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DIGESTIBILITY OF ADDITIONAL CRUDE PROTEIN FROM TROPICAL LEGUMES IN MIXED GRASS-LEGUME RATIONS FOR RUMINANTS

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ABSTRACT

The digestibility of crude protein (CP) from tropical legumes in grass-legume mixed diets was studied based on literature data by regressing the digestible CP (digCP) on the proportion of CP from legumes in the diet. *In vivo* studies reporting on CP concentration and *in vivo* CP digestibility values of ruminants fed diets with tropical legumes and grasses with no other feed, were selected for the analysis (56 publications, 213 dietary treatments (150 legume forages, 63 grasses)). First, observations were classified into categories based on the CP concentration of the control grass using the first and the third quartile of the grass CP concentration (LOW, MEDIUM, and HIGH grass quality). Second, legumes were divided based on their growth habit: herbs, shrubs, and trees. Based on the slopes and coefficients of the regressions of the digCP supply on the proportion of CP from legumes, CP digestibility of legumes was higher than that of LOW quality grasses, but lower than that of MEDIUM and HIGH quality grasses. Furthermore, the digestibility of the additional CP from legumes was higher when combined with MEDIUM quality grasses (0.493) compared with those of LOW quality (0.432), while it decreased when combined with HIGH quality grasses (0.305). No differences appeared in the digestibility of additional CP from legumes depending on their growth habit (range 0.415 to 0.421). These results can help optimize the assimilation of CP supplemented by tropical legumes.

Keywords: legume forages, crude protein digestibility, grass quality.

INTRODUCTION

Legume forages are valuable resources with the potential to improve the nutritional status of ruminants, particularly regarding the crude protein (CP) supply due to their higher nitrogen concentration compared with forages of the Poaceae family (i.e., grasses). This is particularly relevant in tropical regions where grasses and other commonly used forages (e.g., straws, stover) have low concentrations of CP. However, there is evidence that for diets evaluated under iso-nitrogenous conditions or when the effects of legumes are corrected by CP concentration in the diet, CP digestibility (CPD) of diets containing legumes may be lower than that of diets without legumes (e.g., Castro-Montoya and Dickhoefer, 2018; da Silva et al., 2017). That decrease in CPD implies that the supply of digestible CP (digCP), which is the protein that can be used

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for maintenance and productive purposes, might be lower than expected based solely on the increment in CP concentration in the diet. The phenomenon needs be understood in order to develop management strategies intended to avoid such losses.

Castro-Montoya and Dickhoefer (2018) found that the effects of including legumes in the diet are dependent on the quality of the grass substituted, with CPD of diets with only legume silages as forage source being lower than CPD in diets containing grasses+legumes, equal to diets containing maize silage+legumes, and higher than diets containing sorghum silage+legumes, where sorghum was typically of lower quality than maize and grasses. Those results clearly reflect an interaction between the basal forage and the additional CP from legumes. Moreover, Poppi and McLennan (1995) stated that the use of legumes may be limited by the loss of protein from the rumen, due to an imbalance between CP and energy in the diet. Indeed, organic matter digestibility (OMD), a proxy of energy supply, is lower in shrub and tree legumes compared with grasses (Castro-Montoya and Dickhöfer, 2020). Similarly, differences in dry matter (DM), CP and fiber digestibility have been reported depending on the growth habit of the legumes (i.e., herbs, shrubs, trees), being high, intermediate or low for diets containing herbaceous, tree, or shrub legumes, respectively (Castro-Montoya and Dickhöfer, 2018; Tiemann et al., 2008). Likewise, clear differences have been reported between herbs, shrubs and trees in terms of fiber and energy concentrations, as well as on the proportion of fiber-bound N (Castro-Montoya and Dickhoefer, 2020), which could influence CPD.

