RUMINANT NUTRITION

Modification of the summative equation to estimate daily total digestible nutrients for bermudagrass pasture

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Abstract

In forage-animal nutrition modeling, diet energy is estimated mainly from the forage total digestible nutrients (TDN). As digestibility trials are expensive, TDN is usually estimated using summative equations. Early summative equations assumed a fixed coefficient to compute digestible fiber using the lignin-to-neutral detergent fiber (NDF) ratio. Subsequently, a structural coefficient (φ) was added to the summative equations to reflect an association between lignin and cell wall components. Additional modifications to the summative equations assumed a constant φ value, and they have been used as a standard method by many commercial laboratories and scientists. For feeds with nutritive values that do not change much over time, a constant φ value may suffice. However, for forages with nutritive values that keep changing during the grazing season owing to changes in weather and plant maturity, a constant φ value may add a systematic bias to prediction because it is associated with the variable lignin-to-NDF ratio. In this study, we developed a model to estimate φ as a function of the day of the year by using the daily TDN values of bermudagrass [*Cynodon dactylon* (L.) Pers.], a popular warm-season perennial grass in the southern United States. The variable φ model was evaluated by using it in the TDN equation and comparing the estimated values with the observed ones obtained from several locations. Values of the various measures of fit used—the Willmott index (WI), the modeling efficiency (ME), R^2 , root mean square error (RMSE), and percent error (PE)—showed that using the variable φ vis-à-vis the constant φ improved the TDN equation significantly. The WI, ME, R^2 , RMSE, and PE values of 0.94, 0.80, 0.80, 2.5, and 4.7, respectively, indicated that the TDN equation with the variable φ model was able to mimic the observed values of TDN satisfactorily. Unlike the constant φ , the variable φ predicted more closely the forage nutritive value throughout the grazing season. The variable φ model may be useful to forage-beef modeling in accurately reflecting the impacts of plant maturity and weather on daily forage nutritive value and animal performance.

Key words: bermudagrass, forage, summative equation, total digestible nutrients

Abbreviations

DE	digestible energy
DOY	day of the year
EE	ether extract
^m dEE	modified digestible ether extract
ME	modeling efficiency
^m TDN	modified TDN
NDF _u	NDF unavailable
^o dEE	original digestible ether extract
^o TDN	original TDN
PAF	processing adjustment factor
PE	percent error
RMSE	root mean square error
WI	Willmott index

Introduction

Bermudagrass [*Cynodon dactylon* (L.) Pers.] is a persistent, warm-season perennial grass in the southern United States and provides the basis for most of the animal production systems during mid-spring through mid-fall (Taliaferro et al., 2004; Butler and Muir, 2006; Anderson et al., 2016; Rouquette et al., 2020). Of the various cultivars of bermudagrass grown in this region, “Coastal” has played a significant role in livestock production since 1943 (Burton, 1948). As Coastal bermudagrass is mostly defoliation and drought tolerant, remarkably long-lived, widely adapted, promptly input responsive, and highly productive, it has been the most sustainable bermudagrass across this region (Taliaferro et al., 2004).

Forage growth and development are controlled by various environmental and management factors (Minson, 1990). Meteorological conditions can influence the grazing season and impact the quality and quantity of forages produced. To effectively study the effects of these factors on the productivity and sustainability of an agricultural enterprise, simulation modeling is essential (Tsuji et al., 1998; Wallach et al., 2019). The impacts of environment and management on forage mass, animal performance, and income can be studied adequately by using forage-beef models.

Forage nutritive value is one of the significant factors influencing animal performance. In forage-animal nutrition modeling, the animal's diet energy is estimated mainly from the total digestible nutrients (TDN) of the forage used because its digestibility is essentially a function of its energy content (Tedeschi and Fox, 2020). The TDN is directly related to digestible energy (DE) and is useful for characterizing animal feeds and forages. The TDN is the first limiting factor in accurately predicting the useful energy in a feedstuff because it is used to predict DE, which, in turn, is used to predict modeling efficiency (ME), from which net energy may be predicted (Tedeschi and Fox, 2020). The TDN is estimated from the crude protein (CP), ether extract (EE), and carbohydrate (crude fiber and N-free extract) values of feed and feces obtained in digestibility trials (Schneider and Flatt, 1975). Since forage digestibility trials are expensive and laborious, TDN has been mainly estimated using summative equations that include neutral detergent fiber (NDF), CP, EE, lignin, and ash. Then, each organic matter component is multiplied by its theoretical digestibility coefficient.

Based on the ideas outlined by Van Soest et al. (1966), Goering and Van Soest (1970), and Osbourn (1978), Conrad et al. (1984) developed a summative model that estimated TDN using the concentrations of CP, NDF, lignin, and fat. Pointing out that the Conrad et al. (1984) model was based on true digestibility

coefficients, rather than apparent digestibility coefficients, Girard and Dupuis (1988) modified the Conrad et al. (1984) equation by subtracting the fraction of metabolic fecal losses from the true digestibility. Weiss et al. (1992) further improved and expanded the summative equation to make it more theoretically sound and accurate for most of the feedstuffs. They provided more accurate apparent TDN and energy values for feeds that underwent heat damage by discounting TDN for metabolic fecal matter; thus, they suggested a metabolic fecal loss of 7%. The summative TDN equation, as presented by Weiss et al. (1992), is hereafter referred to as the original TDN (^oTDN) equation. The ^oTDN equation has been used by many commercial laboratories and scientists to estimate TDN for a feedstuff. However, the ^oTDN equation has undergone several improvements over time, as discussed subsequently.

The lignin-to-NDF ratio in the cell wall has been used as a measure of fiber digestibility since the total cell wall components of a feedstuff are represented by NDF, and the digestibility of the cell wall components is influenced by lignin (Phillips et al., 1954; Sullivan, 1959; Van Saun and Herdt, 2014). Hypothesizing that the digestibility of fiber could be affected primarily by the encrustation of the cell wall by lignin, thus preventing surface-affixing bacteria from digesting underlying cell walls, Conrad et al. (1984) propounded that the fraction of NDF unavailable (NDF_u) to microbes would be directly proportional to the surface area of lignin (LIG_{SA}) and inversely proportional to the surface area of NDF (NDF_{SA}): $\text{NDF}_u \propto \text{LIG}_{SA} / \text{NDF}_{SA}$. The lignin and NDF in this relationship are required to be quantified in surface areas, whereas they are commonly measured in volumes. Thus, the lignin and NDF volumes needed to be converted into surface areas, where the surface area of a geometric object is equal to the two-thirds power of its volume. These conversions led to the expression of $(\text{Lignin}/\text{NDF})^{2/3}$ for the portion of NDF_u and $[1 - (\text{Lignin}/\text{NDF})^{2/3}]$ for available NDF, with both lignin and NDF expressed in volume. For conditions when volumes are not known, and thus weights must be used, Girard and Dupuis (1988) introduced a factor, called the structural coefficient (φ), to the NDF_u relationship: $\text{NDF}_u = \varphi (\text{Lignin}/\text{NDF})^{2/3}$. With the connection of φ with mass, therefore, φ reflects the nature of the association between lignin and cell wall components as a structural coefficient (Girard and Dupuis, 1988). Apparently, Weiss et al. (1992) assumed unity for φ by not including an explicit coefficient in that ^oTDN equation.

