

Review

Ecophysiology of C₄ Forage Grasses—Understanding Plant Growth for Optimising Their Use and Management

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Academic Editor: Cory Matthew

Received: 29 May 2015 / Accepted: 21 July 2015 / Published: 29 July 2015

Abstract: Grazing management has been the focus of the research with forage plants in Brazil for many years. Only in the last two decades, however, significant changes and advances have occurred regarding the understanding of the key factors and processes that determine adequate use of tropical forage plants in pastures. The objective of this review is to provide an historical overview of the research with forage plants and grasslands in Brazil, highlighting advances, trends, and results, as well as to describe the current state of the art and identify future perspectives and challenges. The information is presented in a systematic manner, favoring an integrated view of the different trends and research philosophies. A critical appraisal is given of the need for revision and change of paradigms as a means of improving and consolidating the knowledge on animal production from pastures. Such analysis idealizes efficient, sound and sustainable grazing management practices necessary to realize the existing potential for animal production in the tropics.

Keywords: tropical pastures; ecophysiology; morphogenesis; grazing management

1. Introduction

Brazil is a South American country situated between latitudes 5°16'20" S and 33°45'03" S, therefore part of the tropical/sub-tropical region of the world. Animal husbandry and production systems are mainly based on grazed pastures and harvested forages. The country has around 196 million ha of permanent pastures [1], of which around 51% are comprised of cultivated (introduced) species [2], particularly of the genera *Brachiaria* and *Panicum*, all C₄ grasses with high herbage dry matter yield potential. These are very different from most temperate forage grasses, showing a wide range of plant morphology and structure, varying from prostrate/semi-prostrate to tall-tufted erect growing plants [3]. Despite the potential for generating high animal productivity [4] (25–30,000 kg milk/ha per year and 1000–1600 kg body weight gain/ha per year), national average productivity is low (around 800–1000 kg milk/ha per year and 60–100 kg body weight gain/ha per year) [5], the consequence of inadequate empirical management practices. For that reason, focus has historically been given to research on improving the agronomic, nutritional, and productive traits of forage plants and grazing management. Effective progress, however, became more evident when studies started to adopt a more ecological approach and were planned taking into account functional responses related to plant growth, form, and function, favouring the understanding of the associated processes and providing the necessary knowledge basis for planning sound and efficient management practices. In this context, the inclusion of evaluations regarding plant ecophysiology in the experimental protocols during the early 1990s played an important role and represented a turning point in grassland research in the tropics.

Against that background, the objective of this review is to provide an historical overview of the research with tropical forage grasses in Brazil, highlight advances and identify future perspectives and challenges. In spite of the Brazil focus, the findings should be applicable to the same climate worldwide.

2. Forage Grass Research—A Historical Overview

The research with forage plants and pastures in countries with developed animal husbandry systems started in the early 1900s. Among the scientific publications that came out at that time, some became important contributions and references for all the progress and achievements obtained by grassland scientists, even at the present time. Graber [6], cited by Volenec *et al.* [7], was one of the first to report that the concentration of total non-structural carbohydrates (TNC) in roots decreased soon after defoliation during the regrowth phase of alfalfa (*Medicago sativa* L.). Watson [8], cited by Black [9], demonstrated that a measure of the size of the plant photosynthetic apparatus was important in making comparisons of crop yield and productivity, and proposed the concept of leaf area index (LAI). Brougham [10–16] demonstrated the importance of LAI for understanding the relationship between canopy light interception (LI) and herbage accumulation and the interaction between defoliation frequency and severity.

Brougham [10] fitted a sigmoid curve to the variation in herbage mass during regrowth of perennial ryegrass (*Lolium perenne* L.), white clover (*Trifolium repens* L.) and red clover (*Trifolium pratense* L.) mixed swards (variation in herbage mass with time), as well as describing the asymptotic relationship between LAI and LI [12,17]. The author demonstrated that plant growth was a function of canopy light interception and LAI, and that the rate of herbage dry matter accumulation reached a maximum constant

value when there was enough foliage to intercept almost all the incident light. In general, three distinct phases may be identified in a regrowth curve. The first, soon after defoliation, is characterized by an exponential increase in herbage mass with associated increase in rate of herbage accumulation. This phase is highly influenced by plant organic reserves, climatic and edaphic conditions, and residual leaf area after cutting or grazing [12]. The second is characterized by constant rates of herbage accumulation (linear increase in sward herbage mass). During this phase, intra and inter specific competition between plants become increasingly intense, particularly when the sward is close to maximum canopy light interception. During the third phase there is a reduction in herbage accumulation rate, the consequence of a proportionally larger increase in leaf senescence relative to leaf growth caused by leaves having reached their leaf lifespan and severe shading at the bottom of the sward [18].

These studies provided the basis for developing grazing management strategies based on the concepts of LAI and TNC accumulation and mobilization [19–21], despite the difficulties of measuring them. During the 1960s, Smith [22] carried out a series of experiments with alfalfa in the USA with the objective of demonstrating the importance of plant organic reserves and LAI for adequately managing pastures subjected to intermittent defoliation. As a result, the residual LAI and the organic reserve concentration remained as important considerations to be taken into account in planning and idealizing grazing management practices and strategies. Alcock [23] proposed three simple concepts for explaining plant responses to defoliation: (1) total availability and reutilization of organic reserves, (2) root growth, and (3) leaf area development and canopy light interception. The role of organic reserves had already been recognized as important for a long time [24], but with no applied results, since no grazing management strategy was produced based on it, except for harvesting alfalfa. The same happened with root growth. On the other hand, the LAI and LI concepts were used and studied in a series of experiments whose results helped to establish a strong knowledge basis for understanding the process of herbage accumulation of forage plants subjected to defoliation (cutting or grazing) regimes. Brown & Blaser [25] considered the use of LAI to define management practices an oversimplification of the process, arguing that on tall swards there were usually few leaves close to ground level and that lenient grazing would be necessary to ensure enough residual LAI to allow maximum canopy light interception. The authors also argued that on tall swards the photosynthetic efficiency of the leaves positioned at the base of the sward would be lower than that of leaves positioned at the top, resulting in low harvest efficiency and high risk of reduction in tiller population density.

In Brazil, during the first Symposium on Pasture Management, in 1973, it was recognized that there was a complex interplay among LAI, tillering, and TNC reserves in the regrowth of forage plants, and that the knowledge of those relationships in temperate species should be valid for tropical forages as well [26,27]. Jacques [27], however, argued that “despite its importance, the LAI was not enough to plan and sustain adequate management practices”, and highlighted the distinct interests and approaches of the predominant “research schools” at that time (North American and British).

