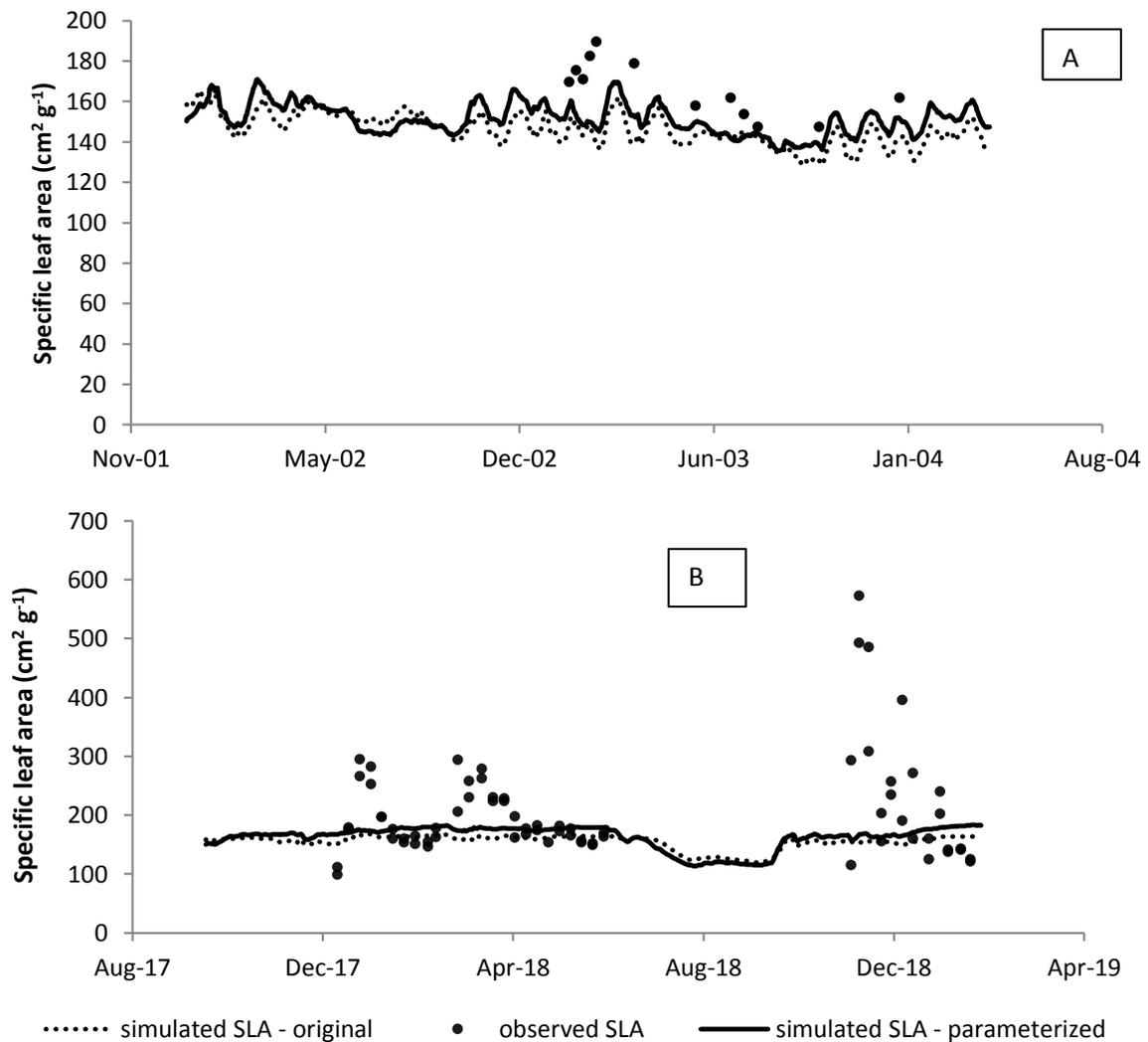
**Figure 7.** Original and parameterized simulated leaf area index (LAI) as a function of date for (A) Tanzânia in Piracicaba, SP, Brazil and (B) Mombaça in São Carlos, SP, Brazil.

