Intake, digestibility and nitrogen utilization of three tropical tree legumes
I. As sole feeds compared to Asystasia intrusa and Brachiaria brizantha

Roger C. Merkel, Kevin R. Pond, Joseph C. Burns, Dwight S. Fisher

Abstract

The tropical tree legumes Paraserianthes falcatoria, Gliricidia sepium, and Calliandra calothyrsus were fed to ram lambs to evaluate their potential as feeds. Dry matter intake, digestibility of dry matter, neutral detergent fiber and nitrogen, and digestible energy content were determined through a digestion study. The herbaceous dicot Asystasia intrusa was included as an underutilized source of nitrogen and Brachiaria brizantha was included as a standard tropical (C₄) grass. Of the tree legumes, C. calothyrsus had the highest level of soluble phenolics (SPHE), averaging 38% of dry matter, and soluble proanthocyanidins (SPRO), averaging 13.7 absorbance units per gram (AU g⁻¹) of dry matter. P. falcatoria was intermediate, averaging 15% SPHE and 4.8 AU g⁻¹ SPRO, with G. sepium the lowest, with 5% SPHE and 0.4 AU g⁻¹ SPRO. Dry matter intake (percent of body weight) was lowest for C. calothyrsus-fed lambs, averaging 2.0%, compared with 3.2% for P. falcatoria and 2.5% for G. sepium. Intakes were similar for A. intrusa and B. brizantha, averaging 2.6%. C. calothyrsus also had the lowest dry matter digestibility, averaging 55%, compared with 61% for P. falcatoria and 63% for G. sepium, which were similar. Highest dry matter digestibility was obtained for A. intrusa, averaging 72%, and B. brizantha, averaging 65%. Forages had similar rank for neutral detergent fiber digestibility.

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Proanthocyanidins in the tree legumes may have bound with cell wall carbohydrates, resulting in a reduction in dry matter and NDF digestibilities. Digestible energy (kcal g\(^{-1}\)) was highest for \textit{G. sepium}, averaging 3.0, and ranged from 2.6 to 2.7 kcal g\(^{-1}\) for \textit{C. calothyrsus}, \textit{P. falcataria}, \textit{A. intrusa} and \textit{B. brizantha}. Fecal N was higher from the lambs fed tree legumes (average, 0.419 g kg\(^{-1}\) BW/day) compared with \textit{A. intrusa} or \textit{B. brizantha} (0.261 and 0.159 g kg\(^{-1}\) BW/day, respectively). This was attributed to higher fecal NDF-N, averaging 0.329 g kg\(^{-1}\) BW/day, from the tree legumes versus 0.162 g kg\(^{-1}\) BW/day for \textit{A. intrusa} and 0.048 g kg\(^{-1}\) BW/day for \textit{B. brizantha}. Consequently, apparent and true N digestibilities were lower for the tree legumes, averaging 61 and 69%, respectively, versus 73 and 84% for \textit{A. intrusa}, and 76 and 93% for \textit{B. brizantha}. Within the tree legumes, \textit{C. calothyrsus} had lowest apparent and true N digestibility, averaging 51 and 57%, while \textit{P. falcataria} and \textit{G. sepium} had apparent and true N digestibilities averaging 67 and 76%. Proanthocyanidins and phenolic compounds in the three legumes, especially \textit{C. calothyrsus}, were associated with reduced forage quality.

**Keywords:** Tree legumes; Proanthocyanidins; Condensed tannin; Digestibility; \textit{Asystasia intrusa}; Digestible energy

### 1. Introduction

Limited nitrogen availability is a major constraint in ruminant production systems in most parts of the world. Tree legumes can be a supplementary source of nitrogen, and other nutrients, in many tropical production systems (Gutteridge and Shelton, 1994). The role of a nitrogen supplement in animal diets is to increase basal diet efficiency. High leaf protein concentration should ideally provide a source of both fermentable and by-pass protein (Raghavan and Krishna, 1993). Condensed tannins and other phenolic compounds in tree leaves, however, may adversely affect digestibility and protein utilization. Many nutritional studies have investigated effects of tree legume supplementation on various diets, but little is known about the digestibility, protein availability and energy content of tree legumes fed alone.