Several of the existing grazing management guidelines have been based on the argument that pasture species should be used under intermittent defoliation regimes such as rotational stocking, generating a series of successive regrowth cycles (sigmoid curves), in order to better use the growth characteristics of forage plants. Under these circumstances, defoliations (grazings or harvests) should happen at the end of the linear growth phase (phase 2) so that maximum average rate of herbage dry matter accumulation could be obtained. Herbage nutritive value under those conditions, however, was usually low and it

could be valuable to interrupt regrowth at an earlier stage with the objective of harvesting better quality herbage [28]. Under continuous stocking, in cases when pastures are maintained at a steady state condition characterized by constant levels of sward LAI, height, or herbage mass, the idea of maintaining LAI to ensure 95% LI would not be valid, since leaf senescence is proportional to leaf growth, resulting in zero or even negative values of net herbage accumulation [29]. In this case, the recommendation would be to manage swards at lower heights and lower LAI relative to intermittent defoliation regimes as a means of ensuring higher rates of herbage accumulation and harvest efficiency of the produced herbage [30].

From the 1960s onwards the “North-American” school started to be influenced by Gerald Mott’s work, with the introduction of the put and take stocking method for adjusting stocking rate in grazing experiments [31]. The method consisted of using fixed groups of animals, called testers, that would represent the experimental unit for measuring animal responses, and another group that would act as stocking rate regulators, which were added to or removed from paddocks as a means of adjusting defoliation intensity based on an arbitrary criterion, originally suggested by Mott as grazing pressure. Grazing pressure was defined as the relationship between animal live weight and herbage mass per unit area [31,32]. By derivation, Mott [31] defined another term, carrying capacity, or the maximum stocking rate that would achieve a target level of animal performance in a specified grazing system. The put-and-take stocking method was more intensively used for research purposes with little use in practical situations, the consequence of the difficulties of its implementation in farm conditions. These concepts were used for many years by several researchers, but, according to Maraschin [33], without fully understanding the underlying principles involved. According to the same author, for efficient use of the herbage produced, stocking rate should always be defined in relation to the carrying capacity of pastures, a condition associated with the optimum grazing pressure. The goal under this approach would be to find an equilibrium between animal performance and animal production per unit area as a means of generating higher economical returns of pasture utilization, but without taking into account aspects of plant ecophysiology and the ecology of grassland ecosystems.

The “North American” school had a strong influence on the research with forage plants and pastures in Brazil for a long time. As a consequence, the emphasis was on describing the growth curve of pastures after cutting or grazing, their seasonality of herbage production, and the morphological and chemical composition of the produced herbage, with no particular attention to dynamic aspects related to plant population and competition for light normally associated with plant recovery after defoliation. Stocking rate and grazing pressure were considered key features and started to be used as control variables (treatments) in grazing experiments. This is corroborated by the large number of conferences on the topic at the Symposium on Pasture Management at ESALQ in Brazil [34–51] and research abstracts published in the Annual Meeting Proceedings of the Brazilian Society of Animal Science [52]. After some time, grazing pressure evolved to the concept of herbage allowance (the amount of herbage on offer per animal), and evidences [53,54] showed that individual herbage intake was maximized when herbage allowance corresponded to three–four times the daily requirement of dry matter [55]. In tropical pastures, after successive grazings, this could result in excessively high levels of herbage on offer characterized by large quantities of dead material and stems, low nutritive value of the herbage, and reduced intake by the grazing animals [56–58]. Mott [59], aware of that limitation, warned that the conversion of the primary production in animal product in tropical pastures would be considerably

different from that in temperate pastures. As a consequence, he suggested that management practices should aim to provide the maximum amount of live tissues with high digestibility to animals, particularly leaves, as a means of increasing intake and performance. This idea led to the concept of green dry matter allowance [60], which evolved to leaf dry matter allowance. These practices were effective in providing a good fit between herbage allowance and animal performance data (as originally reported by Mott [31]) in relation to the traditional asymptotic curve [61], but magnified the problem of excessive herbage mass with high proportions of stems and dead material, with negative implications on herbage and animal production.

Although the conflict between the necessary sward conditions for generating high rates of herbage accumulation and those for achieving maximum intake and performance was evident in the literature since the early 1970s [56–58], harvest efficiency was frequently compromised as a means of favoring high levels of animal performance [31], resulting in low productivity and large dry matter losses to senescence, death, and decay [62]. Better understanding and more sound grazing management practices started to emerge during the 1980s when the results from more detailed studies evaluating the dynamics of plant population and growth became available [18]. Bircham & Hodgson [63] were the first to describe the dynamics of the herbage accumulation in continuously stocked perennial ryegrass swards, and showed that net herbage accumulation was the result of the balance between two concomitant and antagonistic processes—growth and senescence. These respond differently to agronomic and management practices. Consequently, evaluation of herbage accumulation only, *i.e.*, without taking into account the independent processes of growth and senescence, could result in imperfect understanding of patterns of plant and pasture response to defoliation [64]. The results also demonstrated that the herbage accumulation process could be adjusted through manipulation of sward structural characteristics such as LAI, height, and herbage mass, allowing for the development of grazing management targets that could be used to guide and control the grazing process in farm conditions. In this context of strict control of sward structure, the need for multi-year experiments became relatively less important when compared, for example, with experimental protocols that used stocking rate or grazing pressure as control variables, since the factors causing the treatment x year interactions were the same as those causing the treatment x environment and/or the treatment x season of the year interactions.

According to Hodgson [65], effective understanding of how plants and animals respond to variations in sward conditions, and consequently to management, could only be achieved in grazing experiments with rigid control of sward structural characteristics at a given state (continuous stocking management with variable stocking rate) or following a pre-specified pattern of variation (pre and post-grazing conditions of an intermittent stocking management). Korte *et al.* [66], studied perennial ryegrass subjected to cutting regimes characterized by two frequencies and two severities of defoliation, and planned their experimental treatments based on the findings of Brougham during the 1950s, using the 95% LI as the reference condition for initiating defoliation. The authors concluded that during the vegetative growth stage the 95% LI criterion could be used to define the best moment for initiating defoliation and, relative to longer defoliation intervals, would result in greater herbage production with higher proportion of leaves and lower proportion of dead material. That would indicate the ideal harvest point during regrowth (determinant of cutting and/or grazing interval), a condition that would be associated with the end of the linear phase of the sigmoidal growth curve described by Brougham [10]. These findings indicated convergence of the available knowledge and corroborated the central role of

LAI as a determinant of plant responses to grazing, highlighting the need to study and understand aspects related to sward structure, light use, and the balance between growth and senescence as a means of planning and defining efficient grazing management strategies [67]. Chapman & Lemaire [68] reinforced the importance of LAI as a determinant of forage plant responses, and demonstrated that it was the result of the combined expression of the morphogenetic and structural characteristics of plants in a given environment. The paper established a reference point because it integrated the understanding from morphogenetic and ecophysiological studies from experimentation with forage plants, providing the necessary knowledge base for understanding the ecological and functional responses of plants and animals in grazing systems [69].