Additionally, the stem portion to abscise dependent on leaf abscission (PORPT) was decreased from 0.27 to 0.15 (Table 2), which contributed to greater stem mass accumulation and a much better fit for Mombaça simulations (Figure 3b).

### 5.3.1.3. Parameters affecting prediction of specific leaf area and leaf area index

Simulated SLA using the original parameters showed underestimated values for both cultivars during all growth cycles (Figure 8). The parameters and functions affecting SLA were modified to better simulate the relationship between leaf biomass and LAI. The model allows SLA to be influenced by solar radiation, temperature, N stress, and water deficit. The solar radiation effect has two primary parameters, SLAMAX, the thinnest leaf under very low light, and SLAMIN, the thickest leaf under high light situations (but without stress from cold temperature, N stress or water deficit). Therefore, the SLAMIN should be close to the SLAVR, which is the cultivar-specific SLA under standard “optimum” growth conditions. In this context, the SLAMIN and SLAVR parameters were set to  $180 \text{ cm}^2 \text{ g}^{-1}$  which provided simulations with overall higher specific leaf area than the original model parameters. The SLAMAX was decreased to  $320 \text{ cm}^2 \text{ g}^{-1}$  to improve the winter vs summer radiation effect on SLA (Table 2).

To account for seasonal temperature effects on SLA of Tanzânia, the temperature effect on SLA of newly-produced leaves (XSLATM and YSLATM, Table 2) was optimized. Increasing the threshold temperature at which maximum reduction occurs (XSLATM) and decreasing the SLA expansion ratio (YSLATM) at this low threshold temperature, allowed for a larger effect of cool temperature to reduce SLA (this is a look-up function that interpolates between the x-y pairs and uses hourly temperature). This improved the SLA reduction for Tanzânia that occurs during cool months (Figure 8a).



**Figure 8.** Original and parameterized simulated specific leaf area (SLA) as a function of date for (A) Tanzânia in Piracicaba, SP, Brazil and (B) Mombaça in São Carlos, SP, Brazil.

Nitrogen stress effect on leaf expansion and SLA (NSLA) is a new feature in DSSAT V4.7 (not available or used with Lara et al (2012)'s previous adaptation), but had been set as a default to 1.0 (maximum effect) for Marandu palisadegrass based on the work of Pequeno et al. (2018) for CROPGRO-PFM in V4.7, thus simulating strong N stress effects on SLA. This parameter was decreased from 1.00 to 0.75 during the parameterization for *Panicum maximum* (Table 2). These changes improved the simulated effects of N on SLA and maximum SLA for Tanzânia (Figure 8).

The parameterization allowed for good prediction of SLA for Tanzânia (Figure 8a) and mean simulated SLA close to that observed for Mombaça (206 compared with 174  $\text{cm}^2 \text{g}^{-1}$  for observed and simulated values, respectively). Consequently, it resulted in improvements in the simulation of aboveground live biomass regrowth during cool (May to September) and warmer conditions (October to April), with good simulation of LAI for both cultivars (Figure 7).