Therefore, the objective of this study was to explore the differences in the digestibility of the additional CP supplied by tropical legumes when legumes are mixed with grasses of low, medium, or high quality (as assumed from the CP concentration of the grasses), and also depending on their growth habit. The working hypotheses were: 1) when legumes are added to grasses, digestibility of the additional CP will have and inverse relation to the quality of the basal grass; 2) digestibility of the additional CP of legumes will differ between legumes of different growth habits, with herbs and shrubs recording the highest and lowest values, respectively.

MATERIALS AND METHODS

A database was created from studies obtained through systematic web searches (i.e., Scopus, Google Scholar, Scielo) in English, Spanish, and Portuguese. Keywords used for the search were "legumes" and "tropical" or "tropics", together with "cattle", "sheep", "goats", "ruminants", "digestibility", "in vivo", and "protein". Only those studies where tropical legumes substituted tropical grasses in ruminants' (cattle, sheep, goats) diets without any addition of other feedstuffs were selected for this analysis. The studies had to report the CP concentration of the legumes, grasses, and total diet; total tract CPD and OMD of the diet; and the proportion of each forage consumed by the ruminants. A total of 56 studies met these criteria (Table 1). Based on the collected information, the digestible CP supply (g/kg DM) of the diet (a factor of the diet's CP concentration and the total tract CPD of the diet) was calculated. In addition, the proportion (g/kg dry matter (DM)) of the additional CP –deriving from legumes– was calculated based on the proportion of legume and its CP concentration. A summary of descriptive statistics of the variables used for the analysis is presented in Table 2.

All observations were classified into categories depending on the CP concentration of their corresponding control grass. For this, all control grasses were ordered according to their CP concentration, and the first and third quartile of the range of CP was calculated. Those grasses below the first quartile were classified as LOW (CP < 51.0 g/kg DM), those above the third quartile were classified as HIGH (CP > 93.1 g/kg DM), and those between the first and the third quartile were classified as MEDIUM.

Similarly, legumes were classified according to their growth habit using the PLANTS database (https://plants.usda.gov) of the Natural Resources Conservation Service of the United States; to simplify this classification, legumes were divided into: "Herbs" (including forbs, vines, and herbs), "Shrubs" (including subshrubs and shrubs) and "Trees" (including shrub trees and trees). In most studies, the basal forage was offered *ad libitum*.

Statistical analysis

A number of simple linear regressions were performed using the lm function of R software (Version 3.3.1), having the concentration of digestible CP supply in the diet as the response variable and the CP from legumes as the independent variable, following the Lucas Test approach (Lucas, 1964). Regressions were performed separately for each of the grass-quality categories to compare the slopes found depending on the control grass quality. Similarly, regressions were performed separately for herb, shrub, and tree legumes. An additional equation was developed for diets with grasses only by regressing the concentration of digestible CP in the diet on the CP concentration of all control

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Table 2. Summary of descriptive statistics of the variables used for the regression analyses.

Variable	Category	n	average	SD	min	max
According to grass quality						
Legume CP concentration (g/kg DM)	LOW	38	167.5	47.7	99.0	254
	MEDIUM	75	181.0	47.8	95.5	300
	HIGH	35	213.2	49.9	126	301
Control grass CP concentration (g/kg DM)	LOW	36	36.7	9.4	23.0	49.0
	MEDIUM	73	72.5	14.0	51.0	93.1
	HIGH	29	106.6	10.9	93.8	131
Legume proportion in the diet (g/kg DM)	LOW	38	37.7	27.4	10	100
	MEDIUM	75	37.0	18.5	10	100
	HIGH	35	50.2	30.6	10	100
CP from the legume in the diet (g/kg DM)	LOW	38	62.0	42.5	9.9	169
	MEDIUM	75	65.6	36.5	19.0	217
	HIGH	29	78.7	40.2	18.3	167
According to growth habit						
Legume CP concentration (g/kg DM)	Herbs	52	155.2	30.8	99.0	225
	Shrubs	23	153.2	42.7	95.5	256
	Trees	73	216.5	45.4	155.0	301
Control grass CP concentration (g/kg DM)	Herbs	71	75.9	26.6	23.0	112
	Shrubs	36	66.4	24.6	23.0	116
	Trees	97	71.8	27.6	28.1	131
Legume propportion in the diet (g/kg DM)	Herbs	53	42.5	23.3	10	100
	Shrubs	22	42.1	27.1	10	100
	Trees	67	32.6	17.5	10	100
CP from the legume in the diet (g/kg DM)	Herbs	53	66.3	38.7	9.9	201
	Shrubs	21	57.6	35.0	14.4	160
	Trees	67	68.9	36.7	18.3	169