The TDN equations, which have been developed using the feed composition data mostly from the temperate regions, are less applicable to feedstuffs from the tropical regions because of environmental factors such as temperatures (Tedeschi and Fox, 2020). As high temperatures decrease plant digestibility (Van Soest, 1994), the summative equations developed by Weiss et al. (1992) and modified by NRC (2001) using temperate feedstuffs have exhibited the underprediction of TDN for warm-season perennial grasses (Tedeschi et al., 2002; Magalhaes et al., 2009; Azevedo et al., 2011). This underprediction issue could be addressed when using the φ coefficient (Tedeschi and Fox, 2020). Tedeschi et al. (2005) indicated that because of the lack of fresh forages in the database of Conrad et al. (1984), which was used to develop the theoretical equation proposed by Weiss et al. (1992), the ^oTDN equation might underpredict TDN for fresh forages. Tedeschi et al. (2005) suggested that the underprediction could also be due to using a fixed coefficient of 0.75 for NDF digestibility for fresh forages. They theorized that this underprediction could also be ameliorated by using the φ coefficient.

The studies cited above demonstrate that φ is associated with lignin, NDF, and fiber digestibility. Researchers have

established that lignin reduces cell wall digestibility by thickening cell walls and increasing fiber concentrations (Phillips et al., 1954; Sullivan, 1959; Van Soest, 1982; Henderson and Robinson, 1982a, 1982b; Jung and Deetz, 1993; Coleman et al., 2004). Lignin synthesis in plant tissues is preferentially increased with an increase in temperature (Henderson and Robinson, 1982a, 1982b; Van Soest, 1982; Da Silva et al., 1987; Jung and Deetz, 1993; Nelson and Moser, 1994; Coleman et al., 2004). Elevated temperatures have also been associated with increased NDF concentration (Deinum, 1966; Henderson and Robinson, 1982a; Van Soest, 1982; Da Silva et al., 1987), rapid metabolic activity (Van Soest, 1994), and reduced digestibility of warm-season perennial grasses (Deinum, 1976; Wilson and Minson, 1980; Henderson and Robinson, 1982a; Pitman and Holt, 1982; Holt and Conrad, 1986). Studies have shown that lignin (Hart et al., 1976; Woli et al., 2020) and NDF (Beaty et al., 1966; Jolliff et al., 1979; Roth et al., 1990; Marsalis, 2004; Rouquette et al., 2018; Woli et al., 2020) concentrations of bermudagrass are quadratically associated with the day of the year (DOY) during the grazing season. Both lignin and NDF concentrations increased from early spring, reached a peak around late summer, and decreased slightly thereafter until mid-fall. These trends followed the temperature trend during the grazing period, showing the impact of temperature on lignin and NDF concentrations.

Girard and Dupuis (1988) reported that warm-season grasses tended to have a greater φ value (1.8) compared with cool-season grasses (0.9 to 1.3). The greater φ value of warm-season grasses was likely because: 1) they reach flowering maturity more quickly and result in a greater proportion of stem and 2) their tissue digestion is slower because of more tightly packed radial tissue arrangement, a longer hydration or adherence time, and a greater concentration of phenolic compounds, restricting the attachment and colonization of ruminal bacteria (Galyean and Goetsch, 1993). For cool-season grasses, they also noticed that the φ value tended to increase with advancing maturity. As these results were based on limited data, they suggested that further investigations be carried out on φ before its potential use. Based on the findings discussed above that φ could be impacted by temperature and plant maturity or age and the lignin and NDF concentrations could vary daily during the grazing season, we hypothesized that the φ values must be changing daily during the grazing season.

Based on the work of Palmquist (1990), Weiss et al. (1992) subtracted one from EE (% dry matter [DM]) to estimate digestible EE for nonfat feedstuffs, hereafter referred to as the original digestible EE ($^{\circ}\text{dEE}$). However, based on the finding of Palmquist (1991) that the true digestibility of fatty acids declined linearly from 100% to 78% with diets containing the EE of 1 and 8 (% DM), respectively, Tedeschi and Fox (2020) argued that the true digestibility of fatty acids could be computed as $100 - 3.14 \times (\text{EE} - 1)$. Accordingly, they modified the method for estimating digestible EE for nonfat feedstuffs, hereafter referred to as the modified digestible EE ($^{\text{M}}\text{dEE}$).

Furthermore, NRC (2001) added the processing adjustment factor (PAF) to the summative equation to account for the effects of feed particle size, heat, and steam on the digestibility of non-fiber carbohydrates. Although necessary for cereal grains, the PAF is irrelevant for forage grasses. Moreover, Tedeschi et al. (2009), Aguiar et al. (2011), and Tedeschi and Fox (2020) proposed more mechanistic summative equations by incorporating ruminal fractional rates of degradation and passage to compute NDF digestibility. However, using these parameters in the summative equation for forages is not possible at this time due to the lack of data. Similarly, forages lack triglycerides; thus, they do not need the lipid digestibility adjustment proposed by Tedeschi and Fox (2020) in the summative equation. Therefore, the updated TDN equation that is relevant to forage-based feedstuffs—with φ and $^{\text{M}}\text{dEE}$ included in the $^{\circ}\text{TDN}$ —is hereafter referred to as the modified TDN ($^{\text{M}}\text{TDN}$) equation.

The objectives of this study were to 1) compare the $^{\circ}\text{TDN}$ and $^{\text{M}}\text{TDN}$ equations, 2) assess the sensitivity of $^{\text{M}}\text{TDN}$ to the constant φ , and 3) develop a model for estimating φ daily (the variable φ) during the grazing season of bermudagrass.