#### 5.3.1.4. Parameters affecting photosynthesis

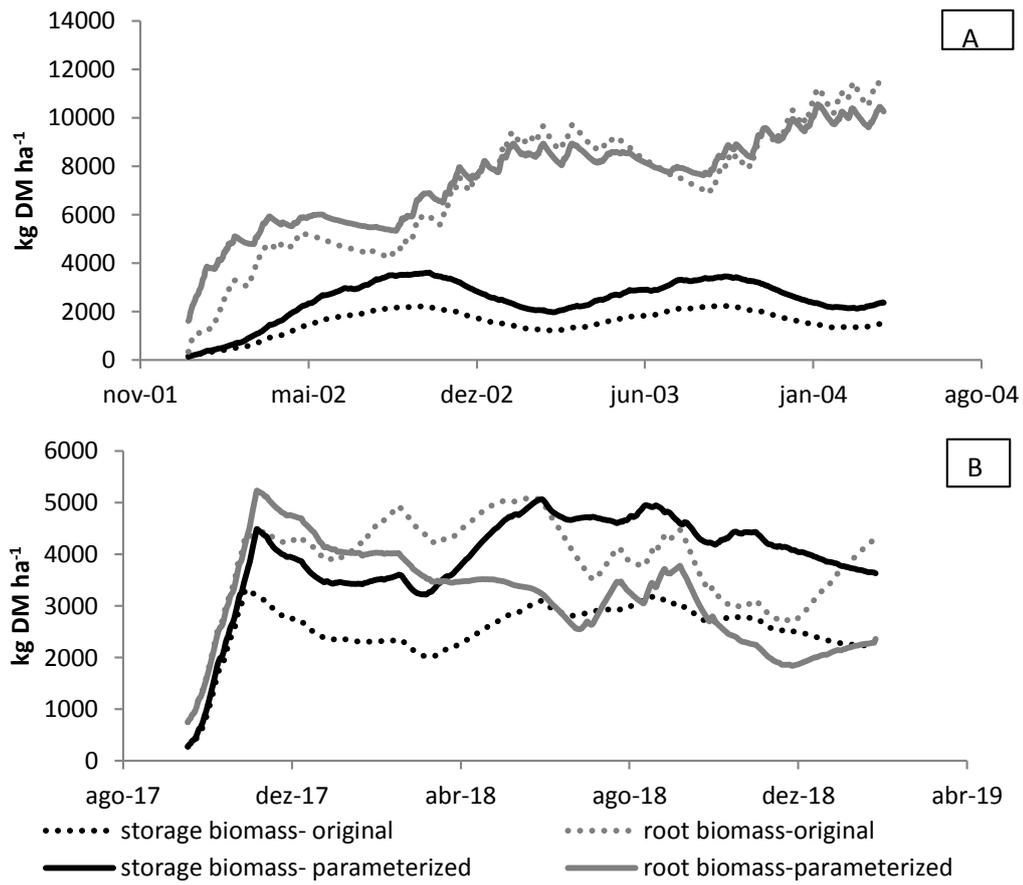
The asymptotic function (FNPGI) defines the daily minimum temperature (night-time) effect on the next day's photosynthesis. That effect was strengthened, increasing the sensitivity to days with low minimum temperatures. Additionally, the base temperature for relative rate of photosynthetic electron transport in response to instantaneous hourly temperature (XLMAXT) was increased (Table 2), also increasing seasonality. Concurrently, the optimum temperature for photosynthesis described by the same pair of temperatures (XLMAXT) (Table 2) was increased to 40 °C. Decreases in photosynthesis due to low temperatures mostly improved Tanzânia aboveground live biomass simulations, while the increase in optimum temperature benefited both cultivars (Figure 4). Light-saturated leaf photosynthesis (LFMAX) is the same for both cultivars and was not changed from the original of 1.91 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (Table 2).

#### 5.3.1.5. Parameters affecting dormancy/partitioning to storage

To decrease production during cool, short daylength months, changes were made to the critical daylength (FNPTD) that increases photosynthate partitioning to storage and less to shoot (guineagrass allocates photosynthates in the stem base and roots but, in the model, there is no specific organ for allocation), and to the relative strength (RDMRT) of daylength effect on FNPTD for the plant to be more sensitive to daylength (Table 2). This was done by increasing the relative sensitivity to daylength (RDRMT) from 0.299 to 0.350 (Table 2) and increasing the lowest daylength value at which the shift of photosynthate partitioning from shoot to the storage is highest (from 9.1 to 10.8 h), while increasing slightly the maximum daylength value at which the shift of photosynthate partitioning from shoot to storage is minimum (from 13.5 to 13.7 h). This change allowed for a stronger effect of daylength with a narrower range of daylength, which decreased the productivity during winter and improved aboveground live biomass accumulation simulation, especially for Tanzânia (Figure 4a).

#### 5.3.1.6. Simulated partitioning to storage and root mass

Modification of the partitioning parameters was done while retaining acceptable partitioning to storage and root mass accumulation, despite lacking collected data. The partitioning to roots was decreased mainly during the early phases of regrowth when grasses tend to prioritize leaf accumulation, while the partitioning to storage was increased slightly during this phase of regrowth (Figure 1). After parameterizing, the model partitioned photosynthate to roots and storage with reasonable long-term and seasonal stability, allowing for the perennation of the plant (Figure 9).

