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Review

Anatomical differences among forage with respect to nutrient availability for ruminants in the tropics: A review

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Different types of forage have been used worldwide in farm animal feeding. However, different microscopic cellular arrangements are clear in the anatomical structure, are due to climatic influences and are reflected in the productivity responses of cattle, especially in comparisons among tropical and temperate grasses. The physical impediment of the plant anatomical structure affects nutrient accessibility to rumen microorganisms. Thus, the objective of the present review was to discuss aspects related to C_3 and C_4 forage plant anatomy and nutrient availability for ruminants, due to the specific structure of each plant tissue, the speed at which the microorganisms can access the cells becomes different animal responses.

Key words: Plant anatomy, digestibility, nutritional value, neutral detergent fiber.

INTRODUCTION

Understanding the anatomical structure of forage can effectively influence nutritional aspects in ruminants. Both grass and legumes are angiosperms. However, their carbon fixation physiology and metabolism can differ among species. In most plants, the CO_2 fixation process includes a 3-carbon molecule as the first stable compound; this process is the C_3 Calvin-Benson cycle (Sharkey and Weise, 2015; Yamaoka et al., 2015). However, in certain plants, the first stable compound is a 4-carbon molecule in a process referred to as the C_4 dicarboxylic acid cycle (Gowik and Westhoff, 2011). The above-described changes imply different morphological traits. Furthermore, C_4 plants are more adapted to light and high temperatures (Valente et al., 2011a). In comparison, C_4 plants require less than 400 g water to produce 1 g dry matter (DM), whereas C_3 plants use 400 g to 1000 g water to produce the same quantity of DM (Odum, 1983). In nature, including forests, C_3 plants

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produce the most photo-assimilates in the world, likely because these plants are more competitive in mixed communities under the effects of shadow casting and little variation in temperature and luminosity (Jardine et al., 2014). When grass is intercropped with legumes in cattle-feeding pastures, high results of degradability are founded (Barcellos et al., 2008; Silva et al., 2010; Zhang et al., 2015). An advantage of intercropping is that legumes exhibit less variation in their nutritional value throughout the year, whereas the grass forage nutrient content decreased in dry seasons (Monteiro et al., 1998; Sage et al., 2015). Intercropping grass and legume forages produces imbalance problems in the pasture because all tropical legumes are C_3 plants, whereas most tropical grasses feature a C_4-type metabolism. In these mixed pastures, C_4 grass exhibits higher growth, and depending on animal management, legumes may disappear due to low persistence and grazing intensity (Carvalho and Pires, 2008a). Tropical C_4 plants exhibit little photorespiration because the high CO_2 levels in the bundle sheath cells accelerate the carboxylase reaction relative to the oxygenase reaction. This effect is relevant at higher temperatures. Thus, C_4 plants have an advantage in hot and bright environments (Van Soest, 1994; Sage and Stata, 2015).

Shaded plants invest relatively higher proportion of photoassimilates in increased leaf area, to maximize capture of the available light. Usually have thin leaves, higher specific leaf area and sheets with lower bulk density. The anatomical changes that occur on leaves develop under low light play an important role in plant adaptation to the conditions imposed by the environment. Generally these changes are related to the increased uptake and utilization of the incident light, feature that limits growth in the shade, increasing photosynthetic efficiency of the plant (Lambers et al., 1998). The increase of leaf area in low light conditions It is directly related to anatomical changes that may occur in the shaded plants as cuticles and thinner epidermis, mesophyll and thinner smaller proportion of palisade parenchyma tissue conductive support and a higher proportion of spaces intercellular and lower stomatal density (Berlyn and Cho, 2000).

In studied with response to levels of artificial shades (0, 50 and 70%) with the objective of determining the acclimation of C_3 and C_4 species of forage species to changes in the luminous environment, Gobbi et al. (2011) worked with C_4 plant signal grass (*Brachiaria decumbens* cv. Basilisk) and C_3 forage peanut (*Arachis pintoi* cv. Amarillo) and concluded that the specific leaf blade of the two species increased linearly as a function of the increasing levels of shading. In signal grass, the increase on specific leaf area was followed by a linear reduction in leaf thickness, with the increasing levels of shade. However, forage peanut leaf thickness was not significantly altered by shade. Stomatal density on adaxial and abaxial leaf surfaces decreased with the increase on levels of shade. The forage species evaluated showed a good acclimation to variations on light intensities, and they are good alternatives to use in environments with low solar radiation levels.