[1] Legumes included in categories LOW, MEDIUM or HIGH depending on the CP concentration of their corresponding control grass.

grasses in the dataset. The regressions were weighted by the study using the inverse of the number of observations as weight. To keep the regressions on the same scale of the studied variables, weights were standardized by dividing each weight by the average of all weights (St-Pierre, 2001).

RESULTS AND DISCUSSION

Effect of basal grass quality on crude protein digestibility of legumes

A total of 56 publications met the criteria for this study, including 216 dietary treatments (150 containing legume forages and 66 controls –grasses only–). The average (± standard deviation) CP of grasses in the LOW, MEDIUM, and HIGH categories were 38.0 (± 8.87), 72.9 (± 14.0) and 107.7 (± 10.5) g/kg DM, respectively. The average CP of legumes in the LOW, MEDIUM, and HIGH grass categories were 167.5 (± 47.7), 181.0 (± 47.8), and 213.2 (± 49.9) g/kg DM, respectively (Table 2). This means that grasses of higher quality are mixed with legumes of higher CP concentration, a condition that factors into the results found.

Of the treatments including legumes, 53, 23 and 74 corresponded to legumes classified as herbs, shrubs, and trees, respectively. The average CP of herb, shrub, and tree legumes were 155.2 (± 30.8), 153.2 (± 42.7), and 216.5 (± 45.4) g/kg DM, respectively (Table 2), which agree with values reported by Castro-Montoya and Dickhoefer (2020).

The regressions in this analysis are interpreted in a similar fashion to the interpretation of a Lucas Test (Lucas, 1964), where the slope of the regression indicates the digestibility of the additional CP in the diet, that is, the CP from legumes. However, this interpretation must be made carefully because the digestibility values observed are not exclusively the result of the characteristics of the CP from legumes, but rather of the interactive effects between the grass and the supplemented legume in the diet, as well as the changes in the diet due to the replacement of a forage by the other. Therefore, it is important to keep in mind that the digestibility coefficients discussed here do not reflect the CP digestibility of the legumes, but the digestibility of the additional CP supplied from legume under different conditions.

When legumes were mixed with poor quality grasses (LOW) (Fig 1A), the additional CP from legumes had a digestibility of 432 g/kg, higher than that of their control grasses (402 g/kg; from digCP supply of 15.3 g/kg DM (intercept) for an average CP concentration of 38.0 g/kg DM). However, when legumes were mixed with grasses in the MEDIUM and HIGH category (Fig 1B and C, Table 1 (Eq. 2-3)), the digestibility of the additional CP from the legumes (493 and 305 g/kg for MEDIUM and HIGH, respectively) was lower than that of their basal grasses (524 and 632 g/kg for MEDIUM and HIGH, respectively).

When comparing the slopes of the regressions between categories, the digestibility of the additional CP differed depending on the quality of the basal grass. The slope of the regression is lower when legumes are mixed with grasses of HIGH quality, and higher when legumes are mixed with grasses of MEDIUM quality. This only partially agrees with the hypothesis, as it was expected that the slopes of the regression would proportionally decrease with increasing grass quality. Poppi and McLennan (1995) stated that significant losses of ingested protein occur at a CP to digestible OM (digOM) ratio beyond 0.21. In the current database, the ratio of CP to digOM in the rations was 0.14 (± 0.07), 0.18 (± 0.06) and 0.26 (± 0.09) for the diets in the LOW, MEDIUM and HIGH quality, respectively. The high ratio of CP to digOM evidences a lack of enough energy relative to the additional CP supplied by the legumes. Similarly, when legumes were mixed with LOW quality grasses, the energy was likely not sufficient for an optimal use of the additional N. However, there is a critical difference between LOW and HIGH categories. When legumes are mixed with grasses of HIGH quality, the imbalance between CP and energy could be corrected by either decreasing the CP concentration of the diet (average CP concentration in the HIGH rations was 145 ± 46.3 g/kg DM) or by supplying additional energy; whereas when legumes are mixed with grasses of LOW quality CP in the diet was already limited (73.5 ± 34.2 g/kg DM), therefore the low efficiency of N use is likely due to a lack of energy.