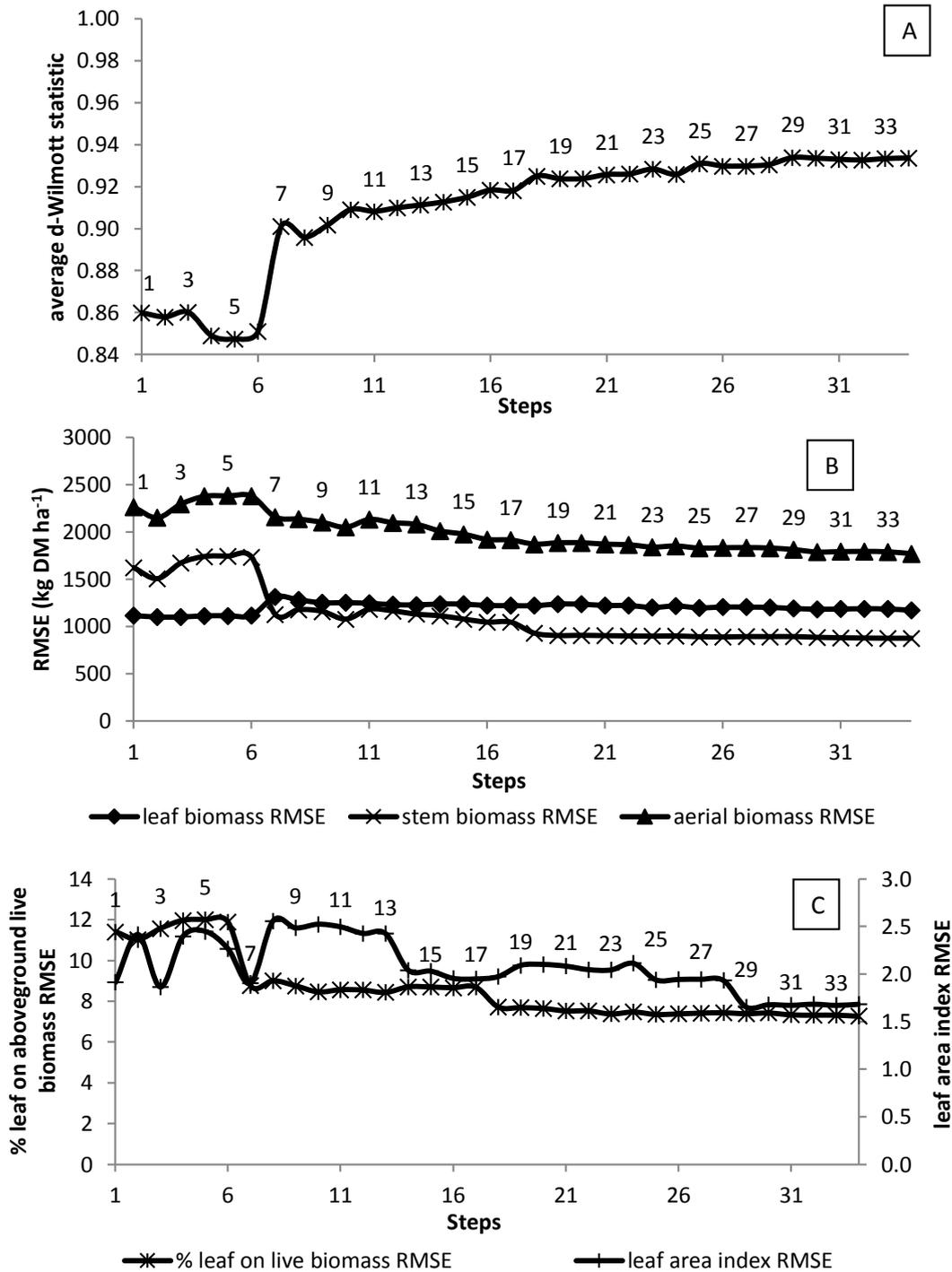


**Figure 9.** Original and parameterized simulated storage organ and root biomass as a function of date for (A) Tanzânia in Piracicaba, SP, Brazil and (B) Mombaça in São Carlos, SP, Brazil.