A great diversity of species of microorganisms present in the rumen environmental, with specific functions, in the degradation of carbohydrates, protein and lipids. However, the knowledge of the interactions between the different species of microorganisms in the rumen ecosystem. Our understanding of characteristics of the ruminal microbial population has opened new avenues of microbial ecology and the use of these nutrients in the plants (Krause et al., 2014; Valente et al., 2016). Thus, the study proposal was to discuss aspects related to C_3 and C_4 forage plant anatomy and nutrient availability for ruminants, due to the specific structure of each plant tissue, the speed at which the microorganisms can access the cells becomes different animal responses.

FORAGE PLANT STRUCTURE

Forage plants are composed of different structures, and the physical and chemical composition of each tissue is directly related to its structure in the plant. Supporting tissues must be densely grouped with thickened and lignified cell walls (Lempp et al., 2000). In photosynthesis-specialized tissues, the cell walls must be thin and non-lignified. Thus, the digestibility potential for given forage is related to the different tissues it comprises (Akin and Robinson, 1982; Batistoti et al., 2012; Cardoso, 2013). Accordingly, higher lignified vascular and sclerenchyma tissue content in a plant lowers the digestibility ratio (Brito et al., 2004; Queiroz et al., 2000b; Valente et al., 2011b,c). As the plant ages, the sclerenchyma cell walls in the leaf blades tend to thicken. In a study on three cultivars of elephant grass, which is tropical forage, Brito and Deschamps (2001) found that the lignified tissue area increased with plant growth in both the leaves and stem. The maturity stage is an important factor that influences the nutritional value of the forage plant (Wilson, 1997, Dabo et al. 1997; Aoki et al., 2013). In grass plants, leaf blades harbor different tissues, including tissues specialized in liquid conduction, tissues specialized in supporting the plant and tissues composed of mesophyll, where photoassimilate synthesis occurs. Conducting tissues are known as vascular bundles and are composed of xylem and phloem. Sclerenchyma is a supporting tissue. However, in grass, supporting and conducting tissues are associated. The epidermis covers the lower and upper outer surface of the plant and can feature a cuticle on its external surface. In grass, the stem is composed of an outermost epidermis and parenchyma tissue with vascular bundles that are scattered as a sub-epidermal sclerenchyma ring surrounding the entire stem (Wilson, 1997). The vascular bundles are similar to the bundles in leaves and can

include a fiber ring (sclerenchyma) around each bundle. In the initial development stages, only xylem is lignified. However, as age increases, the maturation progress proceeds to lignify the sclerenchyma ring and, at a more advanced stage, even the parenchyma where the vascular bundles are inserted (Paciullo, 2000; Smith et al., 2013).

C_4-type forage plant species are anatomically different compared with C_3 plants. Specifically, the mesophyll cells are more densely arranged and form a radial structure around the vascular bundles, which is referred to as Kranz anatomy (Valente et al., 2011a) and is absent in C_3 plants. In a study comparing tropical C_4 and temperate C_3 grass tissue contents, Wilson (1997) showed that the higher mesophyll (rapidly degradable tissue) content in temperate grass produces a better cattle weight gain response than tropical grasses.

PLANT TISSUE CONTENT AND DIGESTIBILITY

Forage plant digestibility depends on its bromatological and histological composition. Although lignin is the major digestibility-limiting factor (Jung and Deetz, 1993), other components can also limit a plant's nutritional value (Bonelli et al., 2013). According to Van Soest (1994), these components include substances with different effects, such as those designed for plant defense through diminishing the forage palatability. Other substances inhibit animal metabolism by hindering bacterial development in the rumen; these include phenylpropanoids, such as lignin, flavonoids, isoflavonoids, other compounds with alkaloid and terpene content and tannins. However, tannins are classified into hydrolysable tannins (HT), with molecular weight between 500 and 3.000 g mol^{-1}, and condensed tannins (CT) with molecular weight up to 20.000 g mol^{-1}, second Cieslak et al. (2013). Tannins can bind proteins, and to a lesser extent metal ions, amino acids, and carbohydrates in aqueous solution (Makkar, 2003). Tannins can antimicrobial effects due to their capacity to bind microbial enzymes or cell wall or membrane proteins, or proteins in the substrate, decreasing microbial attachment and digestion (Morales and Ungerfeld, 2015).