It can be interpreted from the findings of this study that a high CP to digOM ratio (beyond 0.21 as suggested by Poppi and Mclennan (1995)) compromises the utilization of additional CP, but also that a CP to digOM ratio of 0.14 is too low for diets containing only grasses and legumes. The highest digestibility of additional CP when legumes are mixed with MEDIUM quality grasses corresponds to a CP to digOM ratio of 0.18 (± 0.06). This might be the result of a synergy between the grass and the forage, with the grass providing adequate amounts of energy and the legume ensuring sufficient N supply for microbial activity, as suggested by Lüscher et al. (2014).

It is worth mentioning that the low digestibility of the additional CP from legumes when mixed with grasses of HIGH quality was probably related to the overall increase in CP concentration in the diet, as the efficiency of CP utilization shows diminishing increases with higher CP levels (e.g., Castillo et al., 2000). Nevertheless, it is unlikely that all the decrease in CP digestibility is due to those diminishing returns, since other examples of supplementation of grasses with CP-rich ingredients show increases in CP digestibility even when high-quality grasses are the basal forage (Delagarde et al., 1997; Jones-Endsley et al., 1997). This is explained by a higher digestibility of those protein-rich ingredients compared with the supplemented grasses (Bargo et al., 2003), a characteristic that tropical legumes may not always fulfill. Moreover, the average inclusion level of legumes in the HIGH category was 50.2 (± 30.6) g/100 g DM, in contrast to the 37.7 (± 27.4) and 37.0 (± 18.5) g/100 g DM of herbs and shrubs, respectively, which further explains the drop in the additional CP digestibility when legumes are mixed with grasses of HIGH quality.

The present results indicate that the supply of digCP is not proportional to the additional amount of CP in the diet when using tropical legumes. In the current dataset the additional CP supplied by the legumes was 62.0 (± 42.5), 65.6 (± 36.5), and 78.7 (± 40.2) g/kg DM for the LOW,

