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Maximizing Fiber Utilization of Silage in Ruminants

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Abstract

This chapter highlights the importance of fiber digestibility and utilization in ruminants and to summarize the main factors that influence fiber digestibility in silages. Forage provides at least half of the diet of lactating cattle and greatly affects energy and carbohydrate intake. It is important to maximize the intake of digestible carbohydrate from forages, because energy requirements for maintenance and milk production often exceed the amount of energy high-producing cows can consume, particularly in early lactation. There are many approaches used for enhancing fiber utilization in silage and subsequent maximizing energy intake and productivity of dairy cattle. Out of these approaches are: selecting appropriate forages with high fiber digestibility, applying the appropriate agronomic practices such as harvesting at the proper stage of maturity, fertilization, and cutting height at harvest, along with using of esterase-producing inoculants or fibrolytic enzymes have been proposed as approaches to improving the productivity of dairy cattle.

Keywords: feed additive, fiber utilization, nutrient availability, ruminants

1. Introduction

The global livestock industry faces an extensive challenge since a presumed dichotomy exists between the increasing requirements for animal feeding conferred by population growth and consumer concerns regarding the sustainability of livestock production [1]. Meanwhile, the cost of feed grains for livestock has increased substantially in recent years [2]. Thus, there is an increasing interest in using silages as a main source of forages in ruminant's diets, with high nutritive value as an alternative feed source. In high-producing dairy cattle, it is important to maximize digestible carbohydrate intake or increase neutral detergent fiber digestibility (NDFD) from silage because the energy needed for maintenance and milk production often



© 2016 The Author(s). Licensee InTech. This chapter is distributed under the terms of the Creative Commons Attribution License (http://creativecommons.org/licenses/by/3.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. exceeds the amount of energy high-producing cows can consume, particularly in early lactation [3]. One of the main factors that affect silage utilization is the proportion of its potentially digestible fiber fraction, where silage having less than 60% of total fiber content is available for digestion by the ruminant animal [4]. The first section of this chapter will discuss the most important aspects of silage fiber digestibility. The chapter starts by the importance of fiber digestibility, before considering the method used for evaluating fiber digestibility. This is followed by fiber digestion and utilization in ruminants. The chapter ends with sections on the factors that effect on fiber digestibility in silages.

2. Importance of fiber digestibility

Silages are considered the most cost-effective feed resource in ruminant nutrition. Grass and small-grain cereal silages are the main sources of dietary energy, while leguminous silages are considered important sources of protein for ruminant livestock [5]. The quality of silage is an important determining factor in dairy cow performance as the forage accounts for a large proportion of the diet about reaching from 35% up to 100% of dry matter (DM) [6]. For high-producing dairy cows, high-quality silages with lower fiber and higher fermentable concentrates are usually used to meet energy requirements. Nevertheless, inadequate dietary fiber reduces chewing activity, insalivation and rumen pH, and can cause rumen acidosis and laminitis [7]. These can depress fibrolytic microbes and milk production by increasing maintenance demands [8, 9]. National Research Council (NRC) stated that dairy rations should have a minimum of 25% neutral detergent Fiber (NDF), 18.7% of which must come from forage for adequate rumen health. Although rumen fermentation and function can cause negative impacts on dairy cattle fed rations deficient in fiber, excessive level fiber of over 44% may also have negative effects on intake and digestibility [9].

The National Research Council (NRC) recommendations regarding the total NDF and forage NDF contents of dairy rations are presented in Table 1 [9]. In general, the minimum NDF contents that are recommended for dairy ration will depend on the dietary contents of NFC, a physical effectiveness of fiber, and the source of the fiber. It is well established that the fiber from forage sources could induce the salivation and cud-chewing activity than nonforage fiber sources. Consequently, the major factor for evaluating the efficiency of dietary NDF capability is NDF content in forages. It has become very important to prevent acute and subacute rumen acidosis and maintain milk fat level, evaluating the physical effective NDF (peNDF) in diets due to the importance of peNDF in maintaining the rumen pH and fiber digestion. It is well established that the amount of peNDF in the diet is dependent on the chop length of forages, dietary NDF, and forage to concentrate ration content [10]. It has been reported that peNDF intake can stimulate the chewing activity and can minimize the incidence of ruminal acidosis [11]. Many studies have examined the effects of peNDF on lactation performance [12–19]. The peNDF of feed could be calculated from the NDF content multiplied by a physical effectiveness factor (pef). The pef ranges between 0 (not effective at stimulating chewing) and 1 (100% effective at stimulating chewing). Numerous feed models such as Cornell Net Carbohydrate and Protein System (CNCPS) presently use peNDF as an important input for the model to predict lactational performance. The forage and total mixed ration (TMR) particle size distribution recommendation using Penn state particle separator as reported by Heinrichs and Kononoff is presented in **Table 2** [13].