In Brazil, the first papers with information on the morphogenesis and ecophysiology of tropical grasses were published by Pinto *et al.* [70,71]. They reported results on leaf and stem accumulation, average tiller weight, proportion of vegetative and reproductive tillers, and rates of leaf appearance and leaf and stem elongation for andropogon (*Andropogon gayanus* Kunth), guinea (*Panicum maximum* Jacq.), and setaria (*Setaria sphacelata* Schumach.) grasses subjected to two levels of nitrogen fertilization. Gomide [72], in a review paper, showed results from several experiments on plant morphogenesis carried out in Brazil until that date. He indicated that the stabilization of the number of leaves per tiller and of tillers per plant could be a possible indicator for orienting and controlling the grazing management of tropical forage plants. On the other hand, Lemaire [73] argued that the morphogenesis of the main tropical forage species would have to be thoroughly studied in order to provide the necessary conditions for understanding plant responses to changes in management and environment. That introduced a change in research paradigm and to how the experimentation with forage plants would be conducted in the country from then onwards. In this new context, sustainability became an important feature, emphasizing pasture stability and productivity as the main goals to be achieved by the idealized management practices, highlighting the importance of rationalization and integration of the existing knowledge and results [74].

The inclusion of ecophysiology principles and a more integrative approach into the experimental protocols used changed the research with forage plants in Brazil, with key words like plant growth and development, herbage intake, ingestive behaviour, utilization, and conversion starting to be slowly but irreversibly incorporated into the vocabulary of researchers. As a result, knowledge and understanding of plant structural and morphogenetic characteristics became an important tool for determining the adequate sward conditions (height, herbage and leaf mass, LAI *etc.*) to ensure efficient and sustainable animal production from pastures.

3. The Ecophysiology of Tropical Grasses and Grazing Management

Among the commonly most used forage grasses in cultivated grasslands in Brazil are those from the *Brachiaria* (Syn. *Urochloa*), *Panicum*, *Pennisetum*, and *Cynodon* genera. Although they all have an effective vegetative perennation mechanism based on clonal growth (e.g., tillering—vegetative growth resulting in the natural production of potentially autonomous daughter plants—ramets), there is a wide range in plant architecture and growth habit which determines the functional relationships among individuals and the adaptive plasticity of their morphological structures.

Cynodon species and cultivars, as well as their intra and interspecific hybrids, are creeping-type grasses spread either by stolons, rhizomes or both. *Brachiaria*, *Panicum*, and *Pennisetum purpureum* Schum. are tussock-type grasses (also known as caespitose, bunchgrass, tufted grass, or phalanx) characterized by a compact pattern of tiller organization in an erect and clumped growth form and representing the main type of grass plants used in cultivated pastures in Brazil. For this group, there is a wide range of plant size and architectural configurations, which should be considered in order to understand their vegetative perennation mechanisms (e.g., tillering) and adaptation to grazing. Among these tall-tufted growing grasses there are species and cultivars of *Pennisetum purpureum* Schum. and *Panicum maximum* Jacq. with a very high dry matter production potential, which are especially demanding in terms of soil fertility and fertilization. The *Brachiaria* genus has a large variety of morphological types and growth habits varying from small tussock forming plants such as *Brachiaria brizantha* Hochst ex A. Rich Stapf. and *Brachiaria ruziziensis* R. Germ & Evrard, creeping plants such as *Brachiaria humidicola* (Rendle) Schweick, and *Brachiaria purpurascens* Henr. Blumea (Syn. *Brachiaria mutica* (Forsk) Stapf.), to intermediate morphological types characterized by an initial prostrate growth that evolves to an erect form such as *Brachiaria decumbens* Stapf. and *Brachiaria hybrid* cvs Mulato I (*B. ruziziensis* × *B. brizantha*) and Mulato II (*B. ruziziensis* × *B. decumbens* × *B. brizantha*).

According to Cruz & Boval [75], the large phenotypic variability in forage grasses characterized by the wide range of morphological types reveals the need for particular strategies for different species to control canopy development and biomass production. In this context, plant growth and development, leaf turnover, and population dynamics must be analyzed as integrated physiological and adaptive processes that may determine significant changes in the morphological composition of the produced herbage, sward structure, and spreading and colonization pattern. As a result, the recent research with tropical forage grasses has been focused on identifying grazing management strategies that harmonize with and optimize the natural growth cycle of plants, favoring their growth and production. During the last two decades significant progress was made [76] and management targets were generated as a means of transferring this knowledge to practical use [3].

3.1. Morphological Plant Types and Growth

Plant responses to grazing have the objective of maximizing sward leaf area index (LAI) in order to optimize assimilate production and energy supply to plant growth. They are usually integrated and occur at two levels of complexity—the turnover of leaves in individual tillers and the turnover of tillers in tiller population [77]. The LAI is determined by three components: tiller population density, number of leaves per tiller, and leaf size (leaf lamina area). In grasses, leaf size is mainly a function of lamina length, which is controlled by defoliation height, and the number of leaves per tiller is relatively stable, leaving the tiller population density as the component where changes in LAI can be readily expressed [78]. Tiller population density is the result of the balance between tiller appearance and death, which characterizes the tiller population dynamics that influences tiller population stability [79]. These, in turn, determine modifications in the demographic profile of the tiller population, altering the age profile of tillers, sward structure (canopy architecture), photosynthetic efficiency of sward leaf area, and the persistence of the tiller population [80].

