

Energy flows and organic reserves of forage plants

Fluxos energéticos e reservas orgânicas de plantas forrageiras

Flujos de energía y reservas orgánicas de plantas forrajeras

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Abstract

This review addressed the existing energy flows in the pasture ecosystem, as well as the use of organic reserves by forage grasses. The radiant energy is absorbed by the leaves and transformed into chemical energy by which the assimilated carbon is fixed. During the process of assimilation and fixation of C, photochemical, and biochemical processes are carried out, which are influenced by light. Several environmental factors can influence the ability of plants to respond to stimuli. In this sense, energy flows within the pasture system are in constant movement to maintain the forage plant. The direction of energy flow varies with the growth environment of the forage plant, since in addition to affecting the structural characteristics, the environmental factors exert control over the root system. In theory, organic reserves located in roots and stems play a crucial role in the growth of grazed plants, especially in the

first days after defoliation. Therefore, it is important to encourage research involving the reserve organs and their accumulation patterns so that the results can assist in the development of sustainable grazing systems.

Keywords: Carbon; Grasses; Photosynthesis; Nitrogen.

Resumo

Objetivou-se com esta revisão abordar os fluxos de energia existentes no ecossistema de pastagem, bem como o uso de reservas orgânicas por gramíneas forrageiras. A energia radiante é absorvida pelas folhas e transformada em energia química pela qual o carbono assimilado é fixado. Durante o processo de assimilação e fixação do C são realizados processos fotoquímicos e bioquímicos, que são influenciados pela presença de luz. Muitos fatores ambientais podem influenciar a capacidade das plantas em responder à estímulos sofridos. Neste sentido, fluxos energéticos dentro do sistema de pastagem estão em constante movimento para manutenção da planta forrageira. A direção do fluxo energético varia com o ambiente de crescimento da planta forrageira, uma vez que além de afetar as características estruturais, o fator ambiente exerce controle sobre o sistema radicular. Em tese, as reservas orgânicas localizadas em raízes e colmos exercem papel crucial no crescimento de plantas pastejadas, principalmente nos primeiros dias após a desfolhação. Portanto, é importante incentivar pesquisas que envolvam os órgãos de reservas e seus padrões de acúmulo para que os resultados possam auxiliar no desenvolvimento de sistemas de pastejo sustentáveis.

Palavras-chave: Carbono; Fotossíntese; Gramíneas; Nitrogênio.

Resumen

El objetivo de esta revisión fue abordar los flujos de energía existentes en el ecosistema de pastos, así como el aprovechamiento de las reservas orgánicas por parte de las gramíneas forrajeras. La energía radiante es absorbida por las hojas y transformada en energía química mediante la cual se fija el carbono asimilado. Durante el proceso de asimilación y fijación del C se llevan a cabo procesos fotoquímicos y bioquímicos, los cuales están influenciados por la presencia de la luz. Muchos factores ambientales pueden influir en la capacidad de las plantas para responder a los estímulos. En este sentido, los flujos de energía dentro del sistema de pastos están en constante movimiento para mantener la planta forrajera. La dirección del flujo de energía varía con el ambiente de crecimiento de la planta forrajera, ya que además de afectar las características estructurales, el factor ambiental ejerce control sobre el sistema radicular. En general, las reservas orgánicas ubicadas en raíces y tallos juegan un papel crucial en el crecimiento de las plantas pastoreadas, especialmente en los primeros días después de la defoliación. Por lo tanto, es necesario fomentar la investigación que involucre los cuerpos de reserva y sus patrones de acumulación para que los resultados puedan ayudar en el desarrollo de sistemas de pastoreo sostenibles.

Palabras clave: Carbono; Fotosíntesis; Nitrogênio; Pastos.

1. Introduction

In countries where livestock farming is predominantly conducted in pastures, it is common to observe the search for productive sustainability. This objective involves the knowledge about the physiology of the plant in pastoral ecosystems, generating adequate accumulation of forage and animal production, helping in the continuity of the pasture.

The grassland ecosystem is characterized by energy flow dependent on the environment in which the plant is growing. The energy flow within the pastoral system comprises the initial capture of solar energy by vegetation, which converts it into chemical energy through photosynthesis (Costa et al., 2012). Factors such as soil compaction, water availability, intensity and frequency of grazing and shading, among others, modify the development of the forage plant by affecting the photochemical and biochemical processes of photosynthesis.

Photosynthesis is the main source of energy and carbon skeletons for plants, and is related to leaf area and incident light (quantity and quality). In turn, carbon accumulation in the canopy is linked to nitrogen content in the plant, meaning that these two elements are associated with the plant (Ferro et al., 2015).

Grazing modifies the plant's recovery rate and, consequently, its productivity, through changes in the remaining leaf area and the plant's organic reserves (Aranjuelo et al. 2014). Organic reserves are composed of nitrogen and carbon, and serve as a source of energy during periods of stress, ensuring plant survival. They are stored in roots, rhizomes, stolons, and at the base of the stem (Volenc & Nelson, 2020). After defoliation, these organs take on the conditions of an energy source to sustain forage plant growth and persistence.

Therefore, management strategies, such as the frequency and intensity of defoliation and nitrogen fertilization, affect the accumulation of organic reserves and the structure of reserve organs (Soares Filho et al., 2013). Thus, to understand the partitioning of photoassimilates within the forage canopy, it is necessary to understand the factors that determine the accumulation of organic reserves and their use in each plant organ (Irving, 2015). The concentration of reserve compounds in each compartment of the plant is commonly used to express assimilate fluxes. However, the relative importance of plant parts as reserve organs can vary depending on the assimilated concentration and mass accumulation of the storage organs (Islam et al., 2020).

