Research, Society and Development, v. 11, n. 14, e288111435530, 2022
(CC BY 4.0) | ISSN 2525-3409 | DOI: http://dx.doi.org/10.33448/rsd-v11i14.35530

Developmental factors for forage plants and their responses under stress conditions

Fatores de desenvolvimento para plantas forrageiras e suas respostas sob condições de estresse

Factores de desarrollo de las plantas forrajeras y sus respuestas en condiciones de estrés

Received: 09/19/2022 | Revised: 10/17/2022 | Accepted: 10/22/2022 | Published: 10/27/2022

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Abstract
Climate change increases the vulnerability of agricultural production, mainly because it often causes stress to plants. Thus, this review presented the limiting factors in the development of forage plants and how these individuals respond in stressful situations. The factors that are linked to development, consequently with plant production, are water, light, temperature, soil and nutrients. Each of these factors acts differently in plants, from metabolic processes to plant mass productivity. Thus, for plants to develop efficiently, these factors must act within a range that allows them to perform their basic functions of growth and development. However, if one of these growth factors is acting negatively, that is, it is not within the adequate level that the plant needs, it can subject plants to stress conditions, depending on its intensity and duration over the plant. The growth factors directly influence the morphogenic characteristics, and, consequently, the structural characteristics and grazing management, the latter is also considered a limiting factor in the development of plants, due to its importance for animal production, in which a balance between animal and plant productivity. In this sense, understanding how the growth factors act on the development of plants is fundamental for constructing models that help in the efficient management, mainly for grasses under stress conditions and under the pasture system.
Keywords: Solar radiation; Temperature; Water; Soil; Nutrients; Plant stress.

Resumo

As mudanças climáticas aumentam a vulnerabilidade da produção agrícola, principalmente por proporcionarem estresse às plantas. Dessa forma, objetivou apresentar os fatores limitantes ao desenvolvimento de plantas forrageiras e como esses indivíduos respondem em situações de estresse. Os fatores que estão ligados ao desenvolvimento, e consequentemente a produção vegetal, são: água, luz, temperatura, solo e nutrientes. Cada um desses fatores atua de forma diferente nas plantas, desde os processos metabólicos até a produtividade da massa vegetal. Dessa forma, para que as plantas se desenvolvam eficientemente, esses fatores devem atuar dentro de uma faixa que permita a realização de suas funções básicas de crescimento e desenvolvimento. No entanto, caso um desses fatores de crescimento esteja atuando de forma negativa, ou seja, não esteja dentro do nível adequado de que o vegetal necessita, ele tem o potencial de submeter as plantas a condições de estresse, dependendo da sua intensidade e duração sobre a planta. Os fatores de crescimento influenciam diretamente nas características morfogênicas, e, consequentemente, nas características estruturais e no manejo do pastejo, este último é também considerado um fator limitante no desenvolvimento das plantas, devido a sua importância para a produção animal, em que se busca um equilíbrio entre a produtividade animal e vegetal. Portanto, para realizar um manejo da pastagem e do pastejo de forma eficiente e sustentável é necessário entender como as plantas são influenciadas pelos fatores abióticos, que estão ligadas ao seu desenvolvimento e como se comportam em situações de estresse.
Palavras-chave: Radiação solar; Temperatura; Água; Solo; Nutrientes; Estresse vegetal.

Resumen

El cambio climático aumenta la vulnerabilidad de la producción agrícola, principalmente porque suelen causar estrés a las plantas. Así, el objetivo de esta revisión fue presentar los factores limitantes en el desarrollo de plantas forrajeras y cómo estos individuos responden en situaciones de estrés. Los factores que se vinculan con el desarrollo, en consecuencia con la producción vegetal, son: agua, luz, temperatura, suelo y nutrientes. Cada uno de estos factores actúa de manera diferente en las plantas, desde los procesos metabólicos hasta la productividad de la masa vegetal. Así, para que las plantas se desarrollen eficientemente, estos factores deben actuar dentro de un rango que les permita realizar sus funciones básicas de crecimiento y desarrollo. Sin embargo, si uno de estos factores de crecimiento está actuando negativamente, es decir, no está dentro del nivel adecuado que la planta necesita, tiene el potencial de someter a las plantas a condiciones de estrés, dependiendo de su intensidad y duración sobre la planta. Los factores de crecimiento influyen directamente en las características morfogénicas y, en consecuencia, en las características estructurales y el manejo del pastoreo, este último también es considerado un factor limitante en el desarrollo de las plantas, debido a su importancia para la producción animal, en la que se requiere un equilibrio entre animal y vegetal. productividad. En este sentido, comprender cómo actúan los factores de crecimiento sobre el desarrollo de las plantas es fundamental para la construcción de modelos que ayuden en el manejo eficiente, principalmente para gramíneas en condiciones de estrés y bajo el sistema de pastoreo.
Palabras clave: Radiación solar; Temperatura; Agua; Suelo; Nutrientes; Estrés vegetal.