The integration of plant responses determining plant growth in grazed communities was described by Chapman & Lemaire [68] and related to plant morphogenesis. Although originally described for temperate grasses, the approach developed by the authors provided a solid basis for understanding the growth patterns of tropical grasses. During the vegetative growth stage, the morphogenesis of temperate grasses is characterized by leaf appearance, leaf elongation, and leaf lifespan. Since only leaves are produced as above-ground organs, those responses were identified as the major morphogenetic characteristics determining plant and sward structure. Cruz & Boval [75] studied a group of temperate and tropical grasses and proposed the existence of two main morphogenetic types of grasses: tufted and stoloniferous species. According to the authors, while in tufted grasses leaf appearance and final leaf length are related to the length of the sheath tube, in stoloniferous grasses they are related to stolon elongation. In stoloniferous plants, grazing management strategies characterized by lenient defoliation or by high nitrogen availability favor the accumulation of stolons. As a result, leaf appearance rate is increased and final leaf length becomes shorter towards the apex of the stolons. The permanent internode elongation in tropical stoloniferous plants and the stem elongation only during the reproductive stages of growth in temperate grasses differentiate the two morphogenetic types [75]. Although the authors indicated that the growth pattern of tropical tufted grasses would be similar to that of temperate grasses, Cowan & Lowe [81] argued that in tropical tufted grasses stem elongation during the vegetative growth stage was not negligible as for temperate grasses, leading Hodgson and Da Silva [82] to consider stem elongation as an important additional morphogenetic characteristic determining plant responses to grazing for tufted tropical grasses. These are plants with production of both leaves and stems as above-ground organs, a condition that would characterize them as an intermediary plant type. The existence of this intermediary morphogenetic type was initially indicated by Cruz & Boval [75] and recently discussed by Pereira *et al.* [83] for *Brachiaria brizantha* cv. Marandu. The evidence available describes a significant and regular stem elongation process that occurs during the vegetative growth stage of tropical tufted grasses [84] subjected to lenient and/or intermittent grazing which is independent of floral induction.

The tufted growth pattern and its implications to sward structure were originally described for *Panicum maximum* cv. Mombaça under intermittent stocking management [85]. During the early stages of regrowth the main morphological component accumulated is leaf. As LAI increases, competition for light within the sward canopy increases and plants change their growth pattern as a means of optimising light capture through stem elongation. The shift in growth pattern occurs when canopy light interception reaches and exceeds 95% [84]. According to Ballaré [86], during the early stages of regrowth, when LAI is small, the amount of photosynthetic radiation received by the leaves is not affected by neighboring plants, a condition that favors investment in leaf production. However, before any reduction in light availability occurs, small variations in light quality, caused by the preferential absorption of the blue and red wavelengths, and reflection of the far red, can provide plants with information regarding their surroundings [87]. The signaling mechanisms related to changes in the light environment within the canopy allow plants to redirect growth to more favorable patches (areas with better light availability), being common in morphological modifications of tropical grasses associated with shade avoidance responses (in contrast to shade acclimation or tolerance). As a result, the interval between successive defoliations determines the amplitude of the plastic responses plants have to develop [88]. When managed with long regrowth intervals that allow canopy light interception to exceed 95% (e.g.,

maximum light interception— LI_{max}), sward herbage mass is greater but with a higher proportion of stem and dead material relative to leaf, resulting in greater total dry matter production, but smaller leaf dry matter yield [84] and lower nutritive value of the produced herbage [89]. In addition, long grazing intervals characterized by the pre-grazing target of LI_{max} result in a greater proportion of the produced herbage being lost to the soil as a consequence of physical damage and/or rejection, decreasing the efficiency of the grazing process [85,90,91]. The investment in stem elongation results in taller swards with an increased proportion of stems in the upper layers of their vertical profile [92], increasing the difficulty of grazing and in maintaining the post-grazing management targets [93,94]. As a result, the benefit of greater total herbage accumulation is offset by the greater grazing losses when long regrowth intervals are used, indicating that, although herbage accumulation per grazing cycle is smaller when managing with shorter grazing intervals ($LI_{95\%}$), the more frequent defoliation results in larger number of grazing cycles and total herbage accumulation (with higher leaf proportion) than when managing with longer grazing intervals (LI_{max}) [84,91,94,95].

The same pattern of response was later described for *Panicum maximum* cv. Tanzânia [90,92], *Brachiaria brizantha* cv. Xaraés [96,97], *Brachiaria brizantha* cv. Marandu [98], *Pennisetum purpureum* cv. Cameroon [99], *Brachiaria decumbens* cv. Basilisk [100], mulato brachiariagrass (*Brachiaria ruziziensis* x *Brachiaria brizantha* cv. Marandu) [101], *Panicum maximum* cv. Aruana [93], and *Pennisetum purpureum* cv. Napier [94,95], showing consistency within a wide range of morphological types and a strong light effect determining plant growth. More recently, in a study where a forage grass (*Brachiaria brizantha* cv. Piatã) was grown in monoculture or in association with trees (*Eucalyptus* sp.) planted at different densities (181 and 718 trees/ha) and managed under rotational grazing, the importance of light as the determining factor of plant growth and responses was corroborated and expanded, since plant morphogenetic and population dynamic responses were strongly influenced by the amount of photosynthetic radiation available [102]. Under those conditions, a wide range of light availability was generated through regrowth interval, tree density, distance from the tree rows, and season of the year (in this case representing the varying solar angle from summer to winter), illustrating the key role played by light availability within the sward in determining plant growth and herbage production. Further, the evidence suggests that, among the environmental factors, light would determine the potential of herbage production (ceiling LAI), and temperature and water availability (as well as nutrients) would determine if that potential could be realised and, if so, how fast the responses and processes would happen.

3.2. Population Dynamics and Stability

Although adjustments in morphogenetic responses of individual tillers are an important way to maximize leaf area, Matthew *et al.* [78] argued that tiller population density is the main component of sward leaf area when leaf size increase is restricted by defoliation. In plant communities, the beginning of regrowth is characterized by increases in LAI arising from both new tiller production and leaf growth on the existing tillers. However, as regrowth progresses and LAI increases, competition for light within the sward canopy increases, tiller recruitment ceases, and population density starts to decrease. From this point onwards further increase in tiller size and LAI result in reduction in tiller population, characterizing the size-density compensation or self-thinning mechanism described by Matthew *et al.* [103] for

temperate grasses and later corroborated by Sbrissia *et al.* [104,105], Sbrissia & Da Silva [106], and Calsina *et al.* [107] for tropical grasses.