Tropical Legumes also have tannins higher (e.g. *Desmodium, Cajanus*) or less degree (*Arachis, Neonotonia, Centrosema*), which interfere in palatability (decreased) in risk of bloat (reduces), digestion and utilization of protein and forage carbohydrates. However, depending on the nature and concentration of these tannins in forage, some advantages can be obtained, especially at high protein diets (e.g. Leucaena grazed in water). If this protein is not was complexed in part, it is precariously utilized by the animal, since the high rate of degradation in the rumen was not synchronized with the power supply. Then, N losses occur, excreted as urea for example second Barcellos et al. (2008).

In tropical climates, forage typically features less soluble carbohydrate and high cell wall content. Thus, forage tends to exhibit less nutritional value and more structures that are protective against predation. Due to influence by environmental factors, such as long periods of hot nights, plants respire and, when forage grows at higher temperatures, lignification increases. Thus, forage with a C_4 metabolism is typically lower quality (Figueiras et al., 2015). Also, according to Van Soest (1994), the generalization that C_4 plants have a lower nutritive value than C_3 is not universally true, and a few exceptions deserve mention. Corn and sorghum are C_4 plants derived from tropical ancestors. Studies show that corn grown under tropical conditions has a much lower nutritive value than corn grown in a temperate environment. legumes usually have higher levels of crude protein as compared to tropical grasses, which can improve the protein balance in the rumen ecosystem.

Studies on leaf anatomy and its relationship with forage plant nutritional value have been reported (Wilkins, 1972; Wilson, 1976; Rossatto et al., 2015). For tissues that are digested after reaching the rumen, different types of microorganisms must colonize the food particles. The main invasion route seems to be via lacerated epidermal areas. Brito and Deschamps (2001) found that stomata in the epidermis of sheaths and blades were used by microorganisms to access inner tissues. The degradation process begins in the substomatal cavity and progresses through the mesophyll. Rumen bacteria initially digest mesophyll and phloem cells (Hanna et al., 1973; Akin et al., 1973; Akin, 1989). To obtain access to parenchyma bundle sheath cells, microorganisms must first digest the mesophyll or epidermal cells, or the bundle sheath cells must be exposed through physical damage. Thus, the parenchyma bundle sheath cell digestion rate is influenced by the mesophyll cell digestion rate, and the colonization time can decrease as the number of lacerated areas in the epidermis increases. Chewing by the animal can contribute to higher physical degradation of the grass, during both intake and rumination (Krause et al., 2014; Valente et al., 2016).

For the parenchyma bundle sheath and the epidermis, partial digestion is evident after 24 to 48 h of incubation (Bohn et al., 1988; Wilson et al., 1991; Wilson, 1993; Zhang et al., 2015). However, epidermal cells disappear completely after 24 h of incubation (Akin and Burdick, 1975; Sun et al., 2008). Second Moore and Jung (2001) lignification tends to be most intense in structural tissues such as xylem and sclerenchyma are virtually indigestible and remain intact in the ruminal fluid after long incubation times (Figure 1). The reason dry matter digestibility is negatively correlated with lignin concentration is because the concentration of lignin always increases as cell-wall concentration rises, and forage cell walls are always less digestible than cell soluble. There are large differences in lignification between grasses and legumes and also differences in the impact of lignin per se on their forage quality. Lignin concentration of legumes often appears

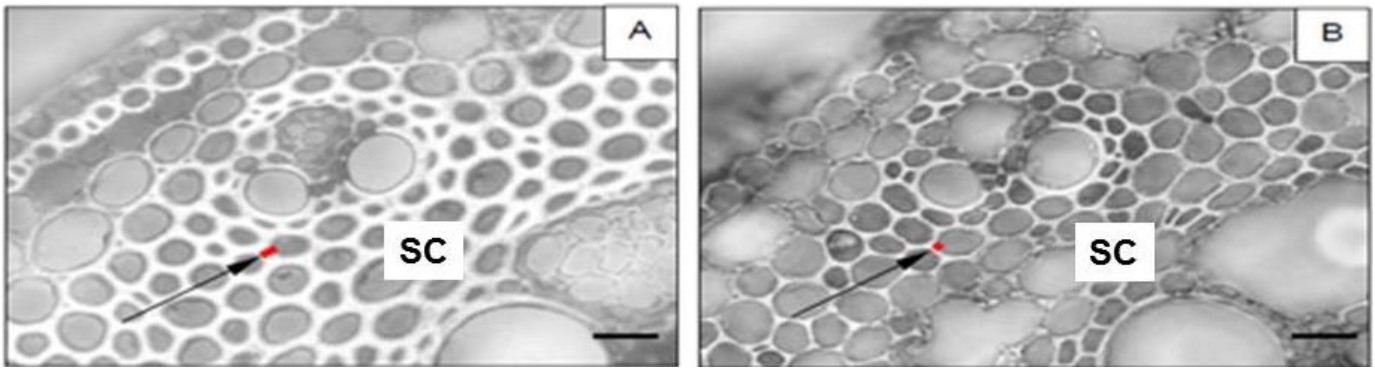

Figure 1. Brachiaria grass stem segment cross-section before (A) and after (B) 46 h of digestion. SC – sclerenchyma cell wall. (—— 15 µm) (Paciullo, 2000).