The morpho-physiological responses of forage grasses depend on the defoliation system adopted and the climate in which they are located. In this context, Silva et al. (2015) reported that grazing management based on organic reserves is still less used because it is little studied compared to morphogenic and structural characteristics. Thus, from a compilation of information, the adoption of technical management criteria produced through knowledge of the morphology, physiology and biochemistry of the plant would be able to result in the development of sustainable grazing goals.

In view of the above, this review addressed issues related to energy flows in the pasture ecosystem and the use of organic reserves by forage grasses.

2. Methodology

This study was written based on scientific articles published in national and international journals about energy flows and organic reserves in forage plants. Thus, this is an exploratory review of a qualitative nature (Pereira et al. 2018) since the bibliographic production on this specific theme were analyzed, highlighting their ideas and subthemes that have more or less relevance within the selected literature.

The inclusion criterion was established as articles published in full, available in Portuguese, English and Spanish languages that evaluated and described how the factors involved in the pasture ecosystem affect the energy flows and organic reserves of forage plants. Articles unrelated to the theme or that did not provide relevant information for the preparation of this review were excluded.

3. Development

3.1 Photosynthesis and photorespiration

Photosynthesis is the transformation of light energy into chemical energy, to promote plant growth. This process occurs in two stages: in the photochemical phase, light energy is converted into chemical energy with the formation of ATP and NADPH, and the release of O₂. In the biochemical phase, there is the fixation of carbon (CO₂) into organic molecules through the Calvin-Benson cycle. The energy produced in the photochemical stage is used in the biochemical stage to form glucose, which is used in the plant's metabolism or transported to the base of the stalk and roots in the form of sucrose, where it can be stored in the form of starch.

The leaf mesophyll is the most active photosynthetic tissue in plants, in the presence of chloroplasts, which are the organelles where photosynthesis occurs. Photosynthesis begins with the absorption of light by the chlorophylls. The chlorophyll a and b groups are the most abundant pigments in plants and absorb wavelengths between 400 and 700 nm, reflecting wavelengths near 580 nm, making their color green (Ferro et al., 2015). Chlorophylls are found in chloroplasts, in a complex of membrane systems called tilacoids, which are associated with proteins to optimize the use of absorbed solar energy (Taiz et al., 2017). Carotenoids are the second largest group of pigments and are considered accessory pigments because they

absorb light at wavelengths between 400 and 500 nm and transmit energy to chlorophyll, contributing to the process photosynthesis (Ferro et al., 2015).

Through carbon fixation, plants can supply their needs for skeletons of organic compounds through the Calvin-Benson cycle, which can be called the pentose reducing cycle and the photosynthetic carbon reduction cycle. In the mesophyll cells, the enzyme ribulose-1,5-biphosphate (RuBP) catalyzes the reaction of CO₂ forming a six-carbon molecule, which is rapidly transformed into two molecules of 3-phosphoglyceric acid (3-PGA). These three-carbon acids are converted into carbohydrates (triose phosphates) by ATP- and NADPH-dependent enzymatic reactions generated in the photochemical step of photosynthesis (Taiz et al., 2017). Thus, plants that have this carbon fixation cycle are called C₃ because they present as their first product two acid molecules with 3 carbons.

The enzyme ribulose-1,5-biphosphate carboxylase/oxygenase, known as *RUBISCO*, is considered the most abundant protein on the planet, and is responsible for converting CO₂ into organic molecules during photosynthesis. However, in addition to reacting with carbon, this enzyme also reacts with O₂ molecules, causing a loss of the carbon fixed in the Calvin-Benson cycle (Nelson & Moore, 2020). According to Volenec and Nelson (2020), this process is called photorespiration and happens when the enzyme RuBP oxygenase reacts with O₂ and forms a 3-PGA molecule and a 2-phosphoglycolate molecule, which is reoxidized to release CO₂. Furthermore, a product formed upon the oxygenation of RuBP, 2-phosphoglycolate, is an inhibitor of the enzyme triose phosphate isomerase and phosphofructokinase, which are involved in the processes of starch and sucrose synthesis (Taiz et al., 2017).

Photorespiration can consume about 30% of the carbon fixed in plant photosynthesis and can be accentuated with increasing temperature and luminosity (Sage et al., 2012). Some plants have developed, through evolution and adaptation, different mechanisms to fix carbon and increase the concentration of this compound near the carboxylation site of Rubisco. Thus, in addition to the C₃ pathway of carbon fixation, there are the C₄ and CAM pathways, where in the former, the phases of photosynthesis are spatially separated (mesophyll cells and vascular sheath) while in the latter group, the reactions are controlled by time (they absorb CO₂ at night and incorporate it during the day).

Species that have the C₄ cycle have, in addition to *Rubisco*, the enzyme phosphoenolpyruvate carboxylase (PEPCase), which does not react with O₂, catalyzes only CO₂ (Volenec & Nelson, 2020). In mesophyll cells, PEPCase reacts with captured atmospheric CO₂ to form a four-carbon compound, oxaloacetate (OAA). They can be transformed into malate and aspartate, and are transported into the vascular sheath. Thus, the four-carbon acids are decarboxylated and release CO₂ that will be fixed by RuBP carboxylase in the Calvin-Benson cycle forming glucose (Taiz et al., 2017). The C₄ carbon fixation pathway limits photorespiration by avoiding CO₂ wastage, allowing plants to thrive in hot, dry climates (Sage et al., 2012).