According to Sbrissia & Da Silva [106], this mechanism ensures that sward LAI remains relatively stable for a wide range of defoliation regimes, highlighting the importance of the vegetative mechanism of plant perennation (tillering) for developing grazing management strategies for tropical grasses. In stoloniferous species like *Cynodon* spp. and aerial-tiller producing grasses such as most tropical grasses, the physiological integration of plants seems to play an important role in adaptation and response to defoliation. Interconnected ramets of clonal plants, although potentially independent, can specialize functionally in performing a limited number of tasks, such as the uptake of resources from above and below ground, carbohydrate storage, vegetative spread, and sexual reproduction [108]. Such specialization and cooperation is comparable to a division of labor in economic systems or in colonies of social animals. The ecological significance of labor division in clonal plants may be found in the increased efficiency of entire clones for exploiting their environments. Preliminary evidences of this pattern of labor division through specialization in development of particular phytomers [109] were reported by Sbrissia *et al.* [104] for Coastcross bermudagrass (*Cynodon* spp.). According to the authors, a new cluster of tillers was formed along a stolon at regular intervals of three phytomers (node with roots and a daughter tiller followed by two successive leaves—Figure 1), suggesting that the first leaf would support root development, the second would support tiller development and the third would support stolon internode elongation. The clonal integration, associated with the labor division, explains the low values of the individual tiller leaf area-to-volume ratio (R value; [110]) recorded for two *Cynodon* spp. cultivars (Coastcross and Tifton-85) (13.1–17.1; [104,105]). Low R values imply that tillers present a small leaf area in relation to their volume, suggesting a reduced ability to use the incident light and, therefore, could be an indicative of reduced competitive ability. However, a plant with low R value could maintain its competitiveness through a higher level of clonal integration, since the R value of an object which is a cluster of similar modules is much greater than the R value of an isolated module [103]. For Tifton-85, assuming a hypothetical clonal integration of four tillers, R values increased (26.2 to 34.8; [105]) and became closer to 50, the reported value for perennial ryegrass [111], leading authors to infer that the natural high competitive ability of *Cynodon* spp. is the result of some degree of clonal integration, since R values of individual tillers are low. This is in line with the argument of De Kroon *et al.* [112], according to whom whole-plant plasticity is the sum of all environmentally induced modular responses plus all interaction effects that are due to communication and behavioral integration of modules.

In tall, tufted, tussock-forming grasses such as elephant grass (*Pennisetum purpureum*) and Mombaça and Tanzania guinea (*Panicum maximum*) grass, tillering is an important component of tussock growth and expansion which determines the efficiency of soil surface occupation through variation in the frequencies of colonized and bare ground areas in the pasture. In this plant type, the proportion of areas with tussocks or bare ground associated with tussock size represent an important indicator of grazing management effect on pasture persistence and productivity. Modifications of the horizontal sward structure in response to grazing were originally reported for rotationally managed Mombaça guinea grass by Lopes [113] and Montagner [114], and demonstrated that in areas with deficient grazing management or not in regular use, the stability of the tiller population was lower, tussock perimeter varied within a wider range (very small to very large tussocks), the proportion of bare ground was

higher, and tiller population density was lower relative to pastures managed in a regular and controlled manner using adequate targets to control grazing [80]. Under those conditions, adjustments in foliage angle were the strategy used by plants to optimize light capture, resulting in 95% canopy light interception at lower sward height (60 cm; [113]). However, during the second year of the experiment, after one year adapting to regular and controlled grazing management, the tiller population density and the proportion of areas with tussocks increased, the proportion of bare ground decreased, the variation in tussock perimeter decreased (very small and very large tussocks disappeared) and the frequency of average size tussocks increased, resulting in 95% canopy light interception at 90 cm [114], the same value reported by Canevalli *et al.* [85] for Mombaça guinea grass. These results showed adaptation of plant population to defoliation regimes used and the importance of tiller and tussock population and size for the necessary adjustments in sward LAI. They also highlight the need to carefully plan experimental treatments and experiments, since there may be the need to allow for sward adaptation to defoliation regimes before starting the measurement period. A more uniform ground cover with smaller tussocks, greater tiller population density, and short distances between tussocks results in more efficient sward carbon acquisition [115] and may also minimize weed encroachment [116].

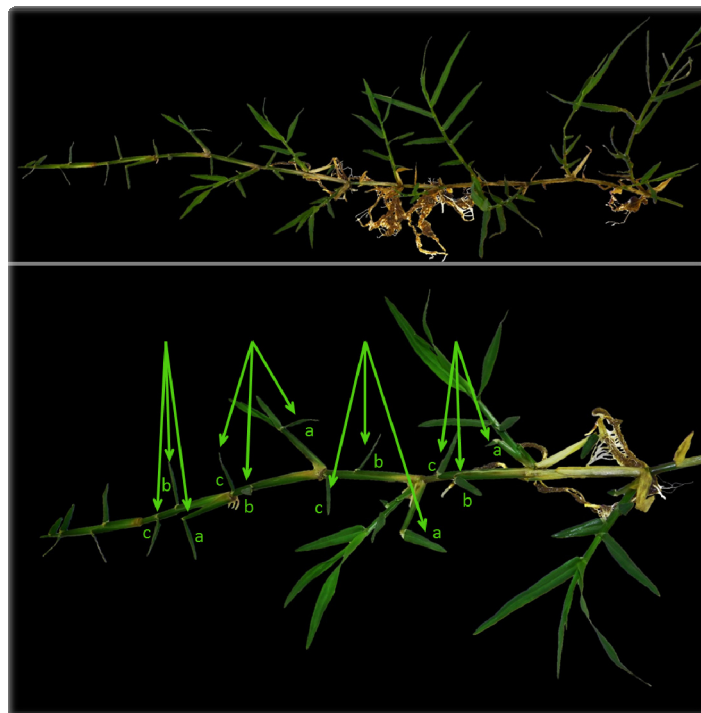


Figure 1. Triplet structure of *Cynodon* spp. cv. Tifton-85 showing cluster formation at regular intervals of three phytomers. Letters a, b and c indicate leaf 1, leaf 2, and leaf 3 of each cluster, respectively.