Three tree legumes, \textit{Paraserianthes falcataria}, \textit{Calliandra calothyrsus} and \textit{Gliricidia sepium}, hereafter referred to as falcata, calliandra and glicidica, respectively, have shown potential as livestock feed in Indonesia (Ibrahim et al., 1988; Rangkuti et al., 1990). Calliandra and glicidica, though native to Central America, were introduced in Indonesia in the early 1900s. In the 1970s, calliandra was widely planted by the State Forest Corporation of Indonesia to provide erosion control, and to also provide firewood and fodder for the use of villagers (NRC, 1983). Glicidica is one of the tree species used for shade in coffee and cocoa plantations in Indonesia. Falcata, formerly called \textit{Albizia falcataria}, is native to the eastern islands of Indonesia, and is one of the world’s fastest growing trees, reaching a height of 7 m in one year under optimal growth conditions (Parrotta, 1990).

An underutilized source of nitrogen for ruminant diets in Indonesia and Malaysia is \textit{Asystasia intrusa}, a herbaceous dicot that is reported to have crude protein concentrations of 21–26% (Ibrahim et al., 1990; Sivaraj et al., 1991; Tuen, 1994). However, asystasia is extremely invasive, and has been designated as a noxious weed by rubber and oil palm plantation owners in Malaysia. Its rapid spread is attributed to both its high degree of
shade tolerance and its establishment from both seed and vegetative propagules. Asystasia ground cover has been reported at 41% in 5-year old stands and 55% in 10-year-old stands in an oil palm plantation (Sivaraj et al., 1993). Because of its competitiveness for soil nutrients and its physical interference with harvesting plantation crops, owners have resorted to either chemical control or hand weeding. However, Chen and Chee (1993) found that asystasia was highly palatable to ruminants and could be controlled by grazing.

The objective of this study was to determine voluntary intake, dry matter, nitrogen and fiber digestibility, as well as the energy content of falcataria, calliandra, gliricidia and asystasia. Phenolic and proanthocyanidin concentrations of the three tree legumes were estimated, and their effects on digestibility and protein utilization determined. The perennial C₄ grass *Brachiaria brizantha* was included as a standard.

2. Material and methods

2.1. General

The experiment was conducted at the Sungai Putih Research and Assessment Installation for Agriculture Technology (RAINAT), North Sumatra, Indonesia. The research station is about 50 m above sea level (3°N and 99°W) and has a tropical climate. Rainfall averages 1800 mm annually, with no distinct dry season (Gatenby et al., 1993).

2.2. Experimental forages

Seedlings of falcataria and calothyrsus, and vegetative cuttings of sepium were established in 0.25 ha plots to provide the tree legume forage for the study. Trees were planted in rows 2 m apart with 50 cm spacing within a row. Four- to seven-month-old regrowth (2–2.5 m) was cut to about 1 m, and the leaves — consisting of the rachis, rachilla and leaflets — were stripped by hand from each stem. Asystasia was harvested in the flowering stage prior to seed set from a well-established, naturally occurring pure stand growing in the shade under rubber trees. *B. brizantha*, a perennial C₄ grass having medium shade tolerance (Wong, 1991) and potential for producing under rubber (Ng, 1991; Thai et al., 1995) was included as a standard forage. Brachiaria was harvested in the vegetative state from pastures at the research site by hand cutting to a 10–20 cm stubble.

All forages were harvested by 0800 hours each day. The compound tree leaves and asystasia received no further processing prior to feeding, but brachiaria was cut into 20 cm lengths to aid its placement in mangers.