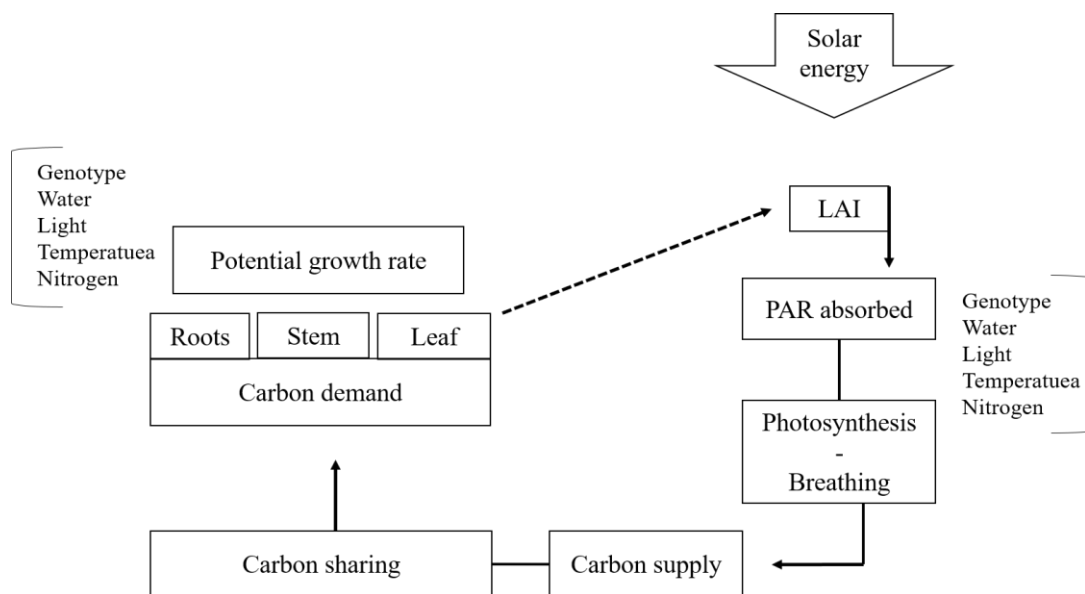
C₃ and C₄ plants differ anatomically and therefore respond specifically to the ecosystem in which they are embedded. In This context, Chicahuala et al. (2018) evaluated the effect of precipitation and temperature on the phenological characteristics of groups of C₃ (*Piptochaetium napostaense*, *Poa ligularis*, *Bromus brevis*) and C₄ (*Digitaria californica*, *Setaria leiantha*, *Eustachys retusa*) plants. In this work, the C₃ grasses started their reproductive cycle before the C₄ grasses. Furthermore, the increase in temperature benefited the growth of tropical climate (C₄) pastures compared to temperate climate (C₃) forages.

3.2 Reserve storage in forage plants

The main physiological process associated with the productive process of plants is photosynthesis, governed mainly, by the availability of light, water, temperature and nutrients (Taiz et al., 2017). Durand et al. (1991) state that the growth of a

pasture can be explained through a model that allows describing the carbon supply through the phenomena of radiation interception, photosynthesis and respiration to supply the use of carbon during plant growth (Figure 1).

Figure 1. Conceptual model of plant growth in relation to photoassimilate distribution and its relationship to environmental components.



*LAI: Leaf area index; PAR: Photosynthetically active radiation. Source: Adapted from Durand et al., (1991).

It is from photosynthesis that the plant community obtains the energy needed for the other morpho-physiological processes that determine plant production, whether it is tillering, production of tissues of the aerial part and roots and accumulation of organic reserves. However, photosynthesis alone does not define the productivity of a plant because other physiological changes caused by the environment can impose limits on the production of forage mass (Silva et al., 2015).

The allocation is the distribution of photoassimilates for storage, growth, and transport. In this sense, the balance between the flows of carbon, nitrogen and water within the grassland ecosystem has a vital relationship to the maintenance of the productive system. According to Gómez et al. (2012), the increased availability of nitrogen in the soil increases the photosynthetic rates of *Brachiaria decumbens* grass (*Urochloa decumbens* syn. *Brachiaria decumbens*) and, consequently, the forage accumulation of these species. Furthermore, the presence of nitrogen in the soil stimulates plant growth through the mobilization of carbon and nitrogen compounds, altering the plant response at physiological levels. Because of this, the use of nitrogen fertilization stimulates the formation of carbon reserves in *Phleum pratense* L. plants, which could be used as a source of energy for plant development (Ould-Ahmed et al., 2014).

Water is also an important component of the system, since severe water deficits promote damage to Rubisco activity and may not be recovered after rehydration (Taiz et al., 2017). Thus, leaf growth and expansion rates may be limited by the production of photoassimilates, which are influenced by the environment by altering the rates of cell division and expansion required for plant development.

The alteration in any of these components causes consequences in the morphophysiology of the forage plant that, in turn, provides adaptation to a specific environmental condition caused by the availability of photoassimilates. However, in addition to the environmental factor in which the plant is embedded, the relative amount of photoassimilates transported to specific regions is variable with plant part and also between cultivars and species (Paraiso et al. 2019).