1. Introduction

In recent decades, climate change has become increasingly discussed among world organizations, countries, and educational and research institutes. The United Nations Organization (UNO), promotes worldwide conventions of member countries to discuss climate change, known as the Conference of the Parties (COP). In 2022, the Intergovernmental Panel on Climate Change (IPCC) Assessment looked at the main effects of climate change on the globe, reporting an increase in extreme weather patterns, such as more persistent droughts due to higher average temperatures and lower average rainfall. These climate changes raise the temperature, enrich the air with carbon dioxide (CO_2), and intensify water stress under plant development (Fariaszewska *et al.,* 2017; Potsch *et al.,* 2019)

In this sense, climate change increases the vulnerability of agricultural production, especially the plant production, susceptible to the stresses that climatic conditions can infer on the development and productivity of plant species. Over the past decades, studies have periodically addressed how the climatic elements influence the growth conditions of plants, especially under stress conditions, focusing on meat and milk production systems, in which pastures are used as the main source of food.

The plant production of forage plants requires water, light, temperature and nutrients, in this case, these elements must find in adequate and balanced conditions for the plant to express its productive potential. In this sense, Blackman (1905) adapted the concept of Liebieg's (1840) law of the minimum to the limiting factors of growth. The author defined that the process that depends on several environmental factors will have its rate or activity regulated by one factor at a time, in such a way that only the increase in the level of this factor increases the rate or activity.

Plant-animal relations in the pasture ecosystem suffer the direct effect of environmental factors, reflecting on the structure of the pasture and, consequently, on animal performance. According to Silva & Nascimento (2007), grazing management, concerning stocking rate and ingestive behavior of animals, is influenced by structural characteristics (proportion of morphological components, leaf/stem ratio, tiller density), and these, in turn, are influenced by morphogenetic characteristics. Therefore, these factors are expressed according to the responses of the plant in relation to the amount of CO_2, nutrient availability, water, solar radiation, temperature, as well as the conditions under which the pasture is managed. Knowledge of the factors that influence the ecophysiology of forage plants is essential to enhance and assist in the development of sustainable management (Silva *et al.*, 2015).

Thus, this review addresses the main factors that affect the development of forage plants and how these individuals respond in stress situations.

2. Growth Factors

Plant growth begins with the process of embryogenesis, in which a single cell is transformed into a multicellular entity with a characteristic organization. In this process, several physiological changes occur at the embryonic level, where the individual begins to be modulated according to the condition it is subjected to. Throughout their development, these individuals make changes in response to the environment, favorable to plant growth, or unfavorable, caused by survival conditions (Taiz *et al.*, 2017). According to these authors, the detection for these readjustments occurs from the sensorial systems, elucidated in the signal transduction process. This process begins with a signal, which can be an environmental stimulus, in which a receptor performs the transduction, and then converts it to trigger the cellular response.

The growth of plants presents a sigmoid behavior, subdivided into three phases: logarithmic phase, characterized by slow growth; linear phase, with an accelerated growth rate (accumulation of dry mass), and the third phase, in which growth is reduced, with an intensification of the senescence process. Regardless of the phase, the development of the forage plant may be influenced by internal factors (genetic changes, phytormones and vitamins) and/or external factors (light, water, temperature, soil, etc.). The phytohormones have the function of regulating the plant's metabolism and plant development, and are divided into five classes: auxins, gibberellins, cytokinins, ethylene and abscisic acid (Mello, 2002).

From a physiological perspective, for plant growth to occur, there needs to be a balance between photosynthetic activity and respiration, that is, there should be a greater photosynthetic rate than respiratory activity. Thus, the production process of forage plants begins with photosynthesis, where the different CO_2 fixation mechanisms reflect on the productive efficiency between C4 and C3 cycle plants. In this sense, the environment directly interferes in plant development, especially in how the plant will express its morphogenic characteristics, that is, the responses to a given stimulus, biotic or abiotic, can change its structural characteristics (Silva & Nascimento Júnior, 2007).

Abiotic factors are physical, chemical, or geological elements of the environment that can affect the plant community in different ways. In this sense, the efficiency of use of forage plants by animals in grazing is closely linked to abiotic factors (Santos et al., 2011). According to Difante *et al.* (2011) and Costa *et al.* (2017), the accumulation of dry mass by the plant is a result of morphogenic responses to the environment, directly interfering with animal productivity (Sbrissia *et al.*, 2018). Thus, it is necessary to know how plants express their morphogenic characteristics through measurements of morphological structures (leaf blade and stem) (Pereira, 2013), allowing to understand how abiotic factors act on the development and vegetative growth.

The forage yield is linked to the quantity and quality of these factors, which, depending on the intensity in the plants, can express these elements positively or negatively. The intensity of a certain growth factor alone or together can lead the plant to stress, which is conceptualized as an adverse condition that inhibits the normal functioning of the organism (Mahajan & Tuteja, 2005), strongly impacts the growth and productivity of forage plants in different ways.