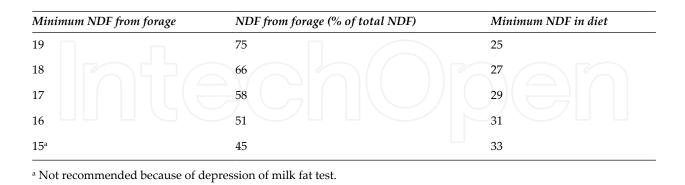


Table 1. Recommended minimum NDF concentration based on the proportion of NDF coming from forage sources [9].

Sieve size	Туре				
	Corn silage	Haylage	TMR		
>19.0 mm	5±3	15 ± 5	5±3		
19.0–8.0 mm	55 ± 10	60 ± 15	40 ± 10		
8.0–1.18 mm	40 ± 10	30 ± 10	40 ± 10		
<1.18 mm	<5	<5	<20		

Table 2. Forage and TMR particle size distribution using Penn state particle separator as reported by Heinrichs and Kononoff [13].

3. Evaluating of fiber digestibility in ruminants

Understanding the mechanism of fiber digestion is very important to accurately estimate the digestible energy of fiber and to improve animal performance. Fiber is digested primarily in the rumen as the result of the dynamic operation that is affected by the chemical nature of the fiber and by the passage and digestion rate of fiber within the digestive tract of the animal. The potentially digestible NDF (pdNDF) and the digestion rate (kd) vary greatly between and within different silage types [14, 17]. The passage rate of fiber (kp) is in the first place influenced by the animal, where the digestion of fiber increases along with increased retention time of feed in the rumen [15, 18]. Several models have been developed to describe the process of digestion in the rumer; some models are simple or complex. Most of these models have been developed by fractional schemes to correlate the disappearance or gas production curves with rumen digestibility of feed components, which assume that the feed component includes at least two portions: a potentially degradable fraction and an undegradable fraction. The potentially degradable portion will be degraded at a fractional rate (per hour), after a discrete

lag time (h). The undegradable fraction is calculated from the longer time of incubation as proposed by Waldo et al. [19] (**Figure 1**). By using this model, Allen and Mertens [21] educed mathematical equations to define fiber digestibility and rumen fill. For fiber digestibility, the following equations were educed:

$$D = (pdNDF(dFINTAKE/dt))/(kd+kp)$$
(1)
$$I = (fi(dFINTAKE/dt))/(kp)$$
(2)

Finally, the rumen fill would be estimated as the sum of the digestible (D) and indigestible (I) fiber pools in the rumen

$$Fill = D + I \tag{3}$$

Eq. (1) shows that digestibility is directly related to (pdNDF) and (kd), and inversely proportional (kd + kp; the rate of total fiber digestibility). Thus, as the ruminal retention time increases (1/kp), the extent of ruminal digestibility increases [22]. The fiber weight in the rumen is dependent on fiber intake per unit of time (dFINTAKE/dt), and parts that are digestible (fd),

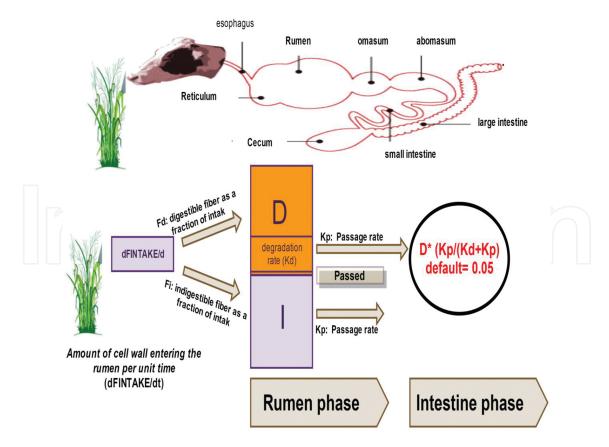


Figure 1. Schematic model of total-tract fiber digestibility. Redrawn from Waldo et al. and Jung and Allen [19, 20].

and indigestible (fi), as well as digestion rates (kd) and passage (kp). Jung and Allen ranked the factors that influence ruminal fill, and the most important element was the fiber content, followed by kp, the fraction that is indigestible, and the lowest factor was the kd [20]. The digestion kinetics of fiber can be measured in vivo using rumen evacuation technique, where cannulated animals are used for measuring the digestible and indigestible fiber pools that flow from the rumen [23]. In spite of the high precision for rumen evacuation technique to estimate rumen digestion kinetics, this technique is unwieldy for routine forage analysis. It has been proved that the use of other biological methods, that is, in vitro or in situ techniques, could give better characterization to degradation kinetics of fibrous fraction of forages. Over the last 50 years, the in vitro system has not been widely used in farm to implement analysis on forages because of its difficulty to perform in farm. This situation has changed in recent years with the use of a shorter digestion time (30 or 48 h) along with the enhancements that occurred in spectral analysis using near-infrared spectroscopies, where the laboratories were facilitated to assess the digestion of forages without the need to obtain rumen fluid. Some mathematical equations have been developed, which can use single time points like 24 or 30 h in vitro NDFD along with fixed lag time and lignin in the forages to calculate the kd rates [24].