3.3 Organic reserves in forage grasses

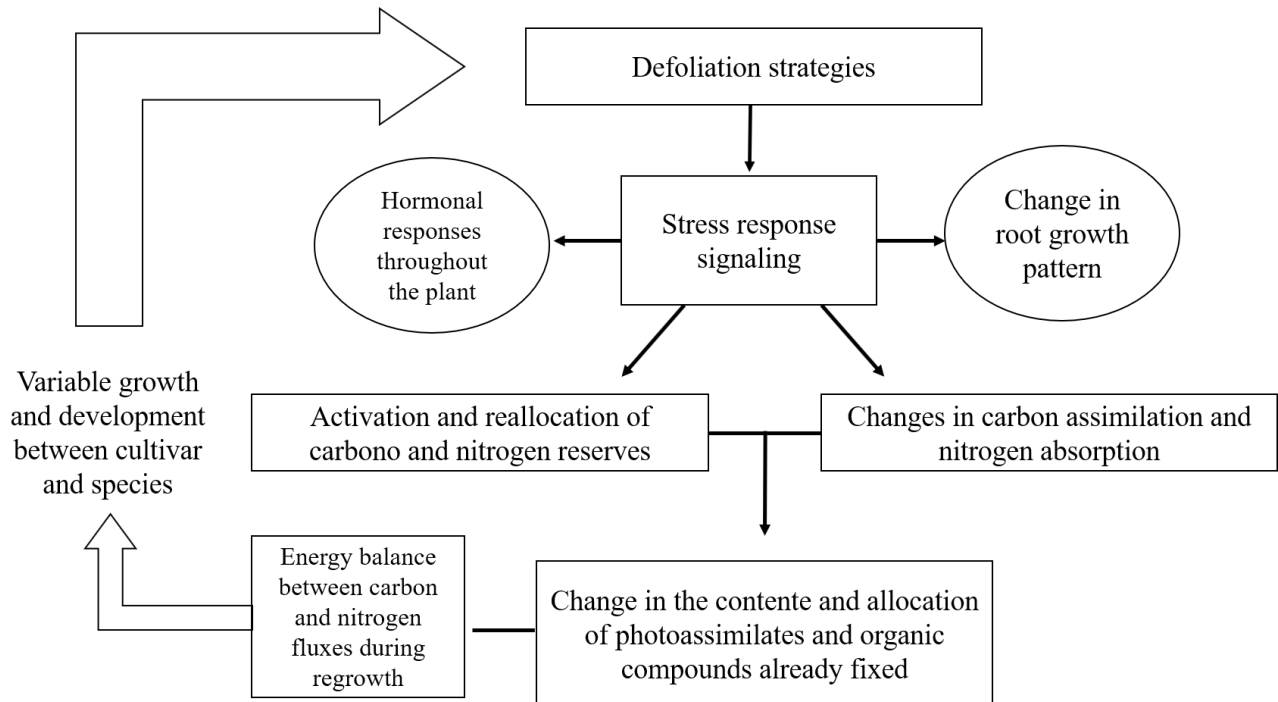
Within the pasture ecosystem, forage plants suffer successive defoliation, the frequency and intensity depend on the grazing strategy used. After defoliation, the reestablishment of the leaf area is a process in which the available resources are used rationally for the formation of photosynthesizing tissues, aiming at plant growth (Lemaire & Chapman, 1996).

Organic reserves are compounds composed of carbon and nitrogen, which are stored by the plant and can be used as a substrates in the processes of maintenance during periods of stress and formation of new tissues for recovery after defoliation and senescence (Volenc et al., 1996). In this sense, these compounds are accumulated in the stems and roots, and can be translocated to the leaves to balance-negative carbon balances imposed by grazing (Nelson & Moore, 2020). The priority of using newly assimilated carbon and nitrogen are for the expansion zones to assist the development in the restoration of forage canopy structures (Irving, 2015; Dierking et al., 2017). Regrowth has two distinct phases: the first, in the short term, through the remobilization of fixed compounds, and the second phase, which occurs in the long term, when the mechanisms of the first phase cannot meet the energy requirement needed for leaf restoration (Lemaire & Chapman, 1996). According to Yang et al. (2013), carbohydrate and nitrogen contents in reserve organs of forage grasses decrease after defoliation, increase again after the restoration of the photosynthesizing area.

As leaf area is restored, some of the fixed carbon is translocated to the roots for storage and to aid in the uptake of nitrogen from the soil (Yang et al., 2013). Thus, carbon and nitrogen in the pastoral system are closely linked and work together for plant restoration after stress.

A model of the regrowth and usage of organic reserves is depicted in Figure 2. After grazing stress, the plant emits hormonal signals, forms organic acids, along with oxidizing enzymes to initiate regeneration. Thus, changes occur in carbon and nitrogen assimilation and activation of organic reserves. At this point, hormonal modification signals to other organs about the stress being experienced, and roots tend to modify their growth pattern and reduce the uptake of nutrients such as nitrogen (Meuriot et al., 2018). There is also a reallocation of organic molecules fixed within a carbon and nitrogen flux, enabling restoration of the defoliated plant by gradually increasing nitrogen uptake by the roots. Importantly, the growth pattern of a forage grass differs between cultivar and species, assuming variations in the morpho-physiological expressions of the plants (Costa et al. 2020ab). Finally, the importance of reserve organ participation may vary depending on the concentration of attached molecules and the size of the organ.