More recently, new evidence on modification of sward horizontal structure in adaptation to grazing management was reported by Pereira *et al.* [94,95] for rotationally managed Napier elephant grass (Figure 2). The authors showed that grazing management interfered with the vegetative mechanism used by plants for perennation by altering the number and the proportion of aerial and basal tillers in tiller population, with consequences on sward horizontal structure and herbage accumulation. Swards under

more frequent defoliation (managed with the $LI_{95\%}$ pre-grazing target) showed a larger contribution of basal tillers, while those subjected to less frequent defoliation (managed with the LI_{Max} pre-grazing target) showed a larger number of aerial tillers per support unit (basal tillers + decapitated tillers), an analogous growth strategy to that associated with the increase in tiller number per integrated physiological unit (IPU) described by Derner *et al.* [117] for the tussock-forming grass *Schizachyrium scoparium* (Michx) Nash. For similar tussock perimeters, swards managed with the $LI_{95\%}$ target showed higher tiller population stability index, higher frequency of tussocks and lower frequency of bare ground relative to those managed with the LI_{Max} target. According to the authors, basal tillers would be responsible for increasing the basal area of tussocks and reducing the sharing of assimilates and nutrients among tillers within an IPU, promoting more uniform distribution of tillers within tussocks, and of tussocks in the area, a condition that would favor carbon acquisition [115] and could increase the growth potential of swards. These differences in patterns of plant distribution between targets of pre-grazing LI show that the duration of the regrowth period (e.g., grazing interval) strongly affects tiller replacement. Similarly, management strategies that favor aerial tillering in tall-tufted tussock forming grasses could adversely affect the dynamics of tussock growth and expansion and the capacity of plants to exploit soil surface, as well as increase the risk of erosion and presence of weeds.

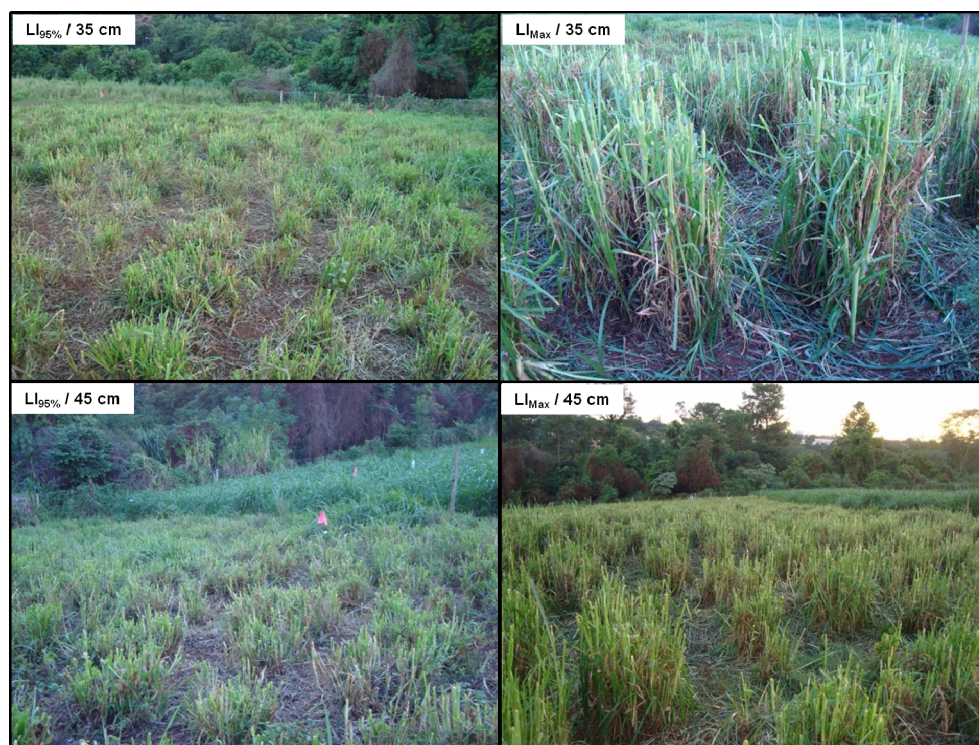


Figure 2. Tussock size and distribution in *Pennisetum purpureum* cv. Napier paddocks subjected to strategies of rotational stocking management characterized by pre-grazing targets of 95% and maximum canopy light interception during regrowth ($LI_{95\%}$ and LI_{Max}) and post-grazing targets of 35 and 45 cm.

In addition to changes in sward structure and in the spreading and colonization ability of plants, tiller appearance and death also interfere with the age profile of the tiller population [80]. Younger tillers (< 2 months old) have higher leaf appearance and elongation rates than old tillers (> 4 months

old) [118,119], highlighting the importance of grazing management as a means of manipulating the age profile of the tiller population. More frequent and/or more intense grazing for intermittent or continuous stocking management, respectively, results in higher intensity of defoliation and, consequently, higher rates of tiller death and appearance (higher turnover in tiller population). Similarly, agronomic practices such as fertilization and irrigation accelerate plant growth and increase the turnover of leaves and tillers, resulting in a younger profile of the tiller population [120]). This was demonstrated by Paiva *et al.* [121] for marandu palisade grass receiving contrasting rates of nitrogen fertilizer. Tiller age has a significant impact on leaf turnover and elongation, with higher values recorded for young relative to old tillers. Young tillers are also more responsive to nitrogen fertilization [119,121], increasing the benefits of agronomic practices and fertilization and also favoring the production of high nutritive value herbage [89], an important condition for ensuring high animal performance.

Seasonal variation in the availability of climatic conditions affects both the number of tillers produced and the longevity of the tiller generations. Periods of high availability of climatic growth factors (e.g., temperature and rainfall), as in late spring and summer, are characterized by high rates of tiller appearance and death and, therefore, short-lived generations. However, the balance between tiller appearance and death is usually positive and results in increased tiller population density. During autumn/winter and early spring, tiller survival increases, although not enough to offset the reduction in tiller appearance, and tiller population density decreases [120,122]. Such variations in tillering dynamics represent a natural cycle of plant growth throughout the year, and occur regardless of the grazing strategy, grazing method, and fertilization level [120].

Similar to the pre-grazing management targets, definition of post-grazing targets is also important and dependent on the plant's resistance and adaptation to grazing, since it interferes with how quick sward leaf area is restored. In general, more severe grazing results in lower sward residual leaf area and herbage mass soon after grazing and, consequently, lower canopy light interception and longer grazing intervals than under more lenient grazing [90,92]. However, these characteristics may be offset by the corresponding higher rates of herbage accumulation, greater herbage removal and higher grazing efficiency in more severely grazed pastures, within certain limits. For Mombaça guinea grass [85], *Andropogon* grass (*Andropogon gayanus* cv. Planaltina [123]), Xaraés palisade grass (*Brachiaria brizantha* cv. Xaraés [96]), and Napier elephant grass [94,95,124] under rotational grazing, similar values of total herbage accumulation have been reported for grazing severities equivalent to a removal of 40%–60% of the pre-grazing height when associated with grazing at LI₉₅%. On the other hand, definition of post-grazing targets also influences the short term rate of herbage intake of grazing animals by interfering with their ability to graze [3]. Carvalho [125] and Carvalho *et al.* [126] described how bite size, biting rate, and intake rate varied from the beginning to the end of grazing of rotationally managed *Cynodon* spp. and *Sorghum bicolor* L. During the first stages of the grazing process the short-term rate of intake remained stable, starting to decrease linearly after 40%–50% removal of the initial height [127]. For *Cynodon* spp. the decrease occurs at a faster rate because succeeding layers of herbage are more restrictive to bite formation than for *Sorghum bicolor* [128]. Similar results were reported for *Brachiaria brizantha* cv. Marandu [129] and for Mulato brachiariagrass hybrid [130]. As grazing progresses and herbage mass decreases towards the end of grazing, the proportions of stem and dead material increase in the consumed herbage as the consequence of the changing plant-part composition of the sward vertical profile [129–131]. This pattern of variation in the short-term rate of intake in relation to the decreasing