### 5.3.2. Main adaptations for improving model performance

The RMSE and d-statistic of the time-series data were averaged over the two cultivars. Because the d-statistic is already normalized within each variable, an average d-statistic over all five variables (Figure 10a) was computed to show step-by-step model improvement, while RMSE of leaf, stem and aboveground live biomass are shown in Figure 10b, and RMSE of leaf percentage in aboveground live biomass and leaf area index are shown in Figure 10c.

The first attempt to modify the partitioning parameters (LFEST, YSTEST, YSREST) had the largest effect toward increasing average d-statistic (Figure 10a, step 7) and decreasing RMSE of percentage leaf and RMSE of stem biomass (Figure 10b and 10c, step 7), although additional adjustments in these parameters were done on steps 15 and 19. Another important step on model improvement was the change made in the MOW input file, increasing the average d-statistic considerably (Figure 10a; step 18) and decreasing RMSE of stem biomass and leaf percentage (Figures 10b and 10c; step 18). The other steps had lesser but consistent relative effects throughout parameterization and were changed iteratively.



**Figure 10.** Wilmott d-statistic and RMSE for aboveground live biomass, leaf biomass, stem biomass, leaf area index and % leaf on aboveground live biomass of the cultivars Tanzânia and Mombaça throughout the steps of parameterization: (A) d-statistic (averaged over all the variables); (B) RMSE of leaf mass, stem mass, and aboveground live biomass; (C) RMSE of % leaf on aboveground live biomass and leaf area index.

## 5.4. Discussion

The major improvement in the model performance was achieved by modifying the biomass partitioning parameters between leaf and stem (Figure 10, step 7) by increasing the partitioning to leaf during early regrowth while increasing partitioning to stem late in the regrowth cycle (the look-up function is described by XLFFEST, YLFEST,

YSTEST and YSREST). In many warm-season grasses, there is stem elongation in later vegetative phases (Santos et al., 1999) which results in increases in stem mass accumulation (Figure 3b, first and third evaluating cycles). Due to the shorter harvest cycle of Tanzânia every 4-8 weeks versus Mombaça at 10-14 weeks, the original simulation of stem accumulation was well performed by the model for Tanzânia but gave poorer performance for Mombaça (Figure 3). The Mombaça cultivar experiment provided data with a much broader range from early regrowth to much later regrowth (larger V-stage), so the changes mostly benefited Mombaça simulations. It is important to state that one set of species, ecotype, and cultivar parameters worked well to simulate both Tanzânia and Mombaça (no cultivar-specific parameters were required). For other cultivars, however, adjustments may be needed. Ideally, no changes in the species file will be necessary, and ecotype and cultivar parameters can be adapted to successfully result in good simulations. Therefore, modeling efforts with other guineagrass cultivars is recommended to further evaluate and improve the *Panicum* model for other cultivars.

At the midpoint to the end of the second evaluating cycle of Mombaça, the plants flowered. *Panicum maximum* is a short-day species (Felippe, 1978; Loch, 1980) with approximate critical daylength of 11.8 hours, when floral initiation can be seen in reproductive tillers (Araujo, 2011). This occurs between the months of April to September in the latitude of Mombaça and Tanzânia experiments (the sites are similar in latitude). The occurrence of the first reproductive tillers (observation of flower primordia) for the Mombaça trial was on 4 April 2018. Thereafter, the number of tillers with flowers primordia increased for about 15 days until the panicles finally started to emerge. Floral initiation (and flowering) terminates leaf initiation and markedly stimulates subsequent stem elongation which raises the apical meristems in conjunction with shifting partitioning from leaves to stem. In addition, the new leaves that had been initiated inside the whorl of leaf sheaths (boot stage) after differentiation of apical meristem from vegetative to reproductive, are shorter (smaller) than vegetative leaves, which also decreases leaf accumulation. It is important to highlight, however, that despite the good results obtained after parameterization, the model still does not simulate flowering for any forage species. For a better simulation of stem elongation due to floral initiation and considerations of the daylength effect, code changes within the model are needed to simulate floral initiation and associated stem elongation, seed growth, and seed maturation. Those aspects were uncoupled with the transition of CROPGRO from annual to perennial species. The issues are not simple, because the model will need to re-initiate the juvenile vegetative state either on an annual basis or more often after harvesting of the reproductive tissues.