Plants, when under stress, receive a series of signals in their receptor cells that trigger responses in an attempt to remain productive and perennial in the ecosystem. One of the main processes affected is photosynthesis, especially by climate change. According to Goh *et al.* (2012), the D1 protein of the photosystem II (FSII) protein complex is sensitive to perturbations caused by stresses, influences the electron transport chain in the chloroplast. Thus, the photosynthetic apparatus is extremely sensitive to stress conditions and can be affected even before morphological damage is observed (Dalberto *et al.*, 2015).

Therefore, knowing and identifying the abiotic (environmental) factors that affect the performance of forage plants and how they interfere with these individuals helps assist in the sustainable management of pasture (Silva *et al.*, 2015), thus ensuring its perenniality and productivity since the damage caused by abiotic factors tend to limit agricultural production effectively.

3. Solar Radiation

The availability of light is considered one of the most relevant factors in plant growth and survival (Guenni *et al.*, 2008). In this sense, the production of biomass can be limited by the ability of the plant to intercept photosynthetically active radiation (PAR) (Monteith *et al.*, 1991) and the efficiency of the conversion of solar energy into photoassimilates in the process of photosynthesis (Ong, 1999). Thus, to ensure the photosynthesis of the plant, solar radiation must have characteristics such as quantity, quality and intensity (Pes & Arenhardt, 2015), because these factors interfere with the physiological level of plant development.

The Sun emits wavelengths ranging from 400 to 3000 nm, however, plants absorb radiation in a spectral range between 400 and 700 nm (RFA). This absorption is allowed by the presence of chlorophyllated tissues, where chlorophyl is the main pigment associated with this process. In addition to the participation of pigments, the leaf area index (LAI), leaf size, leaf distribution angle, age, plant arrangement, time of year and cloudiness (Varlet-Grancher *et al.*, 1989), cultivated species and management practices (Santos *et al.*, 2011) influence the absorption of light by plants.

The efficiency of light absorption for biomass production requires the photosynthetic activity of the leaf, the ability to intercept the radiation and destination of assimilated products (growth, reserve or respiration) (Costa *et al.*, 2012). In this sense, the ability of the species to adapt to low light conditions, i.e. shade, depends on the development of morphological and physiological adjustments to take advantage of the low levels of solar radiation available (Pimentel *et al.*, 2016). Several studies have analyzed the development of plants under shaded (silvipastoral) systems and observed that *Digitaria* and *Urochloa decumbens* (Torres *et al.*, 2017), *Megathyrsus maximum* cv. Massai (Andrade *et al.*, 2004*), Urochloa brizantha* cv. Xaraés and Marandu (Martuscello *et al.*, 2009), have tolerance to shaded environments, depending on the level of shading.

The first consequence of the reduction of luminosity in plants is the decrease in the carbon assimilation rate, having as a consequence the allocation of photo-assimilates preferentially in the aerial part, drastically reducing root growth, studies by Fernandez *et al.* (2004) and Paciullo *et al.* (2010) observed this effect on roots, which at high levels can lead to plant death. The carbon allocation in shaded plants is considered an acclimation mechanism, acting on the increase and recovery of leaf area and stem elongation (Torres *et al.*, 2019), to enhance light uptake (Lemaire, 2001; Anjos & Chaves, 2021), i.e., the plant changes its morphological behavior to compensate for light deficiency.

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Another change in the morphological behavior of plants under shading is the increase in leaf blade length at the expense of the reduction in light intensity (Torres *et al.,* 2019). This event is considered a compensatory effect in the photosynthetic apparatus, because to the low availability of radiation, the plant needs more leaf area to capture light, prioritizing to investing its resources in the formation of leaf tissues. However, the greater length observed in the leaf blades, does not seem to contribute effectively to the increase in dry matter (DM) production (Gobbi *et al.,* 2009; Martuscello *et al.*, 2009), and may be explained by a reduction in the number of leaves to ensure greater penetration of sunlight into the canopy.

Research shows that the reduction in dry matter (DM) production occurs up to a certain level of shading (Torres *et al.*, 2017). According to Paciullo *et al.,* 2008, an increase in DM production can be observed up to 30% shading, which can be attributed to a reduction in tiller population density and an increase in tiller weight.

Photosynthetically active radiation influences the increment of the specific leaf area (Victor *et al.,* 2015) interfering in the leaf area index (LAI) (Gastral and Lemaire, 2015; Gomes *et al.,* 2019), as well as in the tiller population (Queiroz *et al.*, 2018), in which this population can be reduced, but compensated by the increase in the specific leaf area. This compensation effect is considered a mode of plant adaptation to low light conditions.

Tillering is a process that has the axillary bud as the genitor of new tillers (Gastral and Lemaire, 2015), thus, the higher level of shading can interfere in its development, since the reduction of solar radiation favors the production of auxin in the apical meristem (Taiz & Zeiger, 2009), which can block the synthesis or use of cytokinin, a phytormone responsible for tillering in grasses.