In recent times, the feeding studies have found the indigestible neutral detergent fiber (iNDF) after longer incubation time (240 h in vitro or 288 h in situ) was highly correlated with dry matter intake (DMI) and would be used to predict pdNDF [25]. Furthermore, there were sufficient data being created by commercial laboratories. Thus, the iNDF was applied as a new approach rather than using lignin × 2.4 to calculate pdNDF (CB3) and indigestible NDF (CC) using the updated CNCPS 6.5 [25]. It has been found that the model, which could accurately predict NDF digestibility, should partition NDF into iNDF and pdNDF, fractionate feed particles by their retention and passage in the rumen, using a predicted kd by an in vitro system [26]. Based on this approach, Combs developed a new method for predicting fiber digestibility; he used shorter incubation time (24, 30, and 48 h) along with iNDF (240 h) to predict kd (kdCB3) of pdNDF [27]. The CB3 kd rates derived from in vitro analysis were entered in the updated CNCPS model to calculate the ruminal fiber digestibility according to this equation; rumen degradability for $pdNDF = CB3 \times (kdCB3/(kdCB3 + kp))$. Finally, they calculated the in vitro total-tract NDFD (ivttNDFD) assuming that the intestinal digestibility of available NDF (CB3) amount escaping rumen digestion was 5%. Lopes et al. have found that in vivo total-tract NDF digestibility was highly correlated with the ivttNDFD. The regression equation to describe the relationship was described as follows: in vivo total-tract NFDF $(\%) = -3.62 + 1.11 \times \text{ivttNDFD}$ (%) with $R^2 = 0.70$, RMS = 4.27, P-value < 0.01; n = 21 diets. The differences between two methods (ivttNDFD and in vivo total-tract NDFD) were not significant, and mean values varied by only 1% unit, showing promise for this approach [28].

The use of high-resolution spectroscopic techniques (e.g., high-field nuclear magnetic resonance, mid-infrared, Raman spectroscopy, and pyrolysis mass spectrometry) is finding increased usage in forage assessment. These advanced technologies would provide more broad information about a primary nature [29]. A spectroscopic method such as Fourier transform infrared (FT/IR) spectroscopy has been developed as rapid, direct, nondestructive and noninvasive bioanalytical technique [29–37]. Thereby, this technique paves the way to better

understand the quantity, composition, structure, and distribution of chemical constituents and functional groups in a tissue (feed and ingredients) [38–42]. Intrinsic chemical structures were found to effect on nutritive value, degradation characteristics, utilization, and availability of feed [43, 44]. Many studies have reported that AT/IR would accurately predict rumen degradability of DM, NDF, concentrations of lignin, ferulic, and coumaric acids in forage samples [45–47].

4. Fiber digestion and utilization in ruminants

4.1. Plant cell-wall carbohydrates

The forages are diverse in its characteristics, and this uniformity results in variations in quality as an animal feed. Plant cell-wall carbohydrates are the most important components in forages that influence silage quality. There is higher complexity in the utilization of silages due to diversity among forage plants, diversity in the ruminal microorganisms, and interaction between the forage plant cell-wall carbohydrates and microorganisms [48]. Ruminants can digest and degrade plant cell-wall polysaccharides. The plant cell-wall chemistry and anatomical structure will determine the digestion characteristics of cell types [49]. The fiber fraction for the main silages is presented in **Table 3**.

Forage	% DM	ADF	NDF	Hemicellulose	Lignin
Legume silage	37	39	47	8.9	7.7
	30–43	33–44	40-55	4.1–13.6	5.3-10.0
MM legume silage ^a	35	39	52	13.4	6.8
	27–42	35–42	45–59	7.8–18.9	5.4-8.3
MM grass silage	36	39	56	17	6.9
	28-45	35–44	50–63	22	4.7–9.0
Grass silage	31	41	62	21	6.4
	21–41	37–44	55–68	15–27	4.9–7.8
Corn silage	33	26	45	19	2.8
	25–40	22–30	38–51	15–23	2.2–3.5
Winter cereals	29	31	52	21	4.3
	35	39	59	20	6.3

^aMM legume refers to mixed mainly legume forage; MM grass refers to mixed mainly grass forage.

Table 3. Fiber fraction for NDF concentrations based on the proportion of NDF derived from forage sources

The main groups of plant cell-wall carbohydrates are hemicelluloses and cellulose. Cellulose is a water-insoluble β -glucan composed of a linear molecule of *p*-anhydroglucopyranose residues linked by a β -(1 \rightarrow 4) bond. In contrary to cellulose, hemicellulose has various groups of polymers that are characterized with the heterogeneous composition. Xylan is the main

component of hemicellulose and compromises about 30–35% of the cell-wall material of annual plants. The main chain of xylan is composed of 1,4- β -linked D-xylopyranose units [50, 51].