Materials and Methods

Site and data

Data on the average daily gain (ADG) of one-fourth Brahman-three-fourth British-Continental crossbreds grazed on Coastal bermudagrass were obtained mainly from Texas A&M AgriLife Research at Overton, TX (32°29'N, 94°97'W), where numerous grazing experiments have been conducted by various scientists since 1969 (Duble et al., 1971). All protocols and procedures for these grazing studies were approved by the Agriculture Animal Care and Use Committee of Texas A&M AgriLife from the time of initiation of protocols to current (AUP 2017-022A and AUP SOP 2019-015A). Additional ADG data were obtained from the LSU AgCenter Iberia Research Station at Jeanerette, LA (29°58'N, 91°43'W), and from the literature (Utley et al., 1974, 1978, 1981; Greene et al., 1990). The ADG data from each of these sources included several grazing seasons, replications, and weighing periods during the season for each grazing trial, thus resulting in a large number of ADG observations. For simplicity, the ADG values from each location were averaged by the DOY across all seasons, replications, and weighing periods and used in our analyses (Table 1). For instance, Overton, TX, had a total of 746 ADG values belonging to 12 seasons (trials) and several replications and weighing periods in each of these trials. These ADG values were associated with 36 different dates (DOY). By averaging the data by the DOY, thus, we obtained 36 ADG values for this location.

Comparing the $^{\circ}\text{TDN}$ and $^{\text{M}}\text{TDN}$ equations

For a forage-based diet, $^{\text{M}}\text{TDN}$ differs from $^{\circ}\text{TDN}$ concerning the digestible EE function and the coefficient φ . Thus, $^{\circ}\text{TDN}$, which comprises $^{\circ}\text{dEE}$ (equation 1) and unity for φ , was compared with

Table 1. Various sources of the ADG data for 25% Brahman stockers

Source	Location	Seasons	Years	TO ¹	DO
Scaglia, LSU Ag Center	Jeanerette, LA	3	2010 to 2012	144	5
Green et al. (1990)	Homer, LA	4	1982 to 1985	1155	11
Utley et al. (1974, 1978, 1981)	Tifton, GA	8	1968 to 1979	740	17
Rouquette, Texas A&M AgriLife	Overton, TX	12	1976 to 2002	746	36

¹TO, the total number of observed ADG values; DO, the number of observations averaged by the DOY and used for the study.

three versions of $^{\circ}\text{TDN}$: 1) with only φ added to $^{\circ}\text{TDN}$, using 1.8 for φ as suggested by Girard and Dupuis (1988) for warm-season grasses; 2) with only $^{\text{M}}\text{dEE}$ (equation 2) replaced for $^{\circ}\text{dEE}$ in $^{\circ}\text{TDN}$; and 3) with both $^{\text{M}}\text{dEE}$ and φ (1.8) included:

$$^{\circ}\text{dEE} = (\text{EE} - 1) \quad (1)$$

$$^{\text{M}}\text{dEE} = (\text{EE} - 1) [1 - 0.0314 (\text{EE} - 1)], \text{ if } \text{EE} > 1 \quad (2a)$$

$$^{\text{M}}\text{dEE} = (\text{EE} - 1), \text{ if } \text{EE} \leq 1 \quad (2b)$$

For comparative purposes, the daily values of $^{\circ}\text{TDN}$ and $^{\text{M}}\text{TDN}$ were estimated for Coastal bermudagrass forage during the grazing season of mid-spring through mid-fall ($100 \leq \text{DOY} \leq 300$) using the daily values of CP, NDF, lignin, and ash estimated by the nutritive value models (equations 3–6) of Woli et al. (2020) and an average value of 2.4% DM for EE (Burton, 1954; Utley et al., 1978) as inputs to both $^{\circ}\text{TDN}$ (equation 7) and $^{\text{M}}\text{TDN}$ (equation 8). For EE, no daily values were available:

$$\text{CP}_i = 0.0004i^2 - 0.2095i + 39.5 \quad (3)$$

$$\text{NDF}_i = -0.00095i^2 + 0.4713i + 13.9 \quad (4)$$

$$\text{Lignin}_i = -0.00011i^2 + 0.0564i - 2.2 \quad (5)$$

$$\text{Ash}_i = -0.007i + 5.9 \quad (6)$$

$$^{\circ}\text{TDN}_i = \left[\begin{array}{l} 0.98 (100 - \text{NDFN}_i - \text{CP}_i - \text{Ash}_i - \text{EE} + \text{IADICP}) + \\ K_{\text{dep}} \text{CP}_i + \\ 2.25 ^{\circ}\text{dEE} + \\ 0.75 (\text{NDFN}_i - \text{Lignin}_i) \left(1 - \left\{ \frac{\text{Lignin}_i}{\text{NDFN}_i} \right\}^{\frac{2}{3}} \right) \end{array} \right] - 7 \quad (7)$$

$$^{\text{M}}\text{TDN}_i = \left[\begin{array}{l} 0.98 (100 - \text{NDFN}_i - \text{CP}_i - \text{Ash}_i - \text{EE} + \text{IADICP}) + \\ K_{\text{dep}} \text{CP}_i + \\ 2.25 ^{\text{M}}\text{dEE} + \\ 0.75 (\text{NDFN}_i - \text{Lignin}_i) \left(1 - \varphi \left\{ \frac{\text{Lignin}_i}{\text{NDFN}_i} \right\}^{\frac{2}{3}} \right) \end{array} \right] - 7 \quad (8)$$

where $^{\circ}\text{TDN}$ and $^{\text{M}}\text{TDN}$ are apparent TDN for forage-based diets estimated as the original and modified versions of the TDN equation, respectively; EE is ether extract; NDFN (nitrogen-adjusted NDF) = $\text{NDF} - \text{NDICP} + \text{IADICP}$; NDICP (neutral detergent insoluble CP) = $-8.77 + 0.33 \text{ CP} + 0.143 \text{ NDF}$; ADICP (acid detergent insoluble CP) = 0.085 CP ; IADICP (indigestible ADICP) = 0.7 ADICP ; K_{dep} (the true digestibility of CP) = $e^{(-1.2 \text{ ADICP}/\text{CP})}$; $^{\circ}\text{dEE}$ and $^{\text{M}}\text{dEE}$ are the original and modified versions of digestible EE, respectively; e is the Napier constant; φ is the structural coefficient; and i is the i th DOY ($100 \leq i \leq 300$). All the nutritive value variables are expressed in % DM.

The CP, NDF, lignin, and ash models of Woli et al. (2020) were developed by regressing the periodic time-series data on Coastal bermudagrass nutritive value against the DOY. Forage samples for nutritive value, which were collected at Overton, TX, were taken at 2-wk intervals during the growth period of April 1 through November 15. The number of years and the

number of dates (DOY) for which the nutritive value data were available were, respectively, 25 and 1,146 for NDF, 23 and 908 for CP, 2 and 105 for ash, and 5 and 59 for lignin. The forage samples were analyzed sequentially for NDF, acid detergent fiber (ADF), acid detergent lignin (ADL), and ash concentrations using the detergent technique outlined by Goering and Van Soest (1970). The NDF and ADF were determined using a 6-unit refluxing Labconco Digestion and Distillation Apparatus (Labconco Corporation., Kansas City, MO) with fritted glass crucibles for filtering for the years 1969 through 1999 and the ANKOM A200 Fiber Analyzer (ANKOM Technology, Macedon, NY) for the years 2000 and beyond. Lignin was determined as ADL by digesting the forage sample with 72% sulfuric acid and then ashing the sample to determine percent ash and lignin by a difference in sample weight.