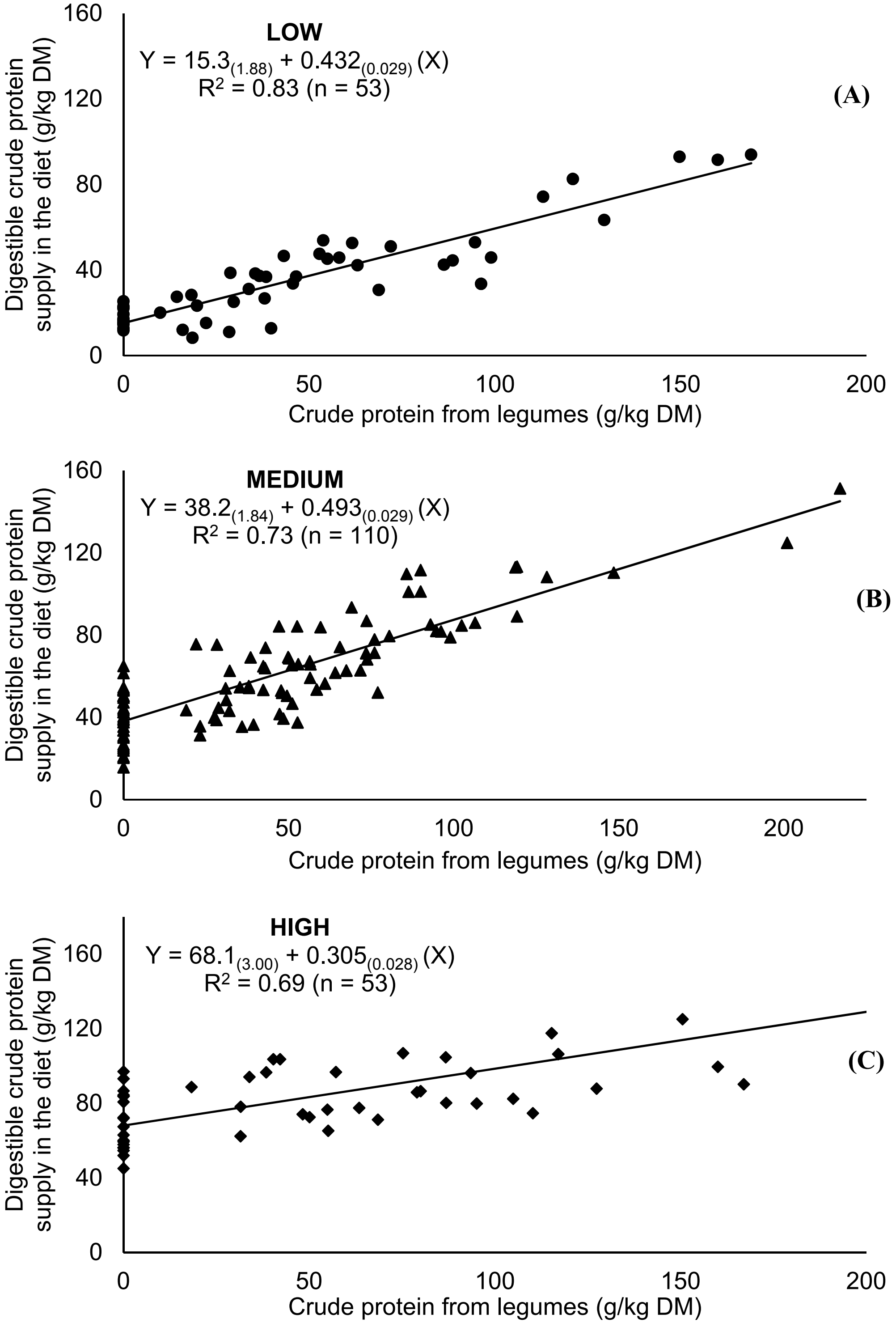

Fig. 1. Scatter plots and regression equations of digestible crude protein supply (g/kg DM) on crude protein from legumes (g/kg DM) when legumes are mixed with grasses of LOW, MEDIUM, or HIGH quality.

MEDIUM, and HIGH categories, respectively. When, factored by the digestibility coefficients found in the current analysis, the supply of digCP was 26.8 (± 18.4), 31.9 (± 18.3), and 23.2 (± 12.8) g/kg DM for legumes combined with grasses in the LOW, MEDIUM, and HIGH category, respectively. The supply of digCP dramatically decreases in the HIGH category compared to that of the MEDIUM category, despite a higher amount of CP supplied in the former.

Commonly, a high correlation between CP concentration and digCP has been assumed for forages (e.g., Miliford and Minson, 1965, Glover et al., 1957). However, those studies related the CP concentration to the CPD of forages fed individually. In this sense, forages with higher CP typically represent younger, less lignified, more digestible materials. Conversely, the current analysis studies the degradability of the additional CP to that provided by grasses. Moreover, the individual feeding of forages does not account for the grass × legume interaction, which is implicit in the results of the current analysis. It is important to keep in mind that when feeding a legume forage, a substitution effect will occur, that is, less grass will be consumed in favour of the legume. This substitution effect is, in most cases, a desired outcome aiming at maximizing protein consumption. However, when decreasing the proportion of grasses in the ration, the supply of energy might be compromised as evidence exists that tropical legumes have lower concentrations of metabolizable energy than tropical grasses (Castro-Montoya and Dickhoefer, 2020).