The collaborative activity of the cellulolytic and noncellulolytic microorganisms in the rumen is critical in fiber digestion [52]. Rumen cell-wall degradation initiated by the attachment of rumen microbes to fiber and the bacterial species specialized to start this attachment/colonization process are the cellulolytic species Ruminococcus albus, R. flavefaciens, and Fibrobacter succinogenes. Rumen fungi and protozoa also colonize and degrade plant fragments to differing degrees [48]. The fermentation of structural carbohydrates by cellulolytic consortium results in the progressive process where volatile fatty acids (VFAs) are liberated at a lower rate than starch fermentation. The fermentation of structural carbohydrates is associated with an increase in the proportion of acetic and butyric acid [53]. Following absorption, the large proportion of acetate is not changed by hepatic metabolism and may be augmented by endogenous acetate production in the liver. The posthepatic supply of acetate to peripheral tissues constitutes a major part of the total energy available to the animal and may be either oxidized to produce adenosine triphosphate (ATP) or used as a substrate in the production of long-chain fatty acids [54]. While ruminally derived butyrate is quantitatively metabolized to b-OH-butyrate during absorption through the rumen epithelium, in posthepatic tissues it has a similar metabolic fate to that of acetate [54].

4.2. Lignin and phenolic acids

Lignin is an indigestible polymer in plants that plays an important role in the structural integrity of plant tissue. Although lignin comprises little of the total structural carbohydrate system in plants, it has been recognized to exert the negative effect on cell-wall polysaccharide digestibility by coating the plant cell-wall polysaccharides from enzymatic hydrolysis [55]. Lignin arises from an enzyme-initiated dehydrogenative polymerization of three originators: p-coumaryl alcohols, coniferyl, and sinapyl. The phenylpropanoid metabolism and shikimic acid pathway lead to the synthesis of lignin intermediates like p-coumaric acid, ferulic acid, and diferulic acid [56], which are converted into coniferyl, sinapyl, and p-coumaryl alcohols and ultimately to guaiacyl, syringyl, or p-hydroxyphenyl lignin, respectively [55].

With the maturation of forage cell walls, the guaiacyl-type lignin changes to lignin-rich syringyl units, and the digestibility of mature cell walls decreased. Taboada et al. found that guaiacyl and syringyl have negative correlation with organic matter or dry matter digestibility in ruminants fed on silages. They concluded that guaiacyl and syringyl could be used as predictors of digestibility than total lignin content in silage [57].

The brown midrib (BMR) mutation in annual C4 grasses such as corn and sorghum results in both a reduction in lignin concentration and a shift in lignin composition to a more guaiacyl-rich polymer [20]. Jung and Deetz have suggested that the improved digestibility of cell walls in BMR mutants is a result of both the reduced lignin concentration and the reduction in syringyl lignin content [58].

Cross-linking of lignin to cell-wall polysaccharides has been reported as additional mechanisms limiting fiber digestibility [20]. In grasses, ferulate and p-coumarate molecules are esterified to arabinoxylans, and some of p-coumarates are the ester or covalent linked to lignin [59]. As forages mature and lignin concentrations increase, ferulates that were esterified to arabinoxylan become etherified to lignin via cross-links between lignin and the cell-wall polysaccharides [60]. The degree of lignin/arabinoxylan cross-linking by ferulates negatively influences cell-wall digestibility to the polysaccharides, which prevents physical access by hydrolytic microbial enzymes to polysaccharides [49]. Model studies utilizing isolated cellulose and xylans, and forage NDF to which phenolic acids have been synthetically esterified, obviously demonstrated that the presence of these phenolic esters negatively effects on cell-wall degradability [61]. However, the reduction in digestibility caused by esterified ferulic acid only limits the degradation rate of polysaccharide, rather than extent, because fungi and ruminal bacteria possess phenolic acid esterases to ultimately remove these impediments to cell-wall digestion [62].

5. Enhancing fiber digestibility and utilization of silage

Ruminal digestibility of forage neutral detergent fiber can range from less than 25% to over 75% for different forage types [9]. Most research with brown midrib mutant corn silage found that lactating dairy cows will consume more DM and produce more milk when fed corn silages that have greater NDFD [63–65]. Oba and Allen found a relationship between NDFD and animal performance and they reported that a 1-unit increase in forage NDFD after 30 h of in vitro incubation was associated with increases of 0.17 kg d⁻¹ of dry matter intake, 0.23 kg d⁻¹ of milk yield, and 0.25 kg d⁻¹ of 4.0% fat-corrected milk [66]. Using high-quality silage in dairy cattle rations could reduce physical rumen fill, allow cattle to consume more feed, and produce more milk [63]. There are many factors that would influence the quality of silage. Such factors include silage species, silage varieties, stage of harvest, cutting height, growing conditions, silage additives, and enzymes.