Assessing the φ sensitivity

Several values of φ were used in TDN computations to explore the response of $^{\text{M}}\text{TDN}$ to φ . The φ values obtained by Girard and Dupuis (1988) ranged from 0.05 to 1.85. For our study, we expanded this range slightly in both directions based on the range of bermudagrass TDN, which generally exceeds 75 in early spring and decreases to 50 or less in late summer. The TDN values of 75 and 50 correspond to the φ values of about -0.6 and 2.2, respectively. Thus, we computed $^{\text{M}}\text{TDN}$ with several values of φ between -0.6 and 2.2.

Evaluating the TDN equations

To evaluate the performance of the TDN model with the variable φ and various values of the constant φ , data on the observed values of TDN were needed. However, no such data were available. The use of TDN values obtained from commercial laboratories for the model evaluation would provide biased results as they are the estimated ones using the $^{\circ}\text{TDN}$ equation or its derivatives. In the absence of other reliable measures to obtain the TDN data, we used a reverse calculation approach. Because the intake of TDN from a feedstuff is directly related with animal performance, we back-converted the measured ADG data (Figure 2a) into probable TDN values (Figure 2b) using a relationship (equation 9; Figure 1) derived from the NRC (1996) data:

Figure 1. The relationship between TDN from a feedstuff and the ADG of a stocker. Adapted from NRC (1996).

$$\text{TDN} = 11.78\text{ADG}^2 + 3.96\text{ADG} + 48.2 \quad (9)$$

where $0 \leq \text{ADG} \leq 1.7$ kg. These ADG-converted TDN values, hereafter, are referred to as the observed values of TDN.

We investigated different statistics to evaluate the performance of the TDN equation because many attributes are involved in assessing the adequacy of model predictability (Tedeschi, 2006). The measures used were the Willmott index (WI) of agreement (Willmott, 1981), ME (Nash and Sutcliffe, 1970), root mean square error (RMSE), percent error (PE), and R^2 . The WI measures the degree to which the observed values are approached by the predicted values. Its values range from zero to one, with zero indicating no agreement between the observed and predicted values and one indicating the perfect agreement. The ME assesses the predictive power of models. Its values range from $-\infty$ to 1, with a greater value meaning the model as a better predictor and one indicating the perfect match between the modeled and observed values. The R^2 describes the proportion of variability in the observed data that can be accounted for by the model. Its values range from zero to one, with zero meaning no agreement between the observed and predicted values and one meaning perfect agreement. The RMSE assesses the error associated with the prediction: the greater the prediction error, the larger the RMSE. The PE, computed as $(\text{RMSE}/\text{mean measured value}) \times 100$, shows the model prediction error relative to the mean of the observed data.

Developing the variable φ model

Results from the φ sensitivity assessment led us to develop the variable φ model to estimate φ on a daily basis. To develop the φ model, an ^mTDN curve for a given φ value was created by computing the daily values of TDN during the bermudagrass grazing season (DOY: 100 to 300) using the φ value in the ^mTDN model. Accordingly, 18 ^mTDN curves were created for different 18 φ values selected from its range of -0.6 to 2.2 . After that, the trendline for the observed values of TDN (Figure 2b) was created and superimposed on the ^mTDN curves. Then, the DOY associated with the intersection between the trendline and the ^mTDN curve of a given φ value was noted. Accordingly, the 18 DOY values associated with the 18 intersections that the trendline made with the 18 ^mTDN curves were collected. Finally,

by regressing the 18 DOY values against the associated 18 φ values, the variable φ model to estimate φ as a function of DOY was developed.

Results and Discussion

The ^oTDN and ^mTDN equations

The ^mTDN equations with φ of 1.8 and with both φ of 1.8 and ^mdEE were significantly different from the ^oTDN equation (Figure 3). These differences were mainly due to the larger value of φ (1.8 vs. 1.0 assumed by ^oTDN). With the increase in φ from 1.0 to 1.8, the digestibility of cell walls plummeted sharply, thus significantly decreasing the TDN concentration. However, the difference between ^oTDN and ^mTDN with just ^odEE replaced by ^mdEE (with no φ coefficient incorporated in the TDN equation) was not significant. This was likely because the EE concentration of the bermudagrass forage was very low (2.4% DM). Accordingly, the ^odEE and ^mdEE values (% DM) of this grass were 1.40 and 1.34, respectively. Thus, the difference in the contributions of these digestible EE values to the TDN value was not significant, as we expected.

Comparisons of ^oTDN and ^mTDN values with and without ^mdEE and φ with the observed (i.e., ADG-converted) values of TDN showed that the performances of the ^mTDN models with the φ value of 1.8 were better than that of the ^oTDN model, which assumes a constant φ value of 1.0 (Table 2). The WI for ^mTDN (0.73) was greater than that for ^oTDN (0.57), indicating that the ^mTDN values were in better agreement with the observed data. Similarly, the ME value for ^mTDN (0.52) was greater than that for ^oTDN (-0.79), indicating that the predictive power of ^mTDN was higher. Moreover, the greater R^2 , RMSE, and PE values for ^mTDN suggested that the performance of ^mTDN was better than that of ^oTDN (Table 2). The performance of ^mTDN , however, was not better than that of ^oTDN when ^odEE , the digestible EE associated with ^oTDN (equation 1), was replaced by ^mdEE , the digestible EE associated with ^mTDN (equation 2), which was likely because the difference between the ^odEE and ^mdEE values was not significant. The performance of ^mTDN with φ of 1.8 was not satisfactory, although it performed better than ^oTDN . The WI of 0.73 showed that the agreement between observed and estimated values was poor. The ME value of 0.52 suggested that the ^mTDN model with φ of 1.8 was not a good predictor.

Figure 2. The ADG (kg) data obtained from various sources in the southern United States (a) and the corresponding values of TDN (% DM) converted from ADG using the relationship $\text{TDN} = 11.78\text{ADG}^2 + 3.96\text{ADG} + 48.2$ (b).