Figure 2. The model of the regrowth mechanism in forage grasses.



Source: Adapted from: Yang et al. (2013); Meuriot et al. (2018).

The success of plant recovery after defoliation is directly linked to reserve compound contents and remaining leaf area. Moreover, these factors act complementary and the importance of each in the physiology of the plant depends on the type of stress suffered (Volenc & Nelson, 2020). The greater residual leaf area after grazing favors regrowth, because it has a greater photosynthetic apparatus, which can contribute to the photosynthesis of the plant. Mombasa grass (*Megathyrus maximus* syn. *Panicum maximum* cv. Mombaça) defoliated with a pre-grazing height of 90 cm, being lowered to 50 cm of residue height showed faster recovery of its leaf area compared to that lowered to 30 cm (Euclides et al., 2017). In this situation, the greater remaining leaf area provided a greater capacity for plant recovery, causing organic reserves to assume a secondary role for regrowth in this case.

Under self-shading conditions, leaves located near the ground may senesce, thus losing their photosynthetic capacity. Thus, in intense defoliation, organic reserves may play a prominent role in new tissue formation, as the remaining leaf area may not be able to sustain canopy recovery (Avice et al., 1996; Gastal & Lemaire, 2015). Therefore, the importance of each factor for the recovery of the defoliated plant will occur in specific situations, and these mechanisms act together and not competitively.

The carbohydrates present in forage plants are classified as structural, being constituents of the cell wall and responsible for maintaining the structure of the plants, and in non-structural (NSC) present in the cell content and involved in various biochemical processes, besides comprising the carbohydrates stored in reserve organs. According to Taiz et al. (2017), carbohydrates accumulated in reserve tissues are classified as monosaccharides (glucose and fructose), oligosaccharides (sucrose and maltose), and polysaccharides (starch and fructans).

The type of reserve carbohydrates in forage plants can vary depending on the photosynthetic mechanisms used. According to Volenc and Nelson (2020), C_3 grasses store mainly fructans as the main reserve carbohydrates, while perennial and annual C_4 grasses accumulate starch and sucrose, respectively. Also according to the authors, while fructans are water-soluble polysaccharides, starch is an insoluble polysaccharide and can be found in the form of amylopectin and amylose.

Additionally, plants can accumulate starch in the amyloplasts of permanent organs being used as an energy reserve, and transiently in chloroplasts, which will be used as an energy reserve for conducting plant biochemical processes during the night (Taiz et al., 2017).

In addition to carbon reserves and remaining leaf area, forage plant recovery after defoliation depends on nitrogen reserves. According to Meuriot et al. (2018), there is internal remobilization of stored nitrogen and recycling of this nutrient from leaf senescence to aid in the leaf recovery process. Nitrogen accumulates in plant tissue in the form of polypeptides, and they must meet the following criteria to be defined as *vegetative storage proteins* (VSPs): (1) proteins must have a preference to be synthesized and accumulated in reserve organs, (2) proteins that are remobilized from reserve organs during the growth phase, (3) proteins whose amount is higher than others in perennial organs (Volenc et al., 1996). According to the authors, during plant recovery, an increase in the activity of proteolytic enzymes, while simultaneously, the contents of soluble proteins present in reserve organs are reduced, resulting in the production of free amino acids, moved to meristematic zones to contribute to the formation of new tissues.

Research conducted with alfalfa (*Mendicago sativa* L.) highlight the importance of nitrogen reserves in the regrowth process, suggesting that carbohydrate reserves would assume a secondary role in this process (Avice et al., 1996, 1997). However, Lu et al. (2017) and Mitchell et al. (2020) reported that nitrogen and carbon reserves work together in the regrowth process of alfalfa, demonstrating the importance of the participation of both in the system.

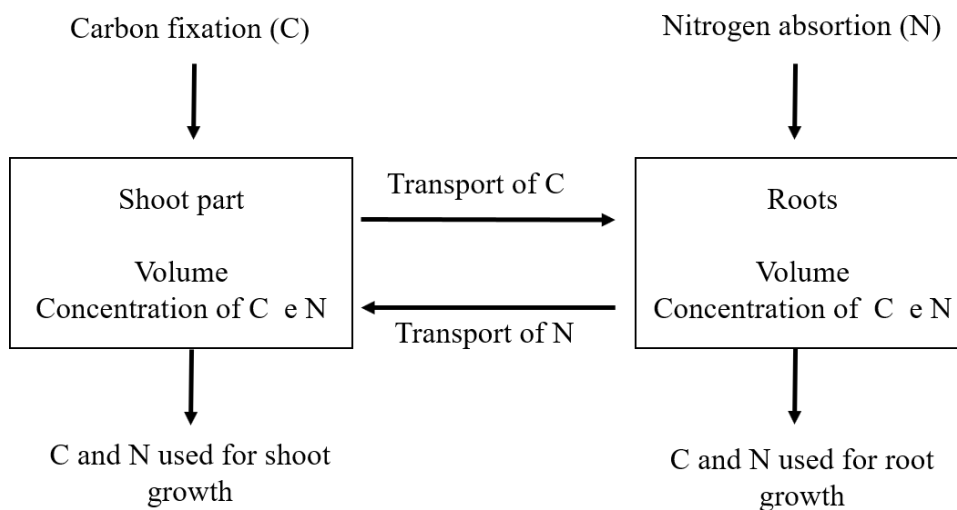
Moscoso and Balocchi (2016) also highlighted the importance of the use of organic reserves (carbohydrate and nitrogen) in perennial bluegrass (*Lolium perene* L.) plants after defoliation, ratifying the role of storage of reserve compounds in the regrowth process of forage grasses. Roche et al. (2017) suggested that in this species, cytokinins act as stress signaling between the leaf sheath and roots, furthermore, they reported increased amino acid synthesis in the growth regions, sustained in the first 24 h, by the remobilization of the plant's nitrogen reserves.