comparable to that of grasses when expressed as a proportion of dry matter. However, when expressed as a proportion of fiber, legumes demonstrate a wider range of lignin concentrations that are generally higher than those of grasses.

Inaccessibility of the secondary cell wall hinders microorganism entry and thus impedes rapid digestion of the plant cell wall, which is due not to its composition but to the time required to access the wall, which can then be excreted in the feces undigested (Wilson, 1997). Cell wall thickness can impede rapid access by the bacteria to initiate the digestive process. Digestion of the sclerenchyma cell wall, for example, requires 48 h. Thus, even if the cell wall is accessible to microorganisms, it will not be fully digested during its residence in the rumen (Krause et al., 2014). Thicker secondary walls require a longer time for full digestion (Akin and Robison, 1982; Monties, 1991). After compiling results from different works on tissue digestion, Akin (1989) suggested dividing C_4 grass leaf tissue into rapidly digestible, *e.g.*, mesophyll and phloem; slowly and partially digestible, *e.g.*, epidermis and vascular bundle sheath cells, respectively; and indigestible tissues, *e.g.*, xylem and sclerenchyma. In C_3 plants, only vascular tissue (except phloem) and the inner bundle sheath, which is observed in certain species, are resistant to digestion, and the sclerenchyma and parenchyma bundle sheath are considered slowly digestible. Tissues such as mesophyll and other types of parenchyma are not lignified, contain a large proportion of metabolites, and are highly degradable. Between these extremes are tissues with intermediate and variable degradability such as phloem and collenchyma (Wilson, 1993). Tissues such as the mesophyll, epidermis and outer bundle sheath are rapidly digested.

In general, C_4 species exhibit more vascular tissue, parenchyma bundle sheath and sclerenchyma content in the leaf blade, whereas C_3 plants feature exceptionally greater mesophyll content, which occupies approximately 60% of the cross-section of such grass (Minson and Wilson, 1980). The C_4 grass mesophyll is more slowly digested, even under rapid ruminal degradation, than C_3 species due to high cell density in C_4 forages. In C_3 species, cells are more loosely arranged and exhibit few cell-to-cell adhesion points. Anatomically, parenchyma sheath degradation seems the greatest cause of digestibility variations among C_4 photosynthetic *Panicum* spp. (Akin, 1982). Non-lignified tissues (collenchyma, chlorenchyma, cambium, phloem, and parenchyma) are more rapidly and almost completely degraded in animal digestive system, whilst lignified tissues, such as xylem vessels and phloem and xylem fibers, typically resist degradation. Epidermal and collenchyma cells develop very thick, but not lignified primary cell walls, which are slowly degradable, whilst waxy cuticle tends to resist degradation (Zorić et al., 2014).

Tissue degradation decreases with plant age. However, according to Carvalho and Pires (2008b), the environment also exerts an influence. Increases in lignified vascular tissue in elephant grass correlate with increasing tissue age, which is more evident in the stem (Brito and Deschamps, 2001). Second, Oliveira et al. (2014) with the aim to determine ruminal degradation of neutral detergent fiber of grasses of the genus *Cynodon* spp., harvested at four cutting ages. Concluded that daily increased in the cutting age, there was a linear reduction in the effective degradability of neutral detergent fiber (NDF) of blade and stem of 0.16 and 0.18%, respectively. The increase in the cutting age had a linear and positive influence on the un-degradable NDF with daily increments for leaf and stem of 0.12 and 0.18%, respectively.