Figure 3. The observed (dots) and estimated (lines) values of TDN for Coastal bermudagrass forage in the southern United States during the grazing season of April through October. Notes: $^{\circ}$ TDN, original TDN equation; $^{\circ}$ TDN, modified TDN equation; $^{\circ}$ dEE, original digestible ether extract; and $^{\circ}$ dEE, modified digestible ether extract. The $^{\circ}$ TDN ($^{\circ}$ dEE + ϕ 1.0) line denotes the $^{\circ}$ TDN equation with $^{\circ}$ dEE and the ϕ value of 1.0, and so forth.

Table 2. Values of various measures used in evaluating the TDN equation with several ϕ values

ϕ value ¹	Measures of fit				
	WI ²	ME	R ²	RMSE	PE
-0.6	0.30	-10.56	0.70	19.4	35.4
-0.4	0.32	-8.80	0.72	17.8	32.6
0.0	0.37	-5.73	0.75	14.8	27.0
0.4	0.44	-3.28	0.76	11.8	21.5
0.8	0.52	-1.43	0.77	8.9	16.2
$^{\circ}$ 1.0	0.57	-0.79	0.77	7.6	13.9
1.0	0.57	-0.74	0.77	7.5	13.7
1.2	0.62	-0.20	0.78	6.2	11.4
1.6	0.70	0.43	0.78	4.3	7.9
$^{\circ}$ 1.8	0.73	0.52	0.78	4.0	7.2
1.8	0.73	0.52	0.78	4.0	7.2
2.0	0.73	0.45	0.78	4.2	7.7
2.2	0.69	0.23	0.78	5.0	9.1
Variable	0.94	0.80	0.80	2.5	4.7

¹The ϕ values preceded by $^{\circ}$ are associated with the original TDN equation and those without any letter are associated with the modified TDN equation.

²WI (Willmott, 1981); ME (Nash and Sutcliffe, 1970); and PE = RMSE/mean observed value $\times$ 100.

The ϕ sensitivity

With an increase in ϕ , where $-0.6 \leq \phi \leq 2.2$, the TDN value of Coastal bermudagrass during the grazing season of April through October ($100 \leq \text{DOY} \leq 300$) decreased linearly on a given day (DOY basis; Figure 4). This decrease was expected because, on a given DOY, digestible NDF was linearly associated with ϕ , and the difference between TDN and digestible NDF was the same for all values of ϕ . The decrease in TDN concentration with an increase in ϕ over the grazing season was curvilinear (Figure 5). That is, the decrease in TDN per unit increase in ϕ was diminishing during April through October. This curvilinear decrease was likely because, with an increase

Figure 4. The relationships of TDN and digestible NDF with the structural coefficient ϕ for Coastal bermudagrass forage grazed on July 9 (DOY = 200).

Figure 5. The observed (dots) and estimated (lines) values of TDN with various values of the structural coefficient ϕ for Coastal bermudagrass forage grazed in the southern United States from April through October. The $\phi = 1.0$ line denotes the original TDN equation.

in ϕ , digestible NDF decreased linearly on a DOY basis and curvilinearly over the grazing season. The curvilinear decrease of digestible NDF was due to the curvilinear relationships of both NDF and lignin concentrations with DOY during the grazing season (Woli et al., 2020). Several studies showed that both lignin and NDF concentrations of bermudagrass were quadratically associated with the DOY during the grazing season, with both lignin and NDF concentrations increasing from early spring, reaching the peaks around late summer, and decreasing slightly thereafter until mid-fall (Beatty et al., 1966; Hart et al., 1976; Jolliffe et al., 1979; Roth et al., 1990; Marsalis, 2004; Woli et al., 2020). These trends have followed the general temperature trend during the forage grazing period (curvilinear: rising from early spring, reaching a peak around mid-summer, and falling thereafter), showing the impact of temperature on lignin and NDF concentrations. An increase in temperature has been associated with increases in lignin and NDF concentrations (Henderson and Robinson,

1982a, 1982b; Van Soest, 1982; Da Silva et al., 1987; Jung and Deetz, 1993; Coleman et al., 2004).

Comparisons of estimated TDN values with the observed ones showed that the performance of the ^mTDN model increased at a diminishing rate with an increase in φ (Table 2). The WI had a logistic relationship with φ , where $-0.6 \leq \varphi \leq 2.2$. With φ , both R^2 and the ME were positively, curvilinearly associated, whereas both RMSE and PE were negatively, curvilinearly associated. The performance of the ^mTDN model, however, was not satisfactory for any values of the constant φ . The maximum values of the WI and the ME, which were associated with the φ of 1.8, were 0.73 and 0.52, respectively, indicating that the predictive power of the ^mTDN model with the constant φ was weak, and the predicted values did not agree reasonably well with the observed data.

The trend of the ^mTDN curves with various φ values during the bermudagrass grazing season (the red, green, and blue lines in Figure 6) compared with the seasonal trend of the observed values of TDN (the dots and the black line in Figure 6) revealed that as the grazing season progressed, the observed value of TDN represented by the trendline was equal to the TDN value estimated by the ^mTDN model with a larger φ value. That is, with an increase in the DOY, the trendline of the observed values intersected the ^mTDN curve of a larger φ value. Thus, the results indicated that φ could be computed as a function of the DOY and prompted us to develop a variable φ model for estimating φ on a daily basis.

The variable φ model

The variable φ model estimates the daily values of φ during the bermudagrass grazing season using the DOY as the predictor variable (equation 10). The association between the DOY and φ was positive, curvilinear (Figure 7):

$$\varphi_i = -0.0051i - \frac{614}{i} + 5.79 \quad (10)$$

where i stands for the i th DOY ($100 \leq i \leq 300$).

The variable φ model assumes that the φ value is about -0.6 at the beginning of the grazing season (around early April) and reaches about 2.2 at the end of the grazing season

(around mid-November; Figure 7). The φ value of -0.6 around the beginning of the season accurately reflected the good nutritive value of bermudagrass in early spring. Unlike the constant φ , the variable φ was able to reflect the forage nutritive value not just during the early part of the grazing season but also during the “summer slump,” a period around mid/late-summer during which the grazing animals in the southern United States typically exhibit a decline in the rate of gain (Sollenberger and Jones, 1989; Coleman and Forbes, 1998; Coleman et al., 2004). The likely causes for this summer slump related to low forage nutritive value are in response to forage maturity and the fluctuations of protein, fiber, and lignin concentrations during the grazing season. Several studies have shown that the CP concentration of a warm-season perennial grass is high during the spring and fall and low during the summer, whereas the lignin and fiber concentrations are low during the spring and fall and high during the summer (Woli et al., 2020). Around

Figure 7. The relationship of the structural coefficient φ with the DOY from April through October.

Figure 6. The observed (dots), trendline (black line), and estimated (colored lines) values of TDN with various values of the structural coefficient φ for Coastal bermudagrass forage grazed in the southern United States from April through October.