The increase in the specific leaf area in shaded conditions results in thinner leaves, making them less resistant to CO_2 diffusion inside the leaf (Gobbi *et al.,* 2011), this influence of solar radiation on the photosynthesis expresses responses in several physiological aspects, one of which is in the increase in chlorophyll concentration per reaction center (Taiz *et al.* 2017), due to the greater accumulation of chloroplasts on the leaf surface, to increase the efficiency in capturing light. Therefore, the reduction of light interferes with the anatomy, morphology and nutrient contents of the forage plant (Anjos & Chaves, 2021).

In this perspective, luminosity can relatively increase protein content when subjected to shading (Faria *et al.,* 2018; Barros *et al.,* 2019), and this same response can be observed in legume forages (List *et al.,* 2019). According to Whatley & Whatley (1982), C4 grasses require a greater supply of energy (higher light intensity) than C4 plants, which results in different anatomical and physiological, and consequently agronomic, characteristics.

Thus, the responses evidenced in the plants in relation to luminosity depend on the quality and intensity of the photosynthetically active radiation available, therefore, the grasses tolerant to shading present morpho-physiological modifications, which give them greater production stability compared to non-tolerant species (Paciullo *et al.,* 2016), when submitted to shaded productive systems.

4. Temperature

Temperature is considered one of the main abiotic factors that determine the distribution, adaptability and productivity of plants. This factor has immediate effects on biochemical (respiration and photosynthesis), physical (transpiration) or morphogenic processes (Gillet, 1984), influencing forage quality (Buxton & Fales, 1994) and acting directly on biomass accumulation.

Plant growth occurs when the plant reaches its photosynthetic efficiency, reached when the temperature is between 25 and 35°C for C4 cycle plants and 20 to 25°C for C3 cycle plants (Taiz *et al.,* 2017), influencing morphogenic characteristics due to its stimulation at meristematic points, promoting cell expansion, observed in leaf and stem elongation rates (Silva *et al.*, 2008). Thus, it is necessary to have an alternation of temperature during the day and night, to ensure maximum photosynthesis during the day and lower respiration rate at night, for better energy conservation, and consequently for plant growth.

These responses observed in the morphogenetic characteristics contribute to the understanding of the influence of temperature on forage plant quality, because to the fact that it directly affects the structural characteristics of the canopy, because the change in stem elongation rates interferes with the leaf/stalk ratio, and consequently in the leaf area index (LAI). These effects can alter the forage accumulation pattern (Gusmão Filho *et al.*, 2020), especially in tropical grasses, as observed by Euclides *et al.* (2008), who, when evaluating Massai and Mombaça, observed a lower forage mass accumulation rate between May and September, which is the period of lowest annual temperature in the Southern Hemisphere.

The period of higher temperature (summer) increases the rates of leaf emergence and elongation, being observed in Decumbens grass (Fagundes *et al.,* 2006) and Xaraés grass (Sousa *et al.,* 2011). Grasses submitted to high temperatures have a higher proportion of cell walls and lower digestibility, mainly due to the greater elongation of the stem. This effect occurs due the temperature accelerates the maturity of forage plants, with changes at the level of tissues, structural composition, increasing cellulose, hemicellulose and lignin, and, in parallel, reduces the cellular content, such as soluble carbohydrates, protein, minerals and vitamins (Santos *et al.*, 2011). Therefore, high temperatures increase the speed of grass development, because of which there is greater deposition of lignin, an indigestible compound for ruminant animals.

The behavior of plants subjected to different temperature levels depends on the mode of CO_2 fixation, i.e., C3 cycle plants tend to limit the rate of photosynthetic CO_2 assimilation, and C4 cycle plants reduce stomatal opening due to the high activity of the PEP carboxylase-PEPcase enzyme, conserving water while fixing carbon dioxide gas (Taiz *et al.*, 2017). In this sense, C3 cycle grasses can maintain growth down to 0°C, however, C4 cycle grasses may have reduced or even ceased dry mass accumulation at temperatures below 15 °C, thus tropical grasses tend to be the most affected by seasonality.

The literature shows that several studies have estimated the lower base temperature (Tbi) grasses, which can be defined as the temperature below which the plant does not develop, with values for elephant grass (*Pennisetum purpureum* cv. Napier) of 13.9°C, *Panicum maximum* and *Brachiaria* grasses around 15°C and *Cynodon* around 12°C (Mendonça & Rassini, 2006; Moreno *et al.*, 2004; Vila Nova *et al.*, 2004). Therefore, knowledge about the base temperature of forage plants is essential to assist in the choice of species because this factor directly influences the process of accumulation of forage mass (Andrade *et al.*, 2016), directly implicating the structural characteristics of the pasture, that is, the nutritive value.