After parameterization, the model was able to simulate biomass partitioning during the early, mid and very late phases of regrowth, which contributed to good simulations of aboveground live biomass accumulation in the later regrowth cycles (Figure 4b) and good leaf biomass simulation during the whole cycle for both cultivars (Figure 6).

A good prediction of biomass partitioning by the model is important, because in pasture-based livestock systems, green leaf accumulation is preferred to stem accumulation due to its high utilization efficiency and nutritive value (Gontijo Neto et al., 2006), which favors high animal productivity and performance. Additionally, the biomass partitioning affects the stubble composition, with consequences for pasture regrowth and perennation. Furthermore, when *Panicum maximum* is cultivated in long cycles, it has the potential to be used as an ethanol source (Jank et al., 2013). In this context, accurately simulating biomass partitioning both in short and long cycles is an important aspect of model improvement when dealing with different grazing strategies (i.e. with herbage removal at different severities and frequencies) and pasture utilization.

Another important issue learned in the parameterization was the need to modify the MOW values of the first and second evaluating cycles (Figure 10, step 18). Harvesting or grazing may cause tiller death because of apical meristem removal. The apical meristems of tillers are found inside the whorl of mature sheaths and their removal is

dependent on cutting height and meristem height and harvesting conditions (Branson, 1953). After meristems are removed, the main tiller senesces and lateral buds may grow due to lack of apical dominance (Richards et al., 1988). However, senescence of nodes and internodes left after harvest may not be detectable in the first days after harvesting thereby causing an apparent decrease in living stem biomass during the following days (Figure 3; see observed data for the first and second evaluating cycles). Thus, considering the total amount of stem left after harvest as the amount measured after ~15 d for the first two evaluating cycles resulted in a better fit over the entire regrowth cycle (Figure 3b). For modeling purposes, special care should be taken when considering data of live aboveground biomass (especially stem) during the first days of regrowth.

One of the features of the CROPGRO-PFM model is that it originated as a model for the simulation of a grain legume model species, which has leaf and petiole abscission due senescence. However, forage grasses tend not to abscise leaves (rather they die and hang on despite senescence) and do not abscise stem tissue (grasses lack petioles). Furthermore, in forage grasses the leaf sheath senesces after leaf laminae senesce, but in reality, the dead leaf sheath material remains on the plant allowing for greater stem accumulation. In this context, the decreases in leaf abscission (ICMP, TCMP and LFSEN) and stem loss (PORPT) associated with senescence in the model are a better representation of grass species (Figure 4). The model does simulate abscised dead tissue with time after each harvest cycle, and comparison of simulated to observed dead foliage mass (data not shown) also confirmed the need to reduce the rate of leaf and stem mass abscission. Available data on dead foliage mass are scarce and there are also sampling issues such as the extent of dead mass carried over from prior regrowth cycles and the extent of dead mass lost to the soil surface with wind, rainfall, and animal tracking.

Along with modifications of senescence and partitioning, to increase production during warm months, the optimum temperature for photosynthetic electron transport (XLMAXT) (Table 2) was increased to 40 °C benefiting productivity of both cultivars during warm months in Brazil's spring and summer. The modified maximum photosynthesis value is consistent with the known optimum temperature for C4 photosynthesis (Pearcy and Ehleringer, 1984).

For the Tanzânia trial, data were also collected during the coolest months of the year (June to August), thus bringing out the need for parameterizing growth under this circumstance. This is an important aspect when parameterizing *Panicum maximum*, as it is usually grown year-round in the tropics, but the decrease in forage supply to feed the animals during winter often has to be complemented with silage or hay. To account for seasonality of production as seen on the Tanzânia trial (Figure 5a), the base temperature for photosynthetic electron transport (XLMAXT) and the lowest night temperature (FNPGL) which defines null photosynthesis during the next day were increased, thus increasing the sensitivity to days with low minimum temperatures and also aiding to decrease production on cool months.