Figure 8. The observed values of TDN (dots) superimposed by the estimates (line) of the modified TDN equation (^mTDN) comprising modified digestible ether extract (^mdEE) and variable φ (φ_{var}) equations during the Coastal bermudagrass grazing season of April through October in the southern United States.

the summer slump, the lignin concentrations of warm-season perennial grasses are the greatest (Hart et al., 1976).

The constant φ , on the other hand, was not able to reflect the forage nutritive values during the entire grazing season. That is, the constant φ could reflect only at a specific time or period of the season. The minimum value studied for φ , -0.6, was able to reflect nutritive value only at the beginning of the season (Figure 5). With an increase in φ , the ability to reflect moved further toward the summer slump. Accordingly, 2.2, the maximum φ value studied, was able to reflect the nutritive value only during the summer slump.

Compared with the constant φ value used for the entire grazing season, the use of the variable φ , a function of the DOY, improved the performance of the ^mTDN model significantly (Table 2; Figure 8). The WI of 0.94, which was close to 1.0, indicated that agreement between the estimated and observed values of TDN was good. The ME value of 0.80 showed that the predictive power of the model was high. The R^2 value of 0.80 suggested that the variability in the observed data could be accounted for by the model fairly well. Values of the above measures, as well as the relatively low values of RMSE (2.5% DM) and the PE (4.7), indicated that the performance of the ^mTDN model with the variable φ was good.

Conclusions

The summative TDN equation has undergone several modifications over time. The inclusion of the structural coefficient φ in the equation during the mid-1980s was a landmark work, especially for the feedstuffs that are pen fed. For these diets, a constant φ value suffices because the nutritive value of the diet in feedlot conditions is consistent with few variations. Our study demonstrated that since the nutritive value of a pasture forage continues changing during the grazing season owing to changes in plant maturity and weather conditions, the φ value had to be variable. Accordingly, in this study, we developed a model to estimate φ as a function of the DOY. Evaluation results showed that the performance of the TDN model for bermudagrass using the variable φ was significantly greater than that using the currently used constant φ . The results further indicated that the TDN model with the variable φ was able to mimic the observed values of TDN well.

For estimating the TDN concentrations of a warm-season perennial grass and energy available for grazing cattle, whose growth and nutrition processes are continuous, the forage-beef modeling community may benefit from the use of the variable φ model, which estimates φ on a daily basis. With this model available, it may be easier for forage-beef scientists to clearly demonstrate the impacts of forage maturity, season, and weather conditions on forage mass, forage nutritive value, animal performance, and the environment.

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Conflicts of interest statement

We, the authors of this manuscript, do not have any actual or potential conflicts of interest that may affect our ability to objectively present or review research or data.

Literature Cited

- Aguiar, A. D., L. O. Tedeschi, F. M. Rouquette Jr, K. C. McCuiston, J. A. Ortega-Santos, R. C. Anderson, D. DeLaney, and S. Moore. 2011. Determination of nutritive value of forages in south Texas using an *in vitro* gas production technique. *Grass Forage Sci.* 66:526–540. doi:[10.1111/j.1365-2494.2011.00809.x](https://doi.org/10.1111/j.1365-2494.2011.00809.x)
- Anderson, W., M. B. Parker, J. E. Knoll, and R. C. Lacy. 2016. Fertilization ratios of N-P₂O₅-K₂O for Tifton 85 bermudagrass on two Coastal plain soils. *Agron. J.* 108:1542–1551. doi:[10.2134/agronj2015.0585](https://doi.org/10.2134/agronj2015.0585)
- Azevedo, J. A. G., S. D. C. Valadares Filho, E. Detmann, D. D. S. Pina, L. G. R. Pereira, K. A. M. D. Oliveira, H. J. Fernandes, and N. K. D. P. Souza. 2011. Prediction of digestible fractions and energy value of agriculture and agro-industrial byproducts for bovine. *Rev. Bras. Zootec.* 40:391–402. doi:[10.1590/S1516-35982011000200022](https://doi.org/10.1590/S1516-35982011000200022)
- Beatty, E. R., D. D. Hayes, and E. E. Worley. 1966. Effect of season of harvesting Coastal bermudagrass on rumen dry-matter disappearance, bulk density, and animal gains. *Proc. Int. Grassl. Congr.* 10:921–923.
- Burton, G. W. 1948. *Coastal bermudagrass*. Cir. 10. Athens (GA): Georgia Agricultural Experiment Station.
- Burton, G. W. 1954. *Coastal bermudagrass*. Bull. NS 2. Athens (GA): Georgia Agricultural Experiment Station.
- Butler, T. J., and J. P. Muir. 2006. Coastal bermudagrass (*Cynodon dactylon*) yield response to various herbicides. *Weed Technol.* 20:95–100. doi:[10.1614/WT-04-318R.1](https://doi.org/10.1614/WT-04-318R.1)
- Coleman, S. W., and T. D. A. Forbes. 1998. Herbage characteristics and performance of steers grazing old world bluestem. *J. Range Manage.* 51:399–407. doi:[10.2307/4003324](https://doi.org/10.2307/4003324)
- Coleman, S. W., J. E. Moore, and J. R. Wilson. 2004. Quality and utilization. In: Moser, L. E., B. L. Burson, and L. E. Sollenberger, editors. *Warm-season (C4) grasses*. Madison (WI): ASA/CSSA/SSSA; p. 267–308.
- Conrad, H. R., W. P. Weiss, W. O. Odwongo, and W. L. Shockey. 1984. Estimating net energy lactation from components of cell solubles and cell walls. *J. Dairy Sci.* 67:427–436. doi:[10.3168/jds.S0022-0302\(84\)81320-X](https://doi.org/10.3168/jds.S0022-0302(84)81320-X)
- Da Silva, J. H. S., W. L. Johnson, J. C. Burns, and C. E. Anderson. 1987. Growth and environment effects on anatomy and quality of temperate and subtropical forage grasses. *Crop Sci.* 27:1266–1273. doi:[10.2135/cropsci1987.0011183X002700060036x](https://doi.org/10.2135/cropsci1987.0011183X002700060036x)
- Deinum, B. 1966. Influence of some climatological factors on the chemical composition and feeding value of herbage. *Proc. Int. Grassl. Congr.* 10:415–418.
- Deinum, B. 1976. Effect of age, leaf number and temperature on cell wall and digestibility of maize. In: van Adrichem, P. W. M., editor. *Carbohydrate research in plants and animals*. Wageningen (The Netherlands): Landbouwhogeschool Wageningen; p. 29–41.
- Duble, R. L., J. A. Lancaster, and E. C. Holt. 1971. Forage characteristics limiting animal performance on warm-season perennial grasses. *Agron. J.* 63:795–798. doi:[10.2134/agronj1971.00021962006300050042x](https://doi.org/10.2134/agronj1971.00021962006300050042x)
- Galyean, M. L., and A. L. Goetsch. 1993. Utilization of forage fiber by ruminants. In: Jung, H. G., D. R. Buxton, R. D. Hatfield, and J. Ralph, editors. *Forage cell wall structure and digestibility*. Madison (WI): ASA/CSSA/ASSA; p. 33–71.
- Girard, V., and G. Dupuis. 1988. Effect of structural and chemical factors of forages on potentially digestible fiber, intake, and true digestibility by ruminants. *Can. J. Anim. Sci.* 68:787–799. doi:[10.4141/cjas88-088](https://doi.org/10.4141/cjas88-088)
- Goering, H. K., and P. J. Van Soest. 1970. *Forage fiber analysis*. Agriculture handbook 379. Washington (DC): USDA.
- Greene, B. B., M. M. Eichhorn, W. M. Oliver, B. D. Nelson, and W. A. Young. 1990. Comparison of four hybrid bermudagrass cultivars for stocker steer production. *J. Prod. Agric.* 3:253–255. doi:[10.2134/jpa1990.0253](https://doi.org/10.2134/jpa1990.0253)
- Hart, R. H., W. H. Marchant, J. L. Butler, R. E. Hellwig, W. C. McCormick, B. L. Southwell, and G. W. Burton. 1976.