4.1 Thermal Stress

Heat stress can occur in two ways, by exposure to low temperature or high temperature. Low temperatures limit growth and productivity because they inhibit metabolic reactions, restrict water absorption, reduce the water potential, prevent the expression of the genetic potential of the plant (Chinnusamy et al., 2007). In this way, plants are classified according to the temperature range, being them: I - cold sensitive plants (<12°C), II - cold tolerant plants (cooling temperature) and III - freeze-resistant plants (Garstka *et al.,* 2007).

The stress caused by low temperature can generate two levels of damage: freezing stress, which can form extracellular ice crystals; and chilling stress, which does not form ice crystals (Taiz & Zeiger, 2013). This sense, many plants can acclimatize to low temperatures or freezing by altering their physiological and biochemical functions, through increased levels of proteins, sugars, amino acids, accumulation of protein and protective osmolytes, changes in photosynthetic electron transport, modifications in the composition of the plasma membrane, inhibition of enzymes, and changes in gene expression, among others (Huner *et al.,* 2003).

According to Taiz & Zeiger (2013), heat stress by cooling causes reduced growth, lesions on the leaves and discoloration, vitrified (translucent) foliage, reduction and/or inhibition of photosynthesis, the generation of ROS (reactive oxygen species), slower translocation of carbohydrates, inhibition of protein metabolism and reduced respiration (Machado *et al.*, 2013), besides causing membrane rigidity, by altering the physical properties of lipids. Stress by freezing forms ice crystals outside and inside the cells, which can physically cut the membranes and organelles, causing cell dehydration since ice can reduce the water potential (Taiz & Zeiger, 2013).

Thus, it has been observed that plants can acclimate to low temperature, changing their physiological and biochemical processes to increase tolerance and survival to this condition. According to Chinnusamy *et al.* (2007), plants from temperate regions tend to have greater ability to acclimate to low temperatures, and that among forage grasses, tropical and subtropical grasses are more susceptible to damage caused by cooling (Machado *et al.,* 2013). According to Kral & Marocco (2019), evaluating five cultivars of summer perennial forage grasses, they observed that Jiggs grass (*Cynodon dactylon*) has greater frost tolerance than Tangola grass (*Brachiaria arrecta* x *Brachiaria mutica*), showing greater lesions on the leaf blades as the temperature would reduce.

High temperature stress can result in biochemical and metabolic alterations, with enzyme inactivation in different metabolic pathways, reduction of photosynthetic activity in the chloroplast and reduction of oxidative phosphorylation in the mitochondria (Araujo *et al.,* 1998); the greatest damage caused by high temperature is observed in the chloroplast and mitochondria. This heat shock response is characterized by the induction of a group of specific genes, which encode proteins called heat shock proteins (group with HSP), which, in turn, are important for the acquisition of thermotolerance (Diogo Junior, 2018).

The impact caused by high temperatures on complex processes such as photosynthesis and respiration depends on the plant genotype and growing conditions (Chaisompongpan *et al.,* 1990). To improve these effects and try to regulate the internal temperature, the participation of water is crucial, in virtue of the fact that plants cannot regulate their internal temperature (Taiz *et al.,* 2017). In summary, heat stress affects a broad spectrum of physiological processes, and is directly associated with water stress.

5. Water

The green biomass is constituting of 95% of water, considered fundamental in plant composition due to its importance for maintaining the functional integrity of biological molecules, cells, tissues and organisms (Chavarria & Santos, 2012). The main functions of water in plants are in the constitution of protoplasm and development of turgescence pressure; in growth, it participates in cell elongation with the absorption of water; in the transport of substances; and in metabolism, performing the dissolution of substances providing H^+ and OH^- ions.

The water requirement of the plant is defined according to the metabolism of CO_2 fixation. C3-type plants require around 550 and 750-g $H_2O.gMS^{-1}$; compared to C4 plants, which require between 250 and 350-g $H_2O.gMS^{-1}$ (Taiz *et al.,* 2017), these values are considered a minimum requirement for biomass production to enable the biochemical processes essential to plants (Lehninger, 2006).

Water participates in several metabolic processes, for example, in the hydrolysis of starch into soluble sugars, mainly during the night, and in the regulation of stomatal opening and closing, enabling CO_2 absorption (Chavarria & Santos, 2012). Furthermore, it is involved in the maintenance of cell turgidity, as well as in the movement and absorption of nutrients for plants through the mass flow process (Taiz & Zeiger, 2009). According to Marenco & Lopes (2005), for the cell to be physiologically active, about 80% to 95% of water must be present in its constitution. About 95% of the water absorbed by the roots is lost by transpiration, and the rest acts providing the biochemical and metabolic reactions for plant growth (Taiz *et al.,* 2017), thus, the distribution and proportion of the roots is essential to meet the water demand in the plant (Chavarria & Santos, 2012).

5.1 Water Stress

Water shortage directly affects basic metabolism, such as photosynthesis, respiration, definition of organ shape and structure, opening and closing of stomata, penetration of the root system into the soil, cell growth and expansion (Santos *et al.*, 2014), as well as the uptake of nutrients from the soil (Freire *et al.*, 2012). The implications of these effects on the plant vary according to the duration and intensity of stress (Araujo Filho & Carvalho, 1997) and the cultivated species (Araújo *et al.*, 2019), and these may develop mechanisms of tolerance and adaptation to such conditions (Silva et al., 2011).