It is not easy to explain the reasons for the reduced CP digestibility when legumes are mixed with HIGH quality grasses, or why the synergism between legumes and grasses becomes less obvious. However, the fiber-bound N, the presence of antinutritive compounds (ANC) and the supply of energy are discussed here as possible explanations. Castro-Montoya and Dickhoefer (2020) found that legumes have a higher ADF-N fraction than grasses (152 vs. 116 g/kg N for legumes and grasses, respectively), which due to their higher N concentration results in a 4.5 times higher ADF-N concentration on DM basis for legumes compared with grasses (3.97 vs. 0.89 g/kg DM). The ADF-N fraction is recognized as non-digestible portion and is expected to be excreted in the faeces, which helps to understand the reduced digestibility of dietary CP when increasing legume proportions are found in the diet. Indeed, Mertens (1979) stated that diets with an ADF-N concentration above 140 g/kg N are at risk of impairing the supply of CP for rumen digestion.

Antinutritive compounds could also aid to decreased CP digestibility (Makkar et al., 2007). However, this is only speculative, as it is not possible to know the type, concentration or activity of ANC in the forages studied, neither their role in the digestion of CP. Moreover, not all legumes included in this study are rich in ANC (e.g., lablab, stylosanthes). Nevertheless, ANC still remains as a possible explanation for the observed effects of legumes on CPD.

An exploration of our data revealed that the estimated digOM of those grasses in the category HIGH would be in average 614 (± 6.7) g/kg DM, whereas that of the legumes would be 566 (± 15.8) g/kg DM. Using those estimates of digOM, the average CP of the grasses in the category HIGH (108 g/kg DM) and the average CP of the legumes included in the study (185 g/kg DM), it is possible to estimate that a CP to DOM ratio of 0.21 is found for a grass to legume ratio of 75:25. Beyond that ratio, higher legume inclusions could lead to a decrease in the use of ingested CP, particularly if a significant portion of that additional CP is bound to fiber, as is the case for tropical legumes. The practical implication of these results is that if tropical legumes are mixed with a high-quality grass and if N use efficiency is to be maximized, the proportion of legumes in the diet should be limited to around 300 g/kg DM. If higher levels of legume inclusion are managed an additional source of energy should be included in the diet. Interestingly, previous studies have demonstrated that higher weight gain, as well as higher efficiency of milk production is achieved with tropical legume levels of inclusion between 200 and 400 g/kg DM (Castro-Montoya and Dickhoefer, 2018; da Silva et al., 2017).

Effect of legumes growth habit on crude protein digestibility

Average (± standard deviation) CP concentrations for herbaceous, shrub and tree legumes were 155.2 (± 30.8), 153.2 (± 42.7), and 216.5 (± 45.4) g/kg DM, respectively being similar to those reported by Castro-Montoya and Dickhöfer (2020). Grasses used as control recorded average CP concentrations of 75.9 (± 26.6), 66.4 (± 24.6) and 71.8 (± 27.6) g/kg DM for the abovementioned forage legumes, respectively.

In contrast to the stated hypothesis, there were no meaningful differences between the digestibility of additional CP from herbaceous, shrub or tree legumes, with digestibility coefficients of 0.415, 0.421, and 0.415, respectively (Fig. 2). Previous studies and reviews showed differences in OM, NDF, and CP digestibility of legumes depending on their growth habit, with shrubs commonly showing a lower digestibility (Castro-Montoya and Dickhoefer, 2018).