- Steer gains under six systems of Coastal bermudagrass utilization. *J. Range Manage.* 29:372–375. doi:[10.2307/3897142](https://doi.org/10.2307/3897142)
- Henderson, M. S., and D. L. Robinson. 1982a. Environmental influences on fiber component concentrations of warm-season perennial grasses. *Agron. J.* 74:573–579. doi:[10.2134/agronj1982.00021962007400030040x](https://doi.org/10.2134/agronj1982.00021962007400030040x)
- Henderson, M. S., and D. L. Robinson. 1982b. Environmental influences on yield and in vitro true digestibility of warm-season perennial grasses and the relationships to fiber components. *Agron. J.* 74:943–946. doi:[10.2134/agronj1982.0021962007400060004x](https://doi.org/10.2134/agronj1982.0021962007400060004x)
- Holt, E. C., and B. E. Conrad. 1986. Influence of harvest frequency and season on bermudagrass cultivar yield and forage quality. *Agron. J.* 78:433–436. doi:[10.2134/agronj1986.00021962007800030007x](https://doi.org/10.2134/agronj1986.00021962007800030007x)
- Jolliff, G. D., A. Garza, and J. M. Hertel. 1979. Seasonal forage nutritive value variation of coastal and coastcross-1 bermudagrass. *Agron. J.* 71:91–94. doi:[10.2134/agronj1979.00021962007100010023x](https://doi.org/10.2134/agronj1979.00021962007100010023x)
- Jung, H. G., and D. A. Deetz. 1993. Cell wall lignification and degradability. In: Jung, H. G., D. R. Buxton, R. D. Hatfield, and J. Ralph, editors. *Forage cell wall structure and digestibility*. Madison (WI): ASA; p. 315–346.
- Magalhaes, K. A., S. C. Valadares Filho, E. Detmann, L. L. Diniz, D. D. S. Pina, J. A. G. Azevedo, F. L. D. Araujo, M. Marcondes, M. Fonseca, and L. Tedeschi. 2009. Evaluation of indirect methods to estimate the nutritional value of tropical feeds for ruminants. *Anim. Feed Sci. Technol.* 155:44–54. doi:[10.1016/j.anifeedsci.2009.10.004](https://doi.org/10.1016/j.anifeedsci.2009.10.004)
- Marsalis, M. A. 2004. *Adaptation of forage bermudagrasses [Cynodon dactylon (L.) Pers.] to the Texas high plains grown under saline and limited irrigation conditions* [PhD dissertation]. Lubbock (TX): Texas Tech University.
- Minson, D. J. 1990. *Forage in ruminant nutrition*. San Diego (CA): Academic Press, Inc.
- Nash, J. E., and J. V. Sutcliffe. 1970. River flow forecasting through conceptual models: Part I. A discussion of principles. *J. Hydrol.* 10:282–290. doi:[10.1016/0022-1694\(70\)90255-6](https://doi.org/10.1016/0022-1694(70)90255-6)
- Nelson, C. J., and L. E. Moser. 1994. Plant factors affecting forage quality. In: Fahey, G. C., editor. *Forage quality, evaluation, and utilization*. Madison (WI): ASA/CSSA/SSSA; p. 115–154.
- NRC. 1996. *Nutrient requirements of beef cattle*: 7th rev. ed. Washington (DC): National Academy Press.
- NRC. 2001. *Nutrient requirements of dairy cattle*. 7th rev. ed. Washington (DC): National Academy Press.
- Osborn, D. F. 1978. Principles governing the use of chemical methods for assessing the nutritive value of forages: a review. *Anim. Feed Sci. Technol.* 3: 265–275. doi:[10.1016/0377-8401\(78\)90001-9](https://doi.org/10.1016/0377-8401(78)90001-9)
- Palmquist, D. L. 1990. Time is ripe to change way fat is measured in feedstuffs. *Feedstuffs*. 62:15–17.
- Palmquist, D. L. 1991. Influence of source and amount of dietary fat on digestibility in lactating cows. *J. Dairy Sci.* 74:1354–1360. doi:[10.3168/jds.S0022-0302\(91\)78290-8](https://doi.org/10.3168/jds.S0022-0302(91)78290-8)
- Phillips, T. G., J. T. Sullivan, M. E. Loughlin, and V. G. Sprague. 1954. Chemical composition of some forage grasses I. Changes with plant maturity. *Agron. J.* 46:361–369. doi:[10.2134/agronj1954.00021962004600080003x](https://doi.org/10.2134/agronj1954.00021962004600080003x)
- Pitman, W. D., and E. C. Holt. 1982. Environmental relationships with forage quality of warm-season perennial grasses. *Crop Sci.* 22:1012–1016. doi:[10.2135/cropsci1982.0011183X002200050028x](https://doi.org/10.2135/cropsci1982.0011183X002200050028x)
- Roth, L. D., F. M. Rouquette Jr, and W. C. Ellis. 1990. Effects of herbage allowance on herbage and dietary attributes of Coastal bermudagrass. *J. Anim. Sci.* 68:193–205. doi:[10.1093/ansci/68.1.193](https://doi.org/10.1093/ansci/68.1.193)
- Rouquette, F. M. Jr, V. Corriher-Olson, and G. R. Smith. 2020. Management strategies for pastures and beef cattle in the Middle-South: the I-20 Corridor. In: Rouquette Jr, M., and G. E. Aiken, editors. *Management strategies for sustainable cattle production in southern pastures*. San Diego (CA): Elsevier Academic Press; p. 123–188.
- Rouquette, F. M. Jr, E. van Santen, and G. R. Smith. 2018. Long-term forage and cow-calf relationships for bermudagrass overseeded with arrowleaf clover or annual ryegrass managed at different stocking rates. *Crop Sci.* 58:1426–1439. doi:[10.2135/cropsci2017.12.0736](https://doi.org/10.2135/cropsci2017.12.0736)