According to Subbarao *et al.* (1995), the mechanisms of adaptation and/or resistance to water deficiency are divided into three types: escape or escape mechanism, avoidance or delay and tolerance. In the escape or escape mechanism, plants modify their phenological development due to their phenotypic plasticity, completing their life cycle to avoid the damage caused by stress (Wu *et al.*, 2010).

In avoidance or retardation, plants reduce their development, in the sense of less root expansion, reduction in leaf cell expansion, and change in leaf area (Haffani *et al.*, 2014). Regarding tolerance mechanisms, these allow the plant to maintain its metabolism, even under the influence of stress, rearranging some metabolic processes, such as osmotic adjustment and changes in tissue elasticity. According to Taiz & Zeiger (2009), tolerance is the ability of the plant to develop favorable mechanisms for adaptation or acclimatization, with variations between species and in the way stress affects the plant.

Stomatal closure is admittedly the fastest response observed in the plant, to immediately reduce water loss by transpiration. This loss is caused by the pressure gradient formed between the leaves and the atmosphere, and the soil water availability (Araújo Junior *et al.*, 2019), considered an instantaneous response process between the soil-plant-atmosphere system, its control is performed by the guard cells (Lawlor & Cornic, 2002). This response can also be stimulated when leaves or roots show signs of dehydration (Calvacante *et al.*, 2009), controlling transpiration to maintain maximum CO_2 uptake.

Abscisic acid (ABA) is also involved in the opening and closing of stomata, where the guard cells perceive in advance the water shortage in the mesophyll without any reduction in its turgidity, stimulating the closure of stomata (Lima *et al.*, 2007). When there is a slight desiccation of the soil, an increase in ABA concentration is observed in the xylem, probably produced in the meristem under the root coppice, inducing the leaf to stomatal closure and reduction of leaf expansion, therefore, the perception of the lack of water is due to the response sensitivity of the root mediated by ABA, which closes their stomata (Pimentel *et al.*, 2016).

Low water availability affects the development of root biomass, a functional balance between water uptake by the roots and photosynthesis by the aboveground part of the plant is what determines the volume of root biomass. Water stress reduces the allocation of photoassimilates from leaf and stem biomass and increases in roots, altering the share of assimilates in roots and aboveground (Mc Michael & Quisemberry, 1993), therefore, an adaptive mechanism to water deficit is the production of roots at greater depths in the soil to gain greater access to soil moisture (Taiz *et al.*, 2017).

Among the physiological changes that water deficit cause in plants, the first to be affected is photosynthesis (Pinheiro & Chaves, 2011), through the reduction of the carbon assimilation rate due to stomatal limitation, with increased stomatal resistance to water outflow and CO_2 ingress; and non-stomatal, which includes pigment degradation, photosystem inactivation, and reduced activity of Calvin cycle enzymes (Ashraf & Harris, 2013), reducing plant productivity.

Another factor that contributes to stomatal closure under conditions of low water availability is the reduction in stomatal conductance. This is an alternative defense of the plant that uses water more efficiently under water deficit conditions (Arcoverde *et al.*, 2011). According to Perez (1995), the control of osmotic adjustment (accumulation of solutes by the cells) in plants is to maintain their turgidity even at low water potential values. The process of accumulation of osmotically active substances uses amino acids to reduce cell potential, such as proline, for example.

Proline acts by retaining water inside the cell, therefore, higher levels are observed in the periods of water scarcity (Larcher, 2000). this sense, Moreno-Galván *et al.* (2020) and Mendoza-Labrador *et al.* (2021), evaluating the performance of

Indian grass (*Megathyrsus maximus*) and Guinea grass, respectively, under water stress, found a greater accumulation of proline in plants subjected to stress.

The water deficit can potentiate the formation of reactive oxygen species (ROS), where the high concentration of ROS causes great damage to the cell, which can damage proteins, lipids, carbohydrates, and cause harm to photosynthesis through the oxidation of photosynthetic pigments (Taiz *et al.,* 2017), as well as proteins and nucleic acids (Carlin *et al.*, 2012). The observation of increased EROS under water restriction conditions occurs due to the decline in CO_2 contents, which reduces components for Photosystem I, generating reactive species (Pimentel *et al.*, 2016).

The discoloration of photosynthetic pigments is called photooxidation, which consists of a secondary phenomenon, after the reduction of photosynthesis dependent on the occurrence of photoinhibition (Araújo and Deminicis, 2009). Thus, the content of pigments in plants under stress is an indication of adaptation, with a higher content of pigments in pioneer grass when subjected to water stress.

Over the years, research has shown that grasses of the *Brachiaria* genus have greater resistance to low water availability than that of the *Panicum* genus, and these observations are in accordance with the presentation of a higher percentage of roots in deeper soil layers, a response mechanism to water stress (Santos *et al.*, 2013).