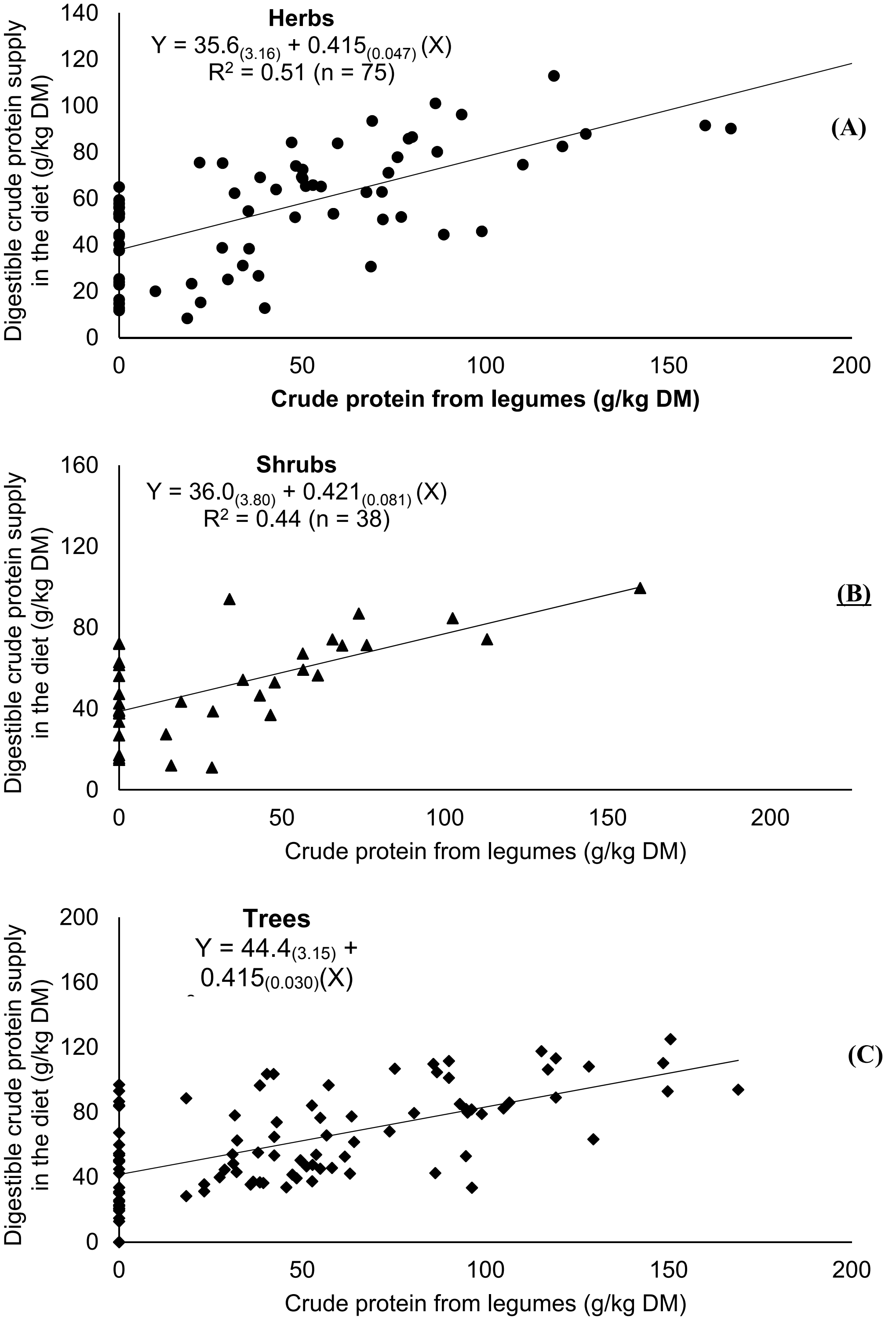

Fig. 2. Scatter plots and regression equations of digestible crude protein supply (g/kg DM) on crude protein from herb (A), shrub (B) or tree (C) legumes (g/kg DM).

Similarly, fiber-bound N was also higher in shrubs compared with legumes in the review of Castro-Montoya and Dickhoefer, 2020.