3.4 Carbon and nitrogen fluxes

The assimilated compounds, mainly carbon and nitrogen, can be used as reserves, and can be mobilized for plant growth under stress conditions. There is a direct relationship between nitrogen availability in the system and the mobilization of carbon reserves since the addition of this nutrient directly influences forage accumulation rates and forage plant tillering (Euclides et al., 2017).

Thus, it is noticeable the relationship between carbon and nitrogen in the pasture system, where both are always present in some chemical reactions that result in the accumulation of biomass and organic compounds. According to Thornley (1972), carbon fixed in the leaf is used for leaf growth or translocated to the roots, while nitrogen absorbed by the roots can be used for leaf or root growth (Figure 3). According to Irving (2015), the model developed by Thornley provides a comprehensive understanding of biomass allocation in grasses, starting from a simple and easily understood concept. Understanding carbon and nitrogen partitioning depends on environmental factors that determine, in turn, the size of the reservoir of these elements and their mobilization in the plant (Poorter et al., 2012).

Figure 3. Model of carbon and nitrogen concentration and fluxes in root and aboveground growth.



Source: Adapted from Thornley (1972).

The partitioning of photoassimilates can be seen as part of the morphophysiology of the plant and can be interpreted following a decreasing hierarchy of priority of carbon allocation between different plant organs: growing leaves, stems and roots (Durand et al., 1991). In this bias, as plants grow, a spatial separation of the plant organs occurs, so a nutrient transport system (xylem and phloem) exists, allowing the exchange of products of nutrient uptake by the roots with those of assimilation by the aboveground part. The xylem is the tissue that transports water and mineral salts from the root system, while the phloem is the tissue that translocates the products of photosynthesis from mature leaves, called sources, to areas of metabolism or storage, called drains (Taiz et al., 2017).

Sources are the organs that produce high concentrations of photoassimilates, which in the case of vegetables, are the mature leaves (Poorter et al., 2012). Drains, in general, are organs that do not produce photoassimilates or do not produce enough to meet their own growth needs (Taiz et al., 2017). During the growth phase, leaves, stalks, and roots are considered drains. During this phase, roots and stems accumulate sugars from photosynthesis and store them in the form of reserve carbohydrates to be used if necessary for the survival of the plant.

The distribution of assimilates in the plant is also dependent on the environmental conditions in which they are inserted. Thus, an organ that was once a drain may become a source, meeting the energetic demands for growth. In this sense, photoassimilates produced by newly expanded leaves are used for their maintenance, as well as to meet the needs of leaf growth zones, root system and supporting tissues (Costa et al., 2012). However, as new leaves develop, the photosynthetic activity of mature leaves is reduced and the senescence process begins, with mainly nitrogen translocation occurring to growth zones (Xing et al., 2019).

When grass growth is accentuated, there is a tendency to reduce the number of leaves and increase the accumulation of stem and dead forage in the forage canopy, caused mainly by self-shading. The decrease in photosynthetic capacity in leaves of advanced age, usually shaded by higher leaves, represents a higher energy expenditure with growth and maintenance respiration, besides altering the redistribution of assimilates for plant development (Costa et al. 2012). Furthermore, according to Gastal and Lemaire (2015) in self-shading conditions, plants invest a greater proportion of photo-assimilates and other resources to increase leaf area. Also, according to the authors, this condition leaves to grow larger and thinner, facilitating the absorption of the little RFA that reaches the shaded areas.

Considering this, Graminho et al. (2014) recorded an increase in the accumulation of stalks as a function of perennial ryegrass plant maturity, which is a result of the change in photo-assimilate partitioning, contributing to the increase in tiller mortality. Furthermore, the transition from the vegetative phase to the reproductive phase (flowering), also contributes to the increase in dead forage because the growth of leaves becomes limited by the decreased supply of photoassimilates for developing leaf tissue (Irving, 2015).

The decrease in photosynthetic capacity of mature leaves is related to the decrease in the quantity and quality of light reaching the lower part of the canopy. In situations where there is no light limitation, high levels of Rubisco must maximize photosynthesis (Irving, 2015). However, as leaves mature and shade, there is degradation of this enzyme and remobilization of nitrogen to new leaves. Although some N loss should be expected in senescent biomass, N remobilization is clearly important in determining plant productivity as it aids in the development of meristematic zones (Xing et al., 2019).

The nutrient requirement of expanded leaves is lower compared to meristematic regions, which are growing. Thus, compounds synthesized in these leaves are carried in the phloem to the drain organs (Volenc & Nelson 2020). Sources supply specific drains, primarily, by proximity between organs. In this case, leaves located in the upper portion supply photoassimilates to the apical meristem and the basal leaves supply the roots (Ferro et al., 2015).

Robin et al. (2018) developed a model of root growth suggesting an equal distribution of carbon among roots of different ages. Here, the use of photoassimilates is divided between maintenance of respiration in the older roots and biomass production in the younger roots. Furthermore, the authors also suggested that the growth of older roots is restricted by the high carbon requirement for their maintenance.