5.2 Hypoxia or Waterlogging Stress

The stress by excess water promotes several changes in chemical, physical and biological processes in the soil, interfering directly in the growth and development of plants (Piedade *et al.*, 2011). The high amount of water in the soil promotes a reduction in oxygen concentration, due to the replacement of air by water in the spaces between the soil structuring particles, being a first effect of excess water.

The flooding of the soil can cause physiological and biochemical disorders in plants. Under these conditions, plants are subject to several implications for their development, which can be observed by reducing leaf expansion, cambial growth and root growth (Herrera, 2013). Additionally, it can lead to inhibition of seed germination and promotion of early senescence, as well as plant death. In waterlogging, the processes of hypoxia (low oxygen availability) or anoxia (absence of oxygen) can occur. Anoxia promotes reduced respiration, fermentative metabolism, inadequate Adenosine Triphosphate (ATP) production, toxin production by anaerobic microorganisms, reactive oxygen species production, and stomatal closure.

Regarding hypoxia, this will stimulates the activity of the 1-carboxylic acid-1-aminocyclopropane (ACC) (synthase and oxidase) in the root apices, causing acceleration in the production of ACC and ethylene, which will trigger the disintegration of cells in the root cortex, provides the formation of aerenchyma (parenchymal tissue with large intercellular spaces), which will facilitate the movement of oxygen (Taiz *et al.,* 2017). this sense, the plant performs metabolic and morphological modifications to adapt to stress conditions, such as the formation of aerenchyma, lenticels, adventitious roots (Lucas *et al.*, 2013; Yin *et al.*, 2010) and growth of new roots, to facilitate gas exchange between plant tissues or between the plant and the external environment (Ferreira *et al.*, 2009).

Research shows that waterlogging affects the specific leaf area (SFA) submitted to total waterlogging (Gonçalves *et al.*, 2012), promotes senescence and leaf abscission in plants intolerant to waterlogging, due to increased abscisic acid (ABA) production and reduced cytokinin, which also influences stomatal closure (Medri *et al.*, 2012). Stomatal closure is a response to reduced photosynthetic rate after waterlogging, directly influences the relative water content in leaves (Coelho *et al.*, 2013).

The stress directly affects photosynthesis and respiration, that is, the primary carbon metabolism pathways. According to Argentia *et al.* (2010), the increase in carbohydrate content demonstrates the shift from aerobic to anaerobic metabolism, significantly affects the availability of energy, demands sugar content to balance the lower production of ATP. Waterlogging promotes a reduction in starch content by inducing the production of enzymes such as alpha-amylase, which hydrolyzes starch and provides an increase in total soluble sugars (TSS) (Peralta *et al.*, 1992).

Under these perspectives, Ramos *et al.* (2011) evaluated the effect of waterlogging in *Brachiaria brizantha* and *Paspalum fasciculatum*, in which the contents of total soluble sugars (TSS), total amino acids (AA) and starch increased in *B. brizantha* under stress condition, in relation to *P. fasciculatum* no changes in these elements were observed, resulting in the fact that this grass is more tolerant to waterlogging conditions than *B.brizantha*.

Dias-Filho *et al.* (2018; 2020), evaluated hybrids of *Brachiaria decumbens* and crosses of *B. brizantha* x *B. decumbens* x *B. ruziziensis* and, under excess water in the soil, observed a reduction in the rate of leaf elongation, consequently, in the production of dry mass of the aerial part, a decrease in the SPAD (Soil Plant Analysis Development) index that correlates with chlorophyll, considering that some genotypes managed to show greater tolerance to waterlogging, especially when the of adventitious roots was observed.

6. Soil and Nutrients

Soil is considered the natural medium for the growth and development of various living organisms, consisting of minerals, organic matter, water, oxygen, and carbon dioxide. For plants, it provides the structure for root support and the contribution of water, oxygen, and nutrients. Additionally, it affects the development of forage plants by influencing the accumulation of minerals in plants, the yield and digestibility of grasses, the resistance of roots to soil penetration and the acquisition of essential resources (Pimentel *et al.*, 2016).

The physical and chemical characteristics of the soil are limiting factors in developing forage grasses. Among the physical characteristics of the soil, the resistance of the soil to root penetration causes physical stress. This resistance is found to a greater extent in compacted soil, and may inhibit cell elongation and impair root growth (Bengough-Glyn *et al.*, 2006). These authors also report that there is a compensatory growth, observing a greater emission of lateral roots, making it an alternative adaptation to this stress, however, this change may leave the plant more susceptible to the effects of water restriction (Pimentel *et al.*, 2016). Silva *et al*. (2020) evaluated different soil water pressures (0, -10, -20, -30, -40, and -50 kPa), found that the higher water pressure in relation to root development of *B. brizantha* cultivars (Piatã, Paiaguás and Braúna), provided greater resources for the production of root biomass, in an attempt to increase access to water, therefore, grasses with higher root production tend to better withstand water stress.