Generally, mesophyll content is positively correlated with digestibility and negatively correlated with cell wall content. On the other hand, parenchyma bundle sheath, vascular tissue and sclerenchyma content are negatively correlated with digestibility and positively correlated with cell wall content (Queiroz et al., 2000a, b). Tropical grasses can exhibit different results for digestion of each leaf tissue. Mesophyll and phloem cells can be rapidly degraded after an incubation period of 12 to 24 h (Márquez et al., 2009), but these tissues have also been found undigested even after 48 h of incubation (Akin et al., 1983). In a study with Tifton 85 and Brachiaria

grasses, Paciullo (2000) found that the mesophyll, parenchyma and phloem cells were the only fully digested cells *in vitro* upon up to 48 h of incubation. During his work with two *Cynodon* spp., Akin (1982) found that the mesophyll and phloem were the first tissues digested. *In situ*, after 24 h of digestion, only xylem and sclerenchyma were detected from temperate climate forage (Gasser et al., 2005). Compared with lignified tissues from palisade grass (*Urochloa brizantha* (Hochst. Ex A.Rich.) R.Webster) and creeping signal grass (*U. humidicola* (Rendle) Morrone & Zuloaga), Brito et al. (2004) found the highest content in palisade grass in the central basal and aerial apical regions.

Barcellos et al. (2008) in a compilation of data to assess the digestibility coefficient for legumes, found 64.4 for *Arachis pintoi,* 49.2 for *Stylosanthes Guianensis,* 44.3 for *Glycine wightii,* 55.6 for *Leucaena leucocephala* and 59.9 for *Medicago sativa.*

When Paciullo (2000) compared digestion among three tropical grasses, Tifton 85, Bermuda grass ((*Cynodon dactylon* (L.) Pers.) exhibited better results than molasses and signal grass species. As for molasses grass (*Melinis minutiflora* P. Beauv.), the high xylem and sclerenchyma content indicates that this species exhibits anatomical traits more typical of forage with lower nutritional value. signal grass species were intermediate compared with the two other species; it exhibited the highest cell wall thickness irrespective of developmental stage, which negatively affected digestion in the cross-sections. The sclerenchyma cell wall digestion rates ranged from 0.007 to 0.018 µm/h depending on the grass species and age and were higher with a 46 h incubation time. Thus, even without lignification, as in young stems, cell wall digestion in ruminal fluid was not complete during the incubation time, which suggests that limited digestion in thick-walled cells (greater than 1 µm) is mainly due to structural problems (Paciullo, 2000). According to Baurhoo et al. (2008), purified lignin can be digested by monogastric and ruminant animals under specific conditions. However, this phenolic polymer does not naturally occur in original plant structures (plant cell walls) and thus is not relevant to the present study.

Lignified vascular tissues exhibit highly significant positive correlations with NDF, acid detergent fibers (ADF) and lignin content and highly significant negative correlations with crude protein (CP) content (Gomes et al., 2011; Mokhele et al., 2012). These tissues exhibit thickened lignified cell walls, which are frequently associated with the slowly digesting fraction and forage fiber content (Queiroz et al., 2000b).

RELATIONSHIP BETWEEN VEGETAL ANATOMY AND CONCEPT THE FIBER IN RUMINANT NUTRITION

For determining forage quality is based on separating several fractions of the forage using detergents. A neutral detergent solution is used to dissolve easily digestible substances, which leaves a fibrous residue referred to as NDF that contains the main plant cell wall components (cellulose, hemicellulose and lignin) and generally corresponds to 600 to 800 g/kg forage DM. Thus, carbohydrates are the main energy source for ruminants both directly through absorbing their monomers in the digestive system and indirectly by conversion into volatile fatty acids through microbial fermentation (Aschenbach et al., 2014). The term fiber is used to define a nutritional rather than an anatomical concept. Fibrous carbohydrates and lignin, which compose the plant cell wall, are slowly digested, exhibit variable nutritional availability and occupy space in the gastrointestinal tract (Van Soest, 1967; Allen, 1996). Fiber methods isolate different chemical constituents in feeds. The fiber with the smallest magnitude is crude fiber, because the strong acid and alkali in this method leaves a residue that is mostly cellulose with variable amounts of lignin and hemicellulose. ADF is next largest in magnitude because it recovers most, if not all, of the polymeric lignin and cellulose in feeds, with some contamination from pectin, hemicellulose, tannin-protein complexes, and ash. Of the three routine fiber methods only NDF isolates all of the insoluble fiber components in plants (hemicellulose, cellulose, and lignin) with some protein contamination. In animal byproduct feeds, NDF isolates the nitrogenous material that is indigestible or slowly digesting and thus meets the requirements of the nutritional definition of fiber. Because ADF does not contain hemicellulose it is not an accurate estimate of fiber in feeds. It was developed as a preparatory step for the determination of lignin and was never intended to be a measure of fiber in feeds (Van Soest, 1994). The concept of physically effective fiber (peNDF) was introduced to account for the physical characteristics of NDF (primarily particle size) that affect chewing activity (saliva secretion) (Yang and Beauchemin (2007). This concept is based on the hypothesis that the fiber in long feed particles (>1 cm) promotes chewing and saliva secretion, which helps neutralize the acids produced during ruminal digestion of feeds. The fiber that promotes chewing is considered physically effective. The peNDF content of the diet can be determined by multiplying the NDF content of the diet by its physical effectiveness factor (pef) second Beauchemin and Yang (2005).