5.1. Silages species

The most practical approach for increasing NDFD is based on increasing the amount of pdNDF in forages. Grass silages often have a greater proportion of pdNDF to indigestible NDF (iNDF) and higher in NDFD than legume silages, but the rate of digestion of legume pdNDF is frequently faster and could increase the total amount of NDF digested in vivo [63, 64]. The chemical and structural features have been identified, which may reduce the fiber digestion. Of these, lignin is the most notably reported [67]. Lignin is supposed to constrain ruminal fiber digestion, which acts as a physical barrier. The involvement of cross-linking of lignin to polysaccharides by ferulate linkages as an additional factor that inhibits the digestion of grass fibers has been identified [20]. However, a similar lignin cross-linking to fiber polysaccharides in legumes has not yet determined. There is an important role for plant anatomy on fiber digestibility [68]. The vascular tissue, sclerenchyma, and stem epidermis are degraded at a slower rate in rumen where they contain a higher amount of indigestible or highly lignified components. Leaf blades C4 grasses are typically less digestible than those in C3 grasses due to the existence of mesophyll cells. In C3 species, stem tissue cell such as parenchyma bundle

sheath, mesophyll, phloem, and epidermal cells are totally degraded, but these tissues are partially or slowly degraded in C4 species. In an earlier study by Akin and Burdick, they found that C4 grasses are less digestible than C3 species due to the existence of vascular tissue and parenchyma bundle sheath cells in larger amounts than in C3 grasses [69].

The total-tract digestibility of whole-crop cereals silage, legumes, and maize silage is often lower than for grass silage. However, the lower digestibility is mostly alleviated by higher feed intake such that energy intake is maintained [70]. Many studies have shown that the partial replacement of grass silage with whole-crop cereals may not have a negative impact on milk production in cows [71]. However, the effects of barley silage on DMI have been inconsistent, which are probably attributable to differences in the quality of the forages between studies. For example, Ahvenjärvi et al. noted a reduction in fiber digestibility when grass silage was replaced with whole-crop barley silage. This reduction in NDFD was related to a lesser pdNDF concentration in the rumen and higher iNDF pool size of barley silage compared with that of grass silage [70].

Whole-crop cereals species also varies in their quality and digestibility, for example, barley and oat silages when harvested at the same maturity stage (milk to soft dough stage) have found to enhance the feed intake and average daily gain in heifers when compared with triticale silage [72]. Furthermore, dairy cows that fed on barley silage have had higher intake than cows fed on oat silage when harvested at the maturity stage (early to a mid-dough stage of maturity). Such difference in feed intake is a consequence of variation in chemical composition and ear:stalk ratio of whole-crop cereals. Barley has more starch than oats and triticale because of the higher ear:stalk ratio in barley. Since most fibers exist in plant stalk, barley contains a lower fiber than oats and triticale when they are harvested at the stage of maturity. The higher starch resulted in a lower fiber content in barley silage, and hence barley can enhance the OM digestion when compared with oats and triticale silages when fed to dairy cows [72].

5.2. Selecting varieties with enhanced NDFD

Another potential method to increase pdNDF is by the use of genetic mutations in forage crops that reduce iNDF and increase the pdNDF fraction of the plant. The brown midrib mutation mutants were discovered for the first time at the University of Minnesota in 1924; the BMR genes have been found in sorghum, Sudan grass, millet, and corn. The BMR corn forage has about 25% less lignin and lower cross-linkages with lignin. Corn silage with the brown midrib mutation has a higher NDFD (34% less lignin and had 19% higher IVNDFD than conventional corn silage) [73–75]. Several studies confirmed the positive effect of feeding BMR corn on DMI and productivity of dairy cattle [76, 77], but responses have not been consistent in all experiments [78]. Ivan et al. compared corn silage with low and high cell-wall content on milk production, and reported that the hybrid with high cell-wall content had greater IVNDFD, increasing DMI and milk yield [79]. Data collected from a Journal of Dairy Science (number of treatments n = 22; **Table 4**) between the year 1999 and 2010 showed a non-significant correlation between IVNDFD in BMR corn silage and milk yield or DMI (P > 0.05, **Figures 2** and **3**). Inconsistent results between experiments may be attributed to various factors such as includ-

ing cows at a different stage of lactation and duration of experimentation or the lack of effect of forages with enhanced NDFD on DMI [82]. Recently, Ferraretto and Shaver performed a meta-analysis to study the effect of corn silage hybrids with different stalk characteristics (conventional, dual-purpose, isogenic, or low-normal fiber digestibility, brown midrib, hybrids with greater NDF but lower lignin contents or high in vitro NDF digestibility, and leafy corn silages) on lactation performance [85]. They found that for every 1-unit increase in ivNDFD the DMI can increase by 0.09 kg/d, although this correlation was not significant (DMI = 0.09ivNDFD + 19.531; R^2 = 0.72, p = 0.40); additionally, they found that for every 1-unit increase in ivNDFD the milk yield would increase by 0.14 kg/d (milk yield = 0.14 ivNDFD + 31; R^2 = 0.87, P = 0.06). It has been reported that the total-tract NDFD response to feeding bm3 corn silage is influenced by the DMI response due to enhanced ivNDFD as reported by Oba and Allen [64]. On the other hand, corn silage type, that is, bm3 versus near-isogenic or conventional corn silage hybrids by dietary forage NDF [82], starch [65], and CP [76] concentration, or supplemental corn grain endosperm type [80] interactions were undetected.