Soil properties such as mineralogy, pH (hydrogen potential), nutrient availability, toxic elements, organic matter and salinity elements constitute the soil and affect plant growth. Low nutrient availability combined high soil acidity can limit the forage production, especially in tropical regions (Townsend *et al.*, 2012). Nutrient deficiency can be linked to the lack of nutrient replenishment or other factors such as drought, waterlogging, and compaction (Pimentel *et al.*, 2016).

The main macronutrients required by plants are nitrogen (N), phosphorus (P), and potassium (K); due to the importance of these nutrients in metabolic processes. According to Taiz *et al.* (2017), nitrogen is the main constituent of chlorophylls, proteins, amino acids, enzymes, among other compounds essential for plant development. Additionally, phosphorus participates in the storage of energy and integrates the sugars participating in photosynthesis, and potassium is linked to the activity of osmotic regulation of the leaf.

Research evaluating nutrient supply, such as nitrogen, has observed biomass accumulation at the expense of nitrogen fertilizer addition (Lopes *et al.*, 2013; Lopes *et al.*, 2017) in the grazing system, as well as changes in increased leaf emergence rate and tillering (Abreu *et al.*, 2020). Nitrogen deficiency can block plant growth because of its implications for vital functions such as photosynthesis.

According to Gomide (1975), phosphorus is an indispensable nutrient in photosynthesis, besides influencing the storage, transport and use of energy in the photosynthesis, its deficiency directly implies the accumulation of biomass. Regarding potassium, its deficiency of causes low growth rates, tillering and thinner stem, besides a yellow-orange coloration on the leaves (Costa *et al.*, 2004). According to Costa *et al.* (2016a, 2016b), P and K promote greater accumulation of forage mass in plants.

7. Grazing

Grazing is considered a limiting factor to plant development, since the interest in productive systems based on pasture is the balance between animal and plant interest. In this sense, it is necessary to perform grazing management to provide the gain and maintain the productive balance. According to Pimentel *et al.* (2016), grazing affects the relationships in the plant community, influences the productivity of grasses, and the production system, so it is necessary to know the aspects that affect them.

Harvesting forage mass by animals is considered an act that causes stress on the plant, and these plants adapt to grazing using alterations in physiological and morphological characteristics. According to Gomide *et al.* (2002), total defoliation of the main tiller limit photosynthesis, compromising root growth; however, when harvesting the mass at a proportion of 50%, root growth is not intensely impaired.

Furthermore, they observed a marked reduction in non-structural carbohydrate content as defoliation intensity increased in Mombasa grass (Gomide *et al.*, 2002). Lupinacci (2002), observed this same behavior for reserve carbohydrates (RC), which, when managed at higher intensity, presented lower accumulation. In this same perspective, Benot *et al.* (2019) observed that carbohydrate concentrations (starch, fructans, sucrose, glucose and fructose) were higher before grazing.

Several studies have been conducted over the years (Rodrigues & Cadima-Zevallos, 1991; Emerenciano Neto *et al.*, 2013; Zhang *et al.*, 2018; Benot *et al.*, 2019) to verify the responses of grazing intensity under the pasture community, both in temperate and tropical grasses. The way the pasture is harvested by the animals (grazing methods) modifies its structural characteristics, consequently, its nutritive value, directly influencing animal consumption and performance.

Thus, the pasture that is not managed by respecting its morphophysiological characteristics tends to present an inferior quality of pasture, than those that are managed by respecting, mainly the height of harvest of the forage mass. Therefore, grazing methods (continuous or rotational grazing) directly influence how the plant responds to these types of management, that is, the rotational grazing method, respecting the pre-harvest and post-harvest height, tends to minimize the effect of this action on the plant, therefore, the grass will have greater conditions to respond positively to regrowth. In this sense, grazing goals are elaborated so that the soil-plant-animal system is productive and sustainable (Silva *et al.*, 2015).

8. Final Considerations

Water, temperature, radiation, soil and nutrients are factors that affect plant development and that may cause limitations under stress conditions. The responses of plants to stress caused by these factors vary according to their intensity, interfering with the physiological, morphological, and structural conditions. The alterations in the photosynthesis will depend on which factor is acting, and the plants may then respond by the mechanism of escape, tolerance, or adaptation.

In forage grasses, changes in behavior are observed at several levels, such as reduced carbon assimilation rate and increased chlorophyll content when subjected to shade; stomatal closure and lower root production when subjected to water stress and low soil humidity; formation of aerenchyma and adventitious roots in the case of flooded environments. Thus, forage plants can remodel their morpho-physiological characteristics, changing their structural features, directly implying the management of grazing. Therefore, to manage pasture and grazing in an efficient and sustainable way, it is necessary to understand how plants are influenced by abiotic factors, which are linked to their development and how they behave in stress situations, so that the management is carried out in a more assertive and productive way.

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