The process of photoassimilate partitioning is also influenced by external factors such as defoliation. After the loss of leaf area by defoliation, drains can become sources, in which stored carbon and nitrogen reserves are mobilized and used for tissue maintenance and aerial part recovery (Iqbal et al., 2012; Dierking et al., 2017). This translocation provides greater agronomic stability and forage production potential, which can favor the sustainability of the production system (Sangoi et al., 2012). Concomitantly, new leaves are issued for the plant to reestablish its photosynthetic capacity (Costa et al., 2017). Thus, momentarily, defoliation reduces plant growth due to the decrease in photoassimilate production. This happens because the presence of leaves is of fundamental importance for the production of photoassimilates, in an amount that supplies the growth needs of roots and aerial parts (leaf + stem) (Moscoso & Balocchi, 2016).

Intense defoliation stress also negatively affects root nodule development in alfalfa (Aranjuelo et al., 2014) and reduces N uptake in perennial ryegrass, particularly in the first days after defoliation (Meuriot et al., 2018). This inverse relationship between remaining leaf area and N uptake suggests that the uptake of this nutrient is associated with photosynthesis, probably by reducing sucrose transport to the roots. In this sense, Louahlia et al. (2008) suggested that the decrease in nitrate uptake after defoliation is a result of sucrose shortage in the root portion since carbon allocation is directed primarily to the growth zones to restore the photosynthetic capacity of the plant.

Pedreira et al. (2017) evaluated Xaraés grass (*U. brizantha* syn. *B. brizantha* cv. Xaraés) subjected to three rotational grazing strategies (28 days fixed, 95 and 100% light interception) and a standard residue height of 15 cm. At the end of two years of experimentation, the authors reported that there was no effect of defoliation strategies on the organic reserves of stalks present in the post-grazing residue forage mass. The lack of difference between the strategies evaluated may be related to the fact that the management was performed at the same residue height of 15 cm, varying only the pre-grazing target.

Soares Filho et al. (2013) reported greater accumulation of carbohydrate reserves in the roots of Tanzania grass (*M. maximus* syn. *P. maximum* cv. Tanzania) at doses of 50 and 100 kg ha⁻¹ year⁻¹ of N than 0 and 150 kg ha⁻¹ year⁻¹ of N, with no difference in the concentration of root nitrogen reserves between the doses studied (Table 1). The authors suggested that the

reduction in root non-structural carbohydrate (NSC) contents at the 150 kg ha⁻¹ year⁻¹ N dose is a result of the greater availability of this nutrient in the soil, which allows a more accelerated development of the forage canopy. In turn, the concentrations of NSC and N at the base of the stalk were higher at a dose of 150 kg ha⁻¹ year⁻¹ of N (Table 1) due to the greater accumulation of forage, green leaves and nitrogen availability.

The results found by Soares Filho et al. (2013) suggested that regardless of the fertilization level used, the highest concentration of NSC in roots occurs in the 20 - 40 cm below the level layer, while the highest concentration of nitrogen is found in the 0 - 10 below level layer (Table 1).

Table 1. Concentrations of non-structural carbohydrates (NSC) and total nitrogen (N) in stem and roots of Tanzania grass under different doses of nitrogen fertilization.

Fertilization level (kg ha ⁻¹ year ⁻¹ of N)	Roots (g.kg ⁻¹)*		Stem (g.kg ⁻¹)*	
	NSC	Total N	NSC	Total N
0	0,47 BC	5,70 A	0,69 B	6,40 C
50	0,65 A	6,00 A	0,87 AB	8,60 B
100	0,55 AB	5,70 A	0,81 AB	9,90 AB
150	0,38 C	6,10 A	0,93 A	10,50 A
Below Ground Layer				
0 – 10 cm	0,44 B	7,60 A	-	-
10 – 20 cm	0,50 B	4,60 B	-	-
20 – 40 cm	0,59 A	4,30 B	-	-

* Values are based on dry matter. For each component and each characteristic, means followed by the same letter in the column do not differ by the Tukey test (P>0.05). Source: Adapted from Soares Filho et al. (2013).

Thus, besides being storage organs for organic reserves, the roots use the carbon compounds for their growth, while the nitrogen reserves are exported to meet the restoration of leaf area. Thus, there is variation between carbohydrate and nitrogen reserves, and their concentrations occur in different root layers. Additionally, it is possible to consider that Tanzania grass has greater nitrogen reserves in the upper root layers, while its greatest carbohydrate reserve is at the base of the stem.

During evaluations of organic reserves in forage grasses, the concentration of organic reserves should be considered, as well as the amount of mass of the storage organ. According to Paraiso et al. (2019), the concentrations of organic reserves in roots and stems can be similar, but the *pool* (total accumulation) differs according to the total mass of each component. In Marandu grass plants, Silva et al. (2014) found higher concentrations (%) of non-structural carbohydrates in the root compared to the stem base. Despite this, the largest *pool* of NSC was found at the base of the stem, as this component showed a higher mass compared to the root. Additionally, Lu et al. (2017) reported that post-grazing alfalfa (*Mendicato sativa*) regrowth was directly related to organic reserve *pools* in roots, rather than their concentrations. Thus, in cases where the grazing strategy and fertilization adopted do not interfere with the contents (%) of reserve components, what will determine the canopy's ability to accumulate organic reserves is the number of storage organs (stolons, stem base, roots) present in the canopy.