sward height during grazing was formally described by Fonseca *et al.* [127,132] and corroborated by Mezzalana *et al.* [128], indicating the potential for manipulating pre- and post-grazing conditions as a means of optimising herbage production and intake in rotationally managed pastures. In general, more frequent defoliations (at 95% canopy light interception) than traditionally used, associated with moderate grazing severity (post-grazing heights around 50% of the pre-grazing height), result in greater leaf dry matter production [84,93,96,124], higher nutritive value [89,90] and intake rate of animals [127–129,132], augmenting animal performance and productivity [133], indicating that rational intensification of grassland use could be an effective way of ensuring sustainability of tropical pastoral systems of animal production. These results are in line with the findings of Knoke *et al.* [134] and provide feasible options for recovering degraded areas, reducing pressure on forest lands and releasing additional area for cropping and food production.

Under grazing, organic reserves are also an important feature to be considered, since they may represent an important source of energy during the early stages of regrowth, particularly when grazing is severe (low stubble heights), favoring regrowth and the competitive ability of plants. According to Matthew *et al.* [103], some grasses may lack organic reserves for bud release to increase tiller population density, a condition that could lead to failure in replacing dead tillers and result in pasture degradation. Despite the importance of stored reserves, the number of grazing studies with tropical grasses evaluating organic reserves is not large. Carvalho *et al.* [135] evaluated the concentration and the amount of total non-structural carbohydrates (TNC) in three *Cynodon* spp. cultivars (Tifton-85, Florakirk, and Coastcross) subjected to a range of grazing intensities under continuous stocking represented by the management heights of 5, 10, 15, and 20 cm. There was no reduction in either concentration or pool of TNC in shoots and roots of any of the grasses as a consequence of more severe grazing. Similar results were reported by Da Silva *et al.* [136] for Marandu palisade grass in an analogous experiment where management heights were 10, 20, 30, and 40 cm. Both experiments showed significant variation in the pool of TNC throughout the year, indicating a strong seasonal effect similar to other species [137]. Recorded values were greater during winter and early spring for both roots and shoots, and there was a reduction in the TNC pool in shoots during periods of active plant growth (late spring and summer). The TNC pool was larger in shoots than in roots, regardless of grazing intensity and season of the year [136], consistent with the findings of White [138], who indicated that the major storage areas of carbohydrate reserves in perennial grasses are usually the lower regions of the stems (stem bases), stolons, crowns, and rhizomes instead of roots.

The results from those experiments indicate the existence of a trade-off between leaf area quantity and quality in swards subjected to varying levels of grazing intensity under continuous stocking management. Under lenient grazing, LAI is high but photosynthetic potential of leaves is low, a consequence of the low light availability within the sward canopy. On the other hand, under severe grazing, swards are capable of compensating the smaller LAI through higher rates of tiller appearance and larger population of younger tillers [122], with greater growth potential than older tillers [121]. Since under continuous stocking management a relatively constant proportion of the sward leaf area is removed [139], the remaining leaf area may be sufficient for supplying assimilates, a condition in which the quality of the sward leaf area is crucial for maintaining plant growth [136]. This highlights the importance of the turnover in tiller population and the tillering process in tropical forage grasses, since the ability to replace tillers ensures rapid restoration of photosynthetic tissues and plant growth.

Under intermittent stocking, part of the initial growth of orchardgrass (*Dactylis glomerata* L.) [140] and perennial ryegrass (*Lolium perenne* L.) [140,141] after defoliation is sustained by assimilates supplied by the organic reserves during the first days of regrowth. However, Ward & Blaser [140] demonstrated that both the reserve carbohydrates and the remaining leaf area (current assimilates supplier) are involved in restoring the carbon balance of plants throughout regrowth. Leaf area restoration and regrowth depend not only on carbohydrate reserves but also on nitrogen reserves [141,142]. Carbon stored as carbohydrate is usually used following defoliation, but nitrogen usually comes from internal remobilization and recycling due to protein turnover associated with leaf senescence [142].

Although the importance of determining limits of grazing severity (management height) for ensuring leaf area restoration, plant growth and persistence is well recognized [143], understanding how defoliation frequency affects carbon and nitrogen reserves in tropical perennial forage grasses is less clear. Turner *et al.* [144] showed that frequent defoliation of orchardgrass (*Dactylis glomerata* L.) resulted in reduced water-soluble carbohydrate assimilation and, therefore, leaf, root, and tiller dry matter accumulation during subsequent periods of regrowth. Lestienne *et al.* [145] showed that defoliation frequency did not substantially affect N uptake, mobilization, and allocation between roots and adult and growing leaves on a plant basis, although tiller number per plant was largely increased under repeated defoliation in perennial ryegrass. In rotationally grazed tropical grasses, it is expected that defoliation severity has a relatively greater impact on mobilization and use of plant organic reserves than on temperate grasses, since it is the defoliation frequency that has been shown to be more related to the turnover of leaves in individual tillers and of tillers in tiller population. However, as discussed previously, some species have shown similar herbage accumulation within a range of grazing severity levels. As a result, field experiments are needed to evaluate whether the high population of young tillers is capable of restoring organic reserve levels during regrowth and to better understand the mechanisms involved with the use of organic reserves by tropical grasses.

In general, defoliation severities equivalent to 40%–60% removal of the initial (pre-grazing) height are within the limits of grazing resistance and use of plants, and ensure favorable conditions for high rates of herbage intake and animal performance when associated with the right pre-grazing management targets. In this context, defoliation frequency is relatively more important than defoliation severity for controlling stem elongation, the main morphological component that determines degeneration of sward structure [84] and imposes restrictions to grazing [3], particularly for tall-tufted grass species such as *Panicum* sp. and *Pennisetum* sp.