The fact that no differences were found when shrubs were fed to ruminants can be explained by the nature of the available data. The proportion of CP from legumes was lower when shrubs were fed compared with the other two legumes (66.3 ± 38.7, 57.6 ± 35.0, and 68.9 ± 36.7 for herbs, shrubs and trees, respectively) (Table 2). Therefore, the diminishing CP digestibility at higher levels of inclusion may not have affected shrubs to the same extent as it may have affected herbs and trees. Moreover, the quality of the grasses supplemented (based on their CP concentration) appeared to be higher in both herbs and trees rather than in shrubs, which, as discussed above, could have compromised the CP digestibility in the former two, resulting in a similar digestibility of additional CP from shrubs compared with trees and herbs. These findings demonstrate that under the right strategy shrub legumes can successfully contribute to the supply of digCP to the same extent as herbs and trees. This strategy would be to include shrubs and grasses of medium quality in diets with intermediate CP concentrations (e.g., 90 to 130 g/kg DM).

It is important to note that the supply of CP and digCP can significantly increase by improving the quality of the grass fed (e.g., by appropriate harvest time, fertilization) or by growing a better quality grass. When a regression was performed of digCP on CP concentration of all the basal grasses in the study, a slope of 0.752 was found (Fig. 3). In this sense, the use of grasses to increase the digCP supply can only be a strategy at low levels of CP requirements, because it is unlikely that CP can be increased beyond (e.g. 120 g/kg DM) based solely on grasses, and in some cases even achieving a CP concentration close to 90 g/kg DM from tropical grasses may be a challenge. Thus, legumes become the ideal forage to further increase CP supply while still maximizing forage utilization.

It is important to mention that tropical legumes are an important fodder in ruminant nutrition and their utilization must be encouraged, not only for their positive effects on animal performance, but also due to several additional benefits associated with legume cropping and their potential to decrease dependency from external sources of protein.

CONCLUSIONS

The digestibility of the additional CP supplied by tropical legumes is affected by the interaction of the legume with the quality of the supplemented grass and it appears to be strongly determined by the energy supply. Therefore, optimizing the energy to protein ratio might be a good approach to maximize the use of the CP supplied by legumes. No differences appeared in the digestibility of additional CP from legumes depending on their growth habit, which indicates that under the right strategy, any type of legume can contribute to increase the protein status of ruminants consuming mixed grass-legume diets.

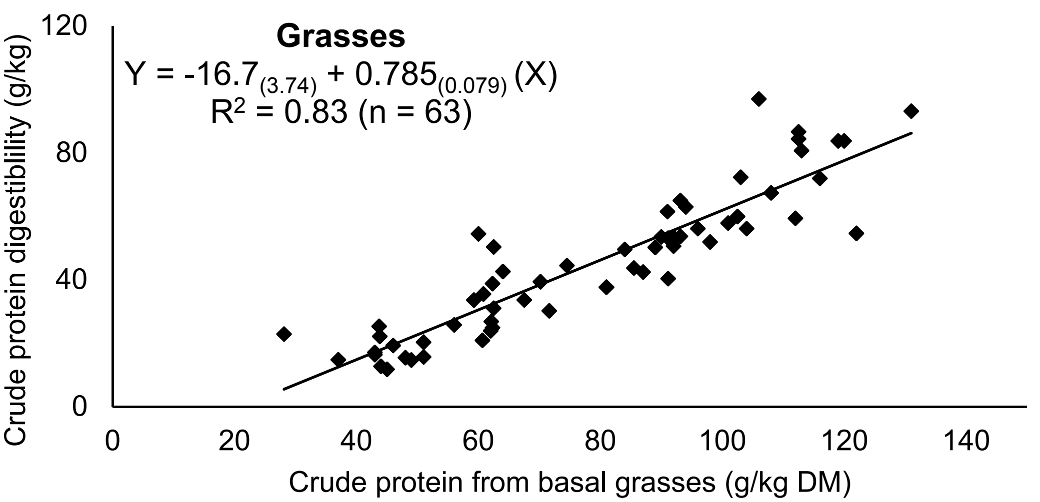

Fig. 3. Scatter plot and regression equation of digestible crude protein supply (g/kg DM) on crude protein from basal grasses (g/kg DM).

The findings of this study indicate that including high levels of legume forages in the diet may lead to the loss of a large proportion of that additional CP if energy is deficient.

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