- Schneider, B. H., and W. P. Flatt. 1975. *The evaluation of feed through digestibility experiments*. Athens (GA): The University of Georgia Press.
- Sollenberger, L. E., and C. S. Jones. 1989. Beef production from nitrogen-fertilized Mott dwarf elephantgrass and Pensacola bahiagrass pastures. *Trop. Grassl.* 23:129–134.
- Sullivan, J. T. 1959. A rapid method for the determination of acid-insoluble lignin in forages and its relation to digestibility. *J. Anim. Sci.* 18:1292–1298. doi:[10.2527/jas1959.1841292x](https://doi.org/10.2527/jas1959.1841292x)
- Taliaferro, C. M., F. M. Rouquette Jr, and P. Mislevy. 2004. *Bermudagrass and stargrass*. In: L. E. Moser B. L. Burson, and L. E. Sollenberger, editors. *Warm-season (C4) grasses (monograph no. 45)*. Madison (WI): ASA/CSSA/SSSA; p. 417–475.
- Tedeschi, L. O. 2006. Assessment of the adequacy of mathematical models. *Agric. Syst.* 89:225–247. doi:[10.1016/j.agsy.2005.11.004](https://doi.org/10.1016/j.agsy.2005.11.004)
- Tedeschi, L. O., and D. G. Fox. 2020. *The ruminant nutrition system: vol. I – an applied model for predicting nutrient requirements and feed utilization in ruminants*. 3rd ed. Ann Arbor (MI): XanEdu.
- Tedeschi, L. O., D. G. Fox, and P. H. Doane. 2005. Evaluation of the tabular feed energy and protein undegradability values of the National Research Council nutrient requirements of beef cattle. *Prof. Anim. Sci.* 21:403–415. doi:[10.15232/S1080-7446\(15\)31238-9](https://doi.org/10.15232/S1080-7446(15)31238-9)
- Tedeschi, L. O., D. G. Fox, A. N. Pell, D. P. D. Lanna, and C. Boin. 2002. Development and evaluation of a tropical feed library for the Cornell Net Carbohydrate and Protein System model. *Sci. Agric.* 59:1–18. doi:[10.1590/S0103-90162002000100001](https://doi.org/10.1590/S0103-90162002000100001)
- Tedeschi, L. O., P. J. Kononoff, K. Karges, and M. L. Gibson. 2009. Effects of chemical composition variation on the dynamics of ruminal fermentable and biological value of corn milling (co) products. *J. Dairy Sci.* 92:401–413. doi:[10.3168/jds.2008-1141](https://doi.org/10.3168/jds.2008-1141)
- Tsuji, G. Y., G. Hoogenboom, and P. K. Thornton. 1998. *Understanding options for agricultural production*. Dordrecht (The Netherlands): Kluwer Academic Publishers.
- Utey, P. R., H. D. Chapman, W. G. Monson, W. H. Marchant, and W. C. McCormick. 1974. Coastcross-1 bermudagrass, Coastal bermudagrass, and Pensacola bahiagrass as summer pasture for steers. *J. Anim. Sci.* 38:490–495. doi:[10.2527/jas1974.383490x](https://doi.org/10.2527/jas1974.383490x)
- Utey, P. R., W. G. Monson, G. W. Burton, R. E. Hellwig, and W. C. McCormick. 1978. Comparison of Tifton 44 and Coastal bermudagrasses as pastures and as harvested forages. *J. Anim. Sci.* 47:800–804. doi:[10.2527/jas1978.474800x](https://doi.org/10.2527/jas1978.474800x)
- Utey, P. R., W. G. Monson, G. W. Burton, and W. C. McCormick. 1981. Evaluation of Tifton 44, Coastal, and Callie bermudagrasses as pastures for growing beef steers. *J. Anim. Sci.* 52:725–728. doi:[10.2527/jas1981.524725x](https://doi.org/10.2527/jas1981.524725x)
- Van Saun, R. J., and T. Herdt. 2014. Nutritional assessment. In: Cebra, C., A. Tibary, L. W. Johnson, D. E. Anderson, and R. J. Van Saun, editors. *Llama and alpaca care: medicine, surgery, reproduction, nutrition, and herd health*. 1st ed. St. Louis (MO): Elsevier Inc; p. 100–123.
- Van Soest, P. J. 1982. *Nutritional ecology of the ruminant*. Corvallis (OR): O & B Books, Inc.
- Van Soest, P. J. 1994. *Nutritional ecology of the ruminant*. 2nd ed. Ithaca (NY): Comstock Publishing Associates.
- Van Soest, P. J., R. H. Wine, and L. A. Moore. 1966. Estimation of the true digestibility by the in vitro digestion of cell walls. *Proc. Int. Grassl. Congr.* 10:438–441.
- Wallach, D., D. Makowski, J. W. Jones, and F. Brun. 2019. *Working with dynamic crop models*. 3rd ed. San Diego (CA): Academic Press.
- Weiss, W. P., H. R. Conrad, and N. R. St. Pierre. 1992. A theoretically-based model for predicting total digestible nutrient values of forages and concentrates. *Anim. Feed Sci. Technol.* 39: 95–110. doi:[10.1016/0377-8401\(92\)90034-4](https://doi.org/10.1016/0377-8401(92)90034-4)
- Willmott, C. J. 1981. On the validation of models. *Phys. Geogr.* 2:184–194. doi:[10.1080/02723646.1981.10642213](https://doi.org/10.1080/02723646.1981.10642213)
- Wilson, J. R., and D. J. Minson. 1980. Prospects for improving the digestibility and intake of tropical grasses. *Trop. Grassl.* 14:253–259.
- Woli, P., F. M. Rouquette Jr, C. R. Long, and L. O. Tedeschi. 2020. Estimating the daily nutritive value of bermudagrass forage for grazing livestock. *Appl. Anim. Sci.* (in press). doi:[10.15232/aas.2020-02087](https://doi.org/10.15232/aas.2020-02087)