4. Future Perspectives and Challenges

The research with forage tropical grasses has shown significant progress since the late 1990s and early 2000s, a consequence of conceptual changes in approach and experimentation strategies. Such change provided the basis for relatively fast progress towards a knowledge of plant functional mechanisms comparable to that already available for temperate grasses. Although part of the same botanical family, temperate and tropical grasses have different photosynthetic pathways, a condition that has a direct influence on some important growth processes. For example, from an ontogenetic point of view, the results have demonstrated that, despite having a similar modular organization (sequential appearance of phytomers on the same tiller), there may be some differences in the dynamics of phytomer

appearance and expansion between C₃ and C₄ grasses. As with C₃ grasses, C₄ grasses have, for a given species, a relatively constant number of live leaves per tiller. However, it is common for the majority of C₄ grasses for the concomitant expansion of two or more leaves and only one senescing leaf on the same tiller. As a result, the senescence rate is greater in a C₄ grass leaf relative to a C₃, suggesting that the former have a faster mobilization of nutrients from senescing leaves for supporting their growth. Another example is related to the stem elongation (stem + pseudostem) process. In contrast with C₃ grasses, C₄ grasses invest in stem elongation during vegetative growth. From an ecological point of view, such a strategy is interesting because it allows tillers to place their leaves in the upper strata of the sward, increasing the range of LAI traversed from the residue after grazing to the light interception capacity at the next grazing and consequently increasing their competitive ability and productivity. If on the one hand there is consistent evidence of a strong correlation between competition for light and high rates of stem elongation in C₄ grasses in the literature, on the other hand there is still the need for a better understanding about a possible ontogenetic programming of plants for producing stems (stem + pseudostem). That is because even with relatively high light availability (low light competition), tillers of tropical grasses can elongate the stem for maintaining the upright form. If the reasons for increasing stem elongation in relatively dense swards (high LAI) seem to be well explained by the amount and quality of the incident light, there is still no explanation for how and why stem elongation occurs in situations where light is not a limiting factor. Nevertheless, these two examples (leaf ontogenesis and stem elongation) are indicators of a likely genetic programming of C₄ grasses that is still not fully understood.

In relation to studies on a plant population level, several experiments have tried to describe the demographic pattern and tillering dynamics as well as the tiller size-density compensation mechanism for tropical forage grasses. In general, the results generated for some important genera such as *Panicum*, *Brachiaria* and *Pennisetum* have shown that tillering occurs at varying rates throughout the year, with a high turnover in tiller population during periods of high availability of resources (especially water) and suitable conditions (temperature) determined by climatic factors (late spring and summer) and a relative transitory instability in tiller population during periods of limited growth (winter and early spring). In spite of that, some studies have demonstrated that there seems to be an interesting interaction between defoliation severity and tiller population stability. For example, there is evidence that maintenance of ideal targets of grazing management for ensuring animal performance (relatively moderate defoliation, regardless of the grazing method used) result in high tiller survival during periods of intense vegetative growth (late spring and summer), favoring population stability without the need for intense tillering. Conversely, as tillers of most grass species have a relatively short period of life (less than six months, on average), there is high mortality during periods of adverse climatic conditions, causing instability in tiller population during autumn and winter. Therefore, it seems reasonable to hypothesize that strategic reductions in grazing management target heights during the autumn/winter period could stimulate tillering at the beginning of the following growing season, increasing population stability and getting pastures back into production earlier in the season. However, the impact of such a management strategy on the dynamics of the tiller population in the long term is still not clear. This highlights the importance of multi-year experiments depending on the question being asked.

Still on a plant population level, it is also important to point out the similarities in the tiller size-density compensation mechanisms found between C₃ and C₄ forage grasses characterized by the

inverse relationship between tiller weight and population density on grazed swards, particularly those managed under different intensities of continuous stocking. Despite that, there is still limited information regarding the dynamics of that mechanism during regrowth of intermittently grazed pastures. A better understanding of the process could have important implications. For example, it is normally accepted in the scientific literature that after severe cutting or grazing the restoration of sward leaf area occurs, mainly, through the recruitment of new tillers from the plant base. As a result, an interesting exercise would be to determine if there would be a maximum residual LAI that would minimize tiller recruitment after grazing, increasing population stability and reducing grazing interval. However, since tillers have a genetically programmed lifespan, studies of this nature would have to consider the trade-offs between the two processes and evaluate whether management strategies that favor tiller survival could hinder plant persistence by reducing their ability to renew tiller population in subsequent grazing cycles.

Finally, several experiments with temperate grasses have shown that mixtures of plants from different species can increase (or at least maintain) the productive capacity of pastures relative to monocultures [146]. That possibility has not yet been seriously considered for tropical grasses. C₄ plants have a wide functional and morphological diversity (e.g., stoloniferous, prostrate, tall-tufted plants), a condition that allows for species combinations and coexistence between them (as corroborated by several experiments on native multi-specific pastures, e.g., [147,148]). For example, *Cynodon* species (stoloniferous/rhizomatous plants) are functionally different from *Pennisetum* species (tall-tufted, tussock forming plants). While the former direct a large proportion of their resources to producing structures like stolons (with large capacity for storing reserves), allowing plants to forage for light and resources horizontally, the latter can invest in structures like aerial tillers capable of occupying higher positions in the vertical strata of the sward, increasing LAI, and increasing light interception. Such functional and morphological diversity of tropical grasses indicates the possibility of coexistence of different plant types in the same area, given their complementary growth habits. This would allow for biodiversity in tropical ecosystems, and could represent a new window of opportunities towards attaining sustainable systems of animal production from pastures in the tropics. It seems that the question is not *whether* it can be done, but *how* to do it. Multi-specific pastures are normally associated with increased carbon sequestration, higher levels of soil organic matter, less evaporation with possible reduction in water stress to plants, increased meso and macrofauna biodiversity in the soil, and increased nutrient cycling [149]. There is no doubt that such benefits would boost multi-functionality and services provided by pastoral ecosystems in the tropics and could have an important economical, environmental, and social impact.

Acknowledgments

Thanks are due to Domicio do Nascimento Jr. for his contribution with the historical overview presented and to Carlos Guilherme Silveira Pedreira for his help in reviewing this manuscript, to the Brazilian National Council for Scientific and Technological Development (CNPq) for the sponsorship provided.

Conflicts of Interest

The authors declare no conflict of interest.

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