Parameterizing the response of SLA to radiation (SLAMIN, SLAVR and SLAMAX) and temperature (XSLATM and YSLATM) resulted in improvements to the prediction of winter versus summer biomass regrowth dynamics, with a good prediction of LAI for both cultivars (Figure 7). However, it was not possible to simulate accurately the Mombaça pattern of SLA variation, which showed high SLA at the beginning of the cycle and systematic decrease until reaching a constant value during mid to late cycle. The high SLA at the start of the regrowth cycles with subsequent decrease towards the end observed in the Mombaça data (Figure 8b), is probably due to the small portion of central venation of the first leaves developed as opposed to the greater portion that appears in leaves as the plant ages (Garcia, 2018). Central venation in C4 leaves has a great proportion of sclerenchyma, lignified vascular tissue and parenchymal bundle sheath (Wilson, 1977), structures that are important for mechanical support of leaf laminae and

which have been reported as having a proportional relationship with leaf length (Queiroz et al., 2000). At the beginning of development and growth, small leaves require little central venation, but as the growth progresses, the central venation of the new and larger leaves become thicker to support these leaves, diminishing SLA. This would also mimic increased lignification of venation with progressive leaf aging (something the model does not simulate at present).

Nitrogen is the nutrient with the greatest effect on warm-season grass growth. In this study we decreased the effect of N stress on reducing SLA (and consequently leaf area expansion) (NSLA) and increased the factor shifting partition of photosynthates from shoot to roots whenever the N stress occurred, allowing for improvements of Tanzânia simulations. The lack of N stress simulated for Mombaça is a result of the extremely large amount of nitrate and ammonium reported in the initial conditions (Table 1). By contrast, the lesser initial nitrate and ammonium, total soil C as well as lesser previous crop residue resulted in simulations with severe N stress for Tanzânia.

Dormancy shift of photosynthate partitioning to storage organs is triggered by decreased daylength and temperature in many grasses such as bermudagrass (*Cynodon spp.*) (Pedreira et al., 2000), elephantgrass (*Pennisetum spp.*) (Macon et al., 2002), limpograss (*Hemarthria altissima* (Poir.) Stapf & Hubbard) (Newman and Sollenberger, 2005), big bluestem (*Andropogon gerardii* Vitman) (Mousel et al., 2005), ryegrass (*Lolium perenne* L.) (Lee et al., 2008; Ourry et al., 1988, 1990, 1994), and palisadegrass (Miles et al., 1996; Rodrigues et al., 2007). These model features were helpful to simulate seasonal growth dynamics and winter dormancy in the present study and for bahiagrass, palisadegrass and the prior version of guineagrass (Rymph, 2004; Pedreira et al., 2011; Lara et al., 2012). We presume that guineagrass, accumulates carbohydrate reserves in stem bases and roots that can be used to fuel regrowth. For the model, the storage organ has no specific location but is a mimic of that situation, as it is not removed by harvesting, but it aids regrowth whenever harvesting occurs. Increasing the relative strength of daylength effect to shift partitioning from shoot to storage/roots (RDMRT), and narrowing the daylength range which defines the maximum and minimum shifting on partitioning (FNPTD) aided to decrease production during the cooler months (June to August), improving aboveground live biomass accumulation simulation, especially for Tanzânia (Figure 4a). After parameterization, the simulations continued to show long-term stability on storage organ and root biomass (Figure 9), which allows for the perennation of the plant and consequently the proper use of the model, especially for long-term simulations.

The parameterized model showed good performance for simulating important aspects of *Panicum maximum* growth dynamics, such as biomass partitioning and seasonality of production. These aspects are important for the model when dealing with different strategies of pasture utilization in different growing conditions.

## 5.5. Conclusion

The original model had good performance for simulating Tanzânia but relatively poor performance for simulating Mombaça growth, although acceptable. After parameterization the model is now able to predict aboveground live biomass accumulation and partitioning in early, mid and long cycles of both experiments, using the same species file. Because assimilate partitioning to leaf and stem affects the quality of forage offered to animals and the quality of stubble left after grazing for the regrowth of the next cycle, a good prediction of the partitioning features during the full regrowth cycle all the way to overly mature is important when considering different grazing strategies and pasture utilization. This model adaptation for *Panicum maximum* will be added as a new crop in a future version of DSSAT and will facilitate further use for evaluating management strategies and evaluating production under new environmental conditions and crop management scenarios.

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