Publication	Treatments $(n = 22)^a$
Ballard et al. [81]	Mycogen corn silage
	Cargill (brown midrib corn silage)
Castro et al. [82]	Normal corn silage
	Brown midrib corn silage
Ebling and Kung, Jr. [83]	Conventional corn silage
	Brown midrib corn silage
Gehman et al. [78]	Dual-purpose corn silage
	Brown midrib corn silage
Ivan et al. [79]	Corn silage with lower cell-wall content
	Corn silage with higher cell-wall content
Oba and Allen [65]	Control corn silage
	Brown midrib corn silage
Oba and Allen [66]	Control corn silage
	Brown midrib corn silage
Taylor and Allen [80]	Control corn silage
	Brown midrib corn silage
Thomas et al. [84]	Dual-purpose corn hybrid
	Leafy corn silage hybrid
Weiss and Wyatt [76]	Dual-purpose corn silage
	High fiber corn silage
Weiss and Wyatt [76]	Dual-purpose corn silage
	Brown midrib corn silage

^aCorrelation analysis between the two variables was performed using the CORR procedure of SAS with the Pearson correlation method, because the variable data are normally distributed. Average of milk yield (38.2 ± 4.360), average of IVNDFD (50.39 ± 9.162).

Table 4. Effects of silage varieties with enhanced 30-h IVNDFD on milk yield. Data have been taken from a number of publications in Journal of Dairy Science (JDS from 1999 to 2010).

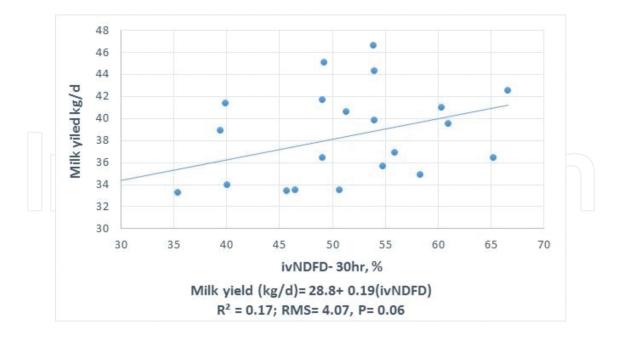


Figure 2. Relationship between in vitro NDFD (30 h) and milk yield with the prediction equation.

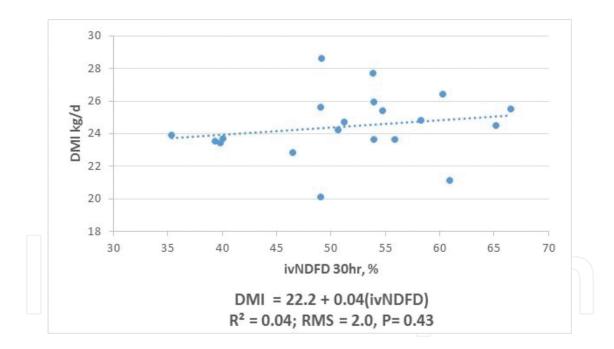


Figure 3. Relationship between in vitro NDFD (30 h) and DMI with the prediction equation.

5.3. Agronomic practices to enhance fiber digestibility

Fiber digestibility is largely dependent on plant maturity. The effect of harvest maturity of whole-crop annual forages is more variable concerning fiber content. Rosser et al. reported a reduction in NDF content by advancing the maturity of barley and oat forage from head elongation to fully ripe, with a reduction in NDF content from 13.8 to 9.6% [86, 87]. By contrast,

the NDF concentration of whole-crop barley was not changed during the milk and soft dough stages, but it increased somewhat between the soft and hard dough stages while this change was not observed in whole-crop oat forage [88]. Bolsen and Berger reported a reduction in total-tract DM digestibility of barley silage at milk stage, compared to advanced, mature stage due to the increasing grain content [89]. By contrast, Rustas et al. found no changes in DM or NDF digestibilities for wheat forage ensiled at milk and dough stages. However, the response regarding NDF digestibility varied for barley forage that was ensiled at milk and dough stages depending on location [89].

With advancing the maturity of grasses silage, their digestibility dramatically drops because the tensile strength of stems increases to support the weight of the plant, besides the leaf-tostem ratio declines [15, 18]. In grass silage, organic matter digestibility dropped from 79% in early growth to 73% in late growth, and NDFD decreased from 73% in early growth to 66% when the plant maturity reached late growth stage. In legumes, NDFD is less than the grasses or small grains during the early vegetative stage of growth but drops slower with advancing maturity.

In corn silage, the stage of maturity has an impact on fiber fraction. The fibrous content has been observed to decline with increasing maturity in whole-corn plants, but no significant change in lignin concentration from early dent to black layer [90]. Coors et al. suggested the observed drop in fiber concentration with increasing maturity to the dilution effect with increasing percentage of grain as the corn plant matures [91]. Fiber concentration of corn stover increases as maturity increases [92, 93].