Silva et al. (2016) evaluated Mulato II grass (hybrid plant of *U. brizantha* x *U. decumbens* x *U. ruziziensis*) under three continuous grazing strategies (10, 25 and 40 cm) and two levels of nitrogen fertilization (50 and 250 kg ha⁻¹ year⁻¹ of N). The authors reported no difference in the concentration of carbohydrate reserves in the root as a function of grazing height or nitrogen dose. However, the carbohydrate *pool* in the root was highly affected by the total root mass, since grazing at 10 cm showed lower root mass and consequently lower accumulation of NSC. Nitrogen reserves were affected only by the rate of nitrogen application, where the application of 250 kg ha⁻¹ year⁻¹ favored the concentration and *pool* of nitrogen compounds in the root (Table 2), through the elevation of root dry mass due to the availability of N in the soil.

Table 2. The concentration and accumulation of nitrogen in the roots of Mulato II grass under two nitrogen fertilization strategies.

Fertilization level	Concentration of N (g.kg ⁻¹)*	Pool of N (g.m ⁻²)*
50 kg.ha ⁻¹ .year ⁻¹ of N	9,1 B	8,6 B
250 kg.ha ⁻¹ .year ⁻¹ of N	10,6 A	11,5 A

* Values are based on dry matter. For each characteristic, means followed by the same letter in the column do not differ by F test (P>0.05). Source: Adapted from Silva et al. (2016).

Paraiso et al. (2019) evaluated Ipyporã (hybrid of *Urochloa ruziziensis* x *U. brizantha*) and Mulato II grass for two years under continuous grazing at 30 cm height. Regardless of cultivar, root mass as well as concentrations and accumulations of organic reserves (carbon and nitrogen) were higher in the first year of evaluation (Table 3) due to higher soil fertility compared in the second year of evaluation. The authors did not highlight whether the root or the base of the stem is more important for the cultivars evaluated, however they reported the importance of these storage organs for the persistence of these forage plants.

Table 3. Total dry mass, concentration and accumulation of nonstructural carbohydrates (NSC) and nitrogen (N) in the roots and stems of *Urochloa* hybrids evaluated over two years.

Variables*	Root		Stem	
	Year 1	Year 2	Year 1	Year 2
Total dry mass (kg.ha ⁻¹)	4500 a	2420 b	2125,0 a	917,5 b
Concentration of NSC (g.kg ⁻¹)	11,7 a	11,7 a	27,3 a	15,0 b
Pool of NSC (g.m ⁻²)	62 a	23 b	180 a	83 b
Concentration of N (g.kg ⁻¹)	8,2 a	8,2 a	5,0 a	4,3 b
Pool of N (g.m ⁻²)	37,6 a	20,1 b	32,6 a	24,2 b

* Values are based on dry matter. For each morphological component and for each variable, means followed by the same letters in the row do not differ by T-test (P>0.05). Source: Adapted from Paraiso et al. (2019).

In this context, the main storage zones of carbon reserves in forage grasses are the base of the stem, stolons and rhizomes (Volenc and Nelson, 2020). However, the authors suggested that research be conducted to study the root of forage plants and their behavior faced with stress. Thus, it is possible to associate the true role of this organ in the regrowth of forage plants.

Thus, research involving organic reserves should include all organs that may serve as a source of energy for the growth of the forage plant. In this context, Volenc and Nelson (2020) state that the storage organs differ between species and these differences must be considered when evaluating their reserves. Thus, the understanding of the relationship between root and residue height after grazing must be better understood, since to show the relevance of the reserve compartments one must consider the accumulation of dry mass of the organs and not only their contents. Additionally, research involving the storage of organic reserves and their relationship with forage canopy structure will help develop grazing strategies that can be applied for the sustainability of the production system (Silva et al., 2015).

Research conducted to address organic reserves in C₄ forage grasses, which consider the contents and concentrations of non-structural carbohydrates as a form of reserve, end up encompassing the fractions of starch, sucrose and fructans present. However, since these plants especially accumulate starch, quantification of this compound may be more appropriate for understanding the mobilization and use of carbohydrate reserves in tropical grasses.

4. Final Considerations

The transformation of light energy into chemical energy through photosynthesis is the most relevant process within forage plant systems. It is from this that forage canopies obtain the energy needed to conduct their morpho-physiological processes. Additionally, it is not only photosynthesis that defines the production capacity of a plant, since all factors present in the ecosystem in which it is inserted affect in some way its development process.

Thus, there is a balance between carbon and nitrogen fluxes within the forage canopy, allowing the plant to obtain enough energy for its maintenance and growth. Generally, carbon and nitrogen can be used by the plant in the form of organic reserves and their distribution throughout the plant will depend on the type of management adopted. Thus, the direction and priority in which the carbon and nitrogen will be allocated is intimately linked directly to the environmental conditions in which the plant is inserted.

Different defoliation and fertilization strategies affect the pattern of organic reserve accumulation in forage plants. Through the defoliation process, reserves assume a priority role in the first days of regrowth, helping reestablish canopy leaf area. Additionally, carbohydrate and nitrogen accumulation patterns depend, besides the environment, on the species or cultivar being evaluated. Thus, it would be interesting to encourage research involving the reserve organs and their accumulation patterns so that the results can aid in understanding their role within the grassland ecosystem.

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