NDF AND INDF BEHAVIOR IN THE RUMEN

Of all routinely measured feed constituents, NDF is most consistently correlated with DM ingestion (Van Soest, 1994). Higher NDF intake occupies more space in the ruminant gastrointestinal tract, which produces a filling effect (Mertens, 2003). Furthermore, due to the lower rate of NDF disappearance in the digestive system, more time is required to reduce the particle size, which is necessary

for escape from the rumen.

Forage fiber or plant cell wall content can be divided into a potentially digestible and indigestible fraction (pdNDF and iNDF, respectively). The digestible fraction of the fiber disappears from the rumen through digestion, fermentation and passage, whereas the indigestible fraction disappears solely through passage (Krause et al., 2014). Notably, particle density is affected by fermentation because the generated and retained gas tends to reduce the specific gravity. As fermentation proceeds and the concentration of potentially fermentable nutrients decreases, the gas production rate decreases, and the density increases, which allows for passage through the reticulo-omasal orifice (Allen, 1996). With the progression of forage maturity, iNDF content increases and decreases the microbial digestion rate of this fraction, which thus affects the fiber particle residence time in the rumen (Jung and Allen, 1995). Microbial growth in animals fed low-quality tropical forage is not yet fully understood. However, additional supplementation with nitrogenous compounds to improve animal performance yielded a balance between digestion and degradation; increased feed intake correlated with increased passage rate (Detmann et al., 2009). Studies on NDF digestibility, which is a heterogeneous fraction composed of two types of carbohydrates, hemicellulose and cellulose, and one phenylpropanoid, lignin, report varying content and physical structure in this fraction among plant species and during the plant life cycle (Gomes et al., 2011). Understanding the iNDF fraction is relevant because it plays an important role in ruminant nutrition. According to Valente et al. (2015), differences in feed particle size are reflected in the iNDF fraction, where a simple change in the particle size from 1 to 3 mm can dramatically increase the expected time for detecting the iNDF in the laboratory after ruminal incubation.

The disappearance of NDF from the ruminal environment is a time-dependent process that integrates the speeds of pdNDF degradation and iNDF escape from the ruminal environment (Ellis et al., 1994). Thus, the entry of new fibrous substrates from forage will only occur when part of the resident mass is removed from the environment through degradation or passage. Accordingly, the pdNDF yield can be maximized by minimizing the ruminal fill effect (Figueiras et al., 2010, 2015). This behavior indicates that removing iNDF from the ruminal system improves NDF intake from low-quality forage.

At an advanced maturity stage, forage exhibits lower degradation and fiber digestion rates, tends to increase ruminal fill and reduces the passage rate (Kp) (Van Soest, 1994). Passage rates can be mathematically calculated based on independent variables related to the animal or diet. In predicting the Kp potential, special attention must be paid to the ingestion of indigestible particles and to the animal's live weight (Cannas and Van Soest, 2000).

Changes in the fibrous particle passage rate seem directly associated with a higher NDF degradation rate (Russell, 2002; Detmann et al., 2014). The pdNDF degradation reduces gas production and increases the relative concentration of the iNDF fraction of the particle, which is typically denser due to higher phenolic compound content.

CONCLUSION

C_4 grass mesophyll is more slowly digested, even under rapid ruminal degradation, than C_3 species due to high cell density in C_4 forages. In C_3 species, cells are more loosely arranged and exhibit few cell-to-cell adhesion points. Tropical forage typically features less soluble carbohydrate and high cell wall content. Lignification tends to be most intense in structural tissues such as xylem and sclerenchyma are virtually indigestible and remain intact in the ruminal fluid after long incubation times.

Plant cell wall lignification is a process that cannot be avoided because it would harm plant structure; however, it hinders nutrient availability for ruminants. Plants with higher growth rate have higher accumulation of lignin hindering access to components of the cell wall by microorganisms because increase the iNDF.

Conflict of Interests

The authors have not declared any conflict of interests.

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