Increasing the height of cutting, which results in leaving a larger proportion of less digestible stalk in the field, may increase the feeding value of silage for lactating dairy cows. It has been reported that corn silage digestibility was enhanced at cutting heights of 45-50 cm. but this at the expense of DM yield [94, 95]. Kruczyńska et al. reported a reduction in hemicellulose, cellulose, and lignin and greater effective degradability of silage that was cut at 50 versus 10 cm [96]. Neylon and Kung examined the effects of corn plant-cutting height and maturity on silage nutrient value. Plants were cut at 12.7 and 45.7 cm as well as harvested between onethird and two-third milk line and then again at black layer [97, 98]. As anticipated, NDF tended to be less in silages that were cut higher, and ADF content decreased significantly. At later maturity, the lignin contents were not influenced by increasing cutting height. The cutting height only influenced in vitro NDF digestibility, with the higher cut being more digestible. By increasing the cutting height of corn silage, the nutritive value was increased by decreasing NDF, ADF, and acid detergent lignin concentration and increasing the starch concentration. They also found that as corn plants were cut higher, there was a tendency for increased milk production and increased feed efficiency in dairy cows. Kung et al. also observed a decrease in fiber fraction concentrations, as well as an increase in starch, and crude protein concentrations as cutting height, was increased [97, 98]. These observations are all logical, because when cutting height is increased, more lignified and less digestible stems are left in the field while increasing the concentration of more digestible leaves and kernels.

It is well established that the nitrogen fertilization can increase the protein content and forage yield and decrease the fiber content. Campos et al. reported a reduction in hemicellulose

content and arabinose proportion of the fiber fraction in Milenio grass by N fertilization. They also found that the fertilization increased fiber digestibility due to increase in (arabinose + glucose):xylose ratio [99].

Environmental temperature has a significant impact on forage digestibility. The forages grown under higher environmental temperature had the higher amount of lignin [100]. Altering the time of seeding can shift the stage of maturity when plants are exposed to greater ambient temperature, moisture availability, and photoperiod intensity. Chow et al. found that the exposure of forages to a lower environmental temperature during heading stage increased IVNDFD [101].

5.4. Silage inoculants

Silage inoculants can be added to the freshly harvested forages to obtain good-quality silage. The first studies on adding inoculants for improving the quality of silage used the inoculants that contain homolactic bacteria (LAB) such as Lactobacillus plantarum, which quicken the drop in silage pH. Nevertheless, this rapid drop in pH inhibits the growth of yeasts, spoilage bacteria, and fungi, as well as plant cell breathing, maintaining the sugars in the silage without decomposition [102]. If this happens, the yeast consumes the lactic acid for its growth causing an augment in silage pH. At this stage, each of yeast and mold can quickly take advantage of sugars for their growth, and reduce the density of nutrients in silage. Due to the occurrence of losses in silage-nutrient density, the studies on developing the inoculant production came up with the second-generation silage inoculants that were generated from Propionibacteria spp. and L. buchneri [102, 103]. Overall, studies have shown that buchneri L. inoculants are more effective in improving aerobic stability of silage than Propionibacteria inoculant. Lactobacillus buchneri is one of heterolactic bacteria, which is able to ferment lactic acid to acetic acid; the acetic acid in turn has an inhibitory effect on the growth of yeast and subsequently prolong the silage shelf life and reduce deterioration of silage nutrients [104]. It was proposed that L. buchneri inoculation would reduce feed intake in ruminant livestock as a result of acetic acid production. However, no effect of inoculant on feed intake has been reported when L. buchneri-treated silage has been fed [105–109].

The first and second generation of inoculants focused only on improving the silage stability without addressing improving the nutrient availability by animals. The main reason for the limited effect in the first and second generation was the inoculants did not produce enzymes that digest the plant cell walls. Thus, the third-generation silage was introduced more recently, through feeding silage inoculated with lactic acid bacteria with ferulic acid esterases activity. Previous studies by Yu et al. have shown that *Aspergillus* ferulic acid esterase and *Trichoderma xylanase* act synergistically to release ferulic acid from feruloyl-polysaccharides in complex plant cell walls [110, 111]. This activity opens the rest of the polysaccharides for more hydrolytic attack and facilitates the accessibility of the main polysaccharide chain to cellulase, thereby increasing the release of reducing sugars [110, 111]. Nsereko et al. performed a screening study on 1000 esterase-producing *Lactobacillus* bacteria and found that half of this number could be able to produce ferulic acid esterase, and run more detailed studies on eight of the bacteria. When compared to untreated perennial ryegrass, all inoculated samples had 9–11% greater

NDFD. Moreover, they found that the inoculation of four corn silage hybrids with a combination of *L. buchneri* and *L. paracasei tolerans* enhanced NDFD by 7% [112, 113]. Several studies have confirmed that esterase enzymes can complement the effects of cellulose and hemicellulase enzymes on plant cell walls, thereby increasing DM or fiber digestibility [114]. Conversely, some studies have reported no effect from adding ferulic acid esterase-producing inoculant on fiber digestibility of silage [115]. Kang et al. reported an enhancement in fiber digestibility when corn hybrids were treated by a third-generation inoculant [116]. The author suggested these effects to the properties of the forage to which they are applied. Other studies have reported improvements in digestibility and steers performance fed barley silage treated with a third-generation inoculant (**Table 2**) [117, 118].

5.5. Using enzymes to enhance fiber utilization

There is increasing interest in using exogenous enzymes as a cost-effective method for improving animal productivity. The main enzyme products marketed for livestock are derived mainly from only four bacterial (*Bacillus subtilis*, *L. acidophilus*, *L. plantarum*, and *Streptococcus faecium*) and three fungal (*A. oryzae*, *T. reesei*, and *Saccharomyces cerevisiae*) species. Other fungal species, including *Humicola insolens* and *Thermomyces lanuginosus*, are being marketed to a lesser extent [119]. Several studies have confirmed that the addition of enzymes to feeds can increase DMI and fiber digestibility [120].

	Uninoculated	Inoculated	P-value				
First generation							
DMI (kg/day)	7.13	7.05	0.40				
Average daily gain (kg)	1.43	1.41	0.70				
Gain: feed DM ratio	0.20	0.20	0.65				
Third generation							
DMI (kg/day)	7.6	7.1	0.02				
Average daily gain (kg)	1.29	1.31	065				
Gain: feed DM ratio	0.17	0.19	0.02				

Table 5. Effects of silage inoculants on feedlot steers performance fed whole-crop barley silage diets inoculated or uninoculated using first and third generation.

Exogenous feed enzymes with fibrolytic activities have been reported to enhance fiber digestion in the rumen [121, 122]. Most of the commercial products that have been investigated in dairy cows have had cellulases and xylanases activates, with proteases and amylases being tested in a minor number of studies. **Table 5** showed some studies that have been performed in dairy cows fed TMR supplemented with enzymes that were characterized by cellulase and/ or xylanase activities. It appeared that the preparations of the current enzyme do not introduce novel enzyme activity into the rumen as they finally increase only the rate and not the extent of digestion of the cell wall [123, 124]. Beauchemin et al. reported that DMI would increase by

 1.0 ± 1.3 kg/d and milk yield by 1.1 ± 1.5 kg/d with the addition of fibrolytic exogenous enzymes to dairy cow diets [125]. It is evident from the dispersion of data from the mean of the responses to the addition of enzymes fibrolytic to ruminant diets were fluctuating. Therefore, it not surprising that the use of enzyme fibrolytic products in the dairy commercial operations is not built broadly.

It is well established that the application of the exogenous enzymes before feeding is more effective when it is applied as a liquid form than as a powder. Meanwhile, spraying enzymes on the wet feed such as silage seems to be more effective than on dry feed such as hay and grain, where the wet feed is easier for enzymes to decompose the complex carbohydrates from polymers. This hydrolysis may enhance and simplify the microbial attachment, and hence reduce the lag time required for microbial colonization [126].

In high-producing dairy cattle, the stage of lactation has an important effect on the efficiency of enzyme additives. For instance, Schingoethe et al. found that the cows in early lactation responded to enzyme supplementation, but they did not detect any effect for enzymes on the cows in mid-lactation [127]. Differences in the response of early- and mid-lactation cows to enzyme supplementation were also reported in other studies [128, 129].

Enzymes that bind to feed seem to be more active, perhaps due to better resistance to proteolytic inhibition in the rumen. In general, the rumen ecosystem was found to have a minor effect on exogenous enzymes as a result of glycosylation [130]. It has also been found that nonglycosylated enzymes could sustain in the rumen and resist the proteolytic activity by ruminal microbiota, but this will be dependent on microbial sources of enzymes [131].

Due to the occurrence of internal fibrolytic enzymes yielded from the rumen bacteria, it is not easy in many cases to define the potential of exogenous enzymes to directly digest carbohydrates alone [132]. There is a synergy between the internal ruminal fibrolytic enzymes and the exogenous enzymes, where exogenous enzymes can enhance the microbial attachment to the forage fiber, here then improving fiber digestibility [133], but the mechanism by which this occurs is not known. It has been found that increasing amount of exogenous enzymes may suppress the ruminal bacteria that digest the fiber, fiber, for example, White et al. [134]. found the lower amount of exogenous enzymes enhanced the rumen bacteria attachment to fiber, in contrast, increase a number of enzymes decrease the microbial activity where exogenous enzymes have competed with ruminal bacteria enzymes for cellulose hydrogen binding sites on forage fiber. Thus, it is recommended to complement the rumen bacterial enzymes with the exogenous enzymes.

6. Conclusion

Silage contains a high content of neutral detergent fiber. Even under optimum conditions, NDF digestibility in the rumen is frequently less than 50%. Improving ruminal fiber degradability could allow cattle to consume more feed and hence increase milk yield. Selecting forage with higher NDFD could be a practical approach to increasing digestible carbohydrate and feed

intake in dairy cattle. Ferulic acid-producing bacteria that are targeted at breaking the bonds between ferulic acid and hemicellulose could be the key to increasing fiber digestibility in ruminants. Addition of enzymes to feeds would increase NDFD. However, responses to feed enzymes are expected to be greatest in situations where digestible energy is the first limiting nutrient in the diet.

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