2.3. Animals and feeding

Twenty 6-month-old ram lambs, weighing 13–22 kg, were used. Ten lambs were St. Croix × Sumatra crossbreed (CS) and the rest were pure Sumatra (S). Lambs were randomly assigned within the breed to form five experimental groups, each consisting of two CS and two S lambs. All the lambs were treated with anthelmintic and then assigned
at random to individual pens for a 10-day feed adaptation period in a concrete barn with a raised slatted floor. The lambs were then moved into digestibility crates in a ground level barn for a further 10 days, with total collection of feces and urine occurring during the last 5 days. Animals had free access to water, but no additional minerals were provided. Animal weights were obtained at the end of the experiment.

Animals were fed, allowing for ad libitum consumption, with about half of their daily dry matter allotment, offered at 0900 hours, and the remainder at 1630 hours. During the experiment, daily orts averaged 34% of the total DM fed (SE = 2.78). The previous day’s refusals were removed and weighed prior to the 0900 hours feeding. Dry matter determinations, conducted at 100°C for 24 h, were made at each feeding on the ‘as-fed’ forage and on the refusals from each animal and dry matter intake calculated. All the five forages were sampled prior to the 0900 hours feeding and dried at 60°C for 72 h for subsequent chemical analyses. Additional samples of the legume trees were taken at both feedings, frozen and freeze dried for subsequent tannin analysis. Because of limited oven- and freeze-drying facilities, all samples were initially frozen until they could be processed further.

The feces and urine collected were weighed following the 0900 hours feeding. About 40% of the daily fecal output was frozen and composited by animal during the 5-day trial. Fecal dry matter was determined by drying at 100°C for 24 h. Urine was collected in plastic buckets, to which 50 ml of 0.5N HCl was added to avoid nitrogen losses. About 5% of the daily urine output was frozen and composited by animal.

2.4. Chemical analysis

All dried forage and fecal samples were ground in a Wiley mill\(^1\) to pass a 1 mm screen. The samples were mixed thoroughly, and a subsample of the forage tissue was ground further in a cyclone mill\(^2\) (Udy Corporation, Fort Collins, CO) to pass a 1 mm screen. Samples were analyzed for organic matter by ashing for 3 h at 500°C. Neutral detergent fiber (NDF), acid detergent fiber (ADF), lignin (LIG), residual NDF (RNDF), and NDF remaining following 48 h in vitro fermentation were determined, according to Goering and Van Soest (1970) and Van Soest and Robertson (1980), and expressed on a dry matter basis. Total nitrogen (N) and N in both NDF and ADF residues (NDF-N and ADF-N) were determined according to the AOAC (1980) and in vitro dry matter disappearance (IVDMD) determined according to Cope and Burns (1971). Freeze-dried forage samples were analyzed gravimetrically for soluble phenolics (SPHE) according to Reed et al. (1985) and for insoluble and soluble proanthocyanidins (IPRO and SPRO) using HCl : butanol (Bate-Smith, 1973; Reed et al., 1982).

Fecal samples were analyzed for N, NDF, ADF, LIG and NDF-N. Fecal metabolic N was determined by difference (total fecal N minus fecal NDF-N) after Van Soest (1982). Urine was analyzed for N concentration by micro-kjeldahl.

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\(^1\) Mention of trade names, warranty, proprietary products, or vendor does not imply endorsement by any of the supporting agencies of the products named or criticism of similar ones not mentioned. All the programs and services by USDA are offered on a nondiscriminatory basis.

\(^2\) Refer footnote 1.
Gross energy content of oven-dried forage was determined through bomb calorimetry (Parr Oxygen Bomb Calorimeter, Parr Instrument Co. Inc., Moline, IL). Digestible energy, in kcal g$^{-1}$, was calculated as the difference between daily gross energy consumption and total fecal energy.

2.5. Statistical analysis

The experiment was analyzed as a completely randomized design with a two-breed by five-feed factorial arrangement in two replicates, using the procedures of SAS (SAS/STAT, 1988). Animal response differences for the 10 treatment combinations were compared using a set of seven non-orthogonal contrasts. Differences were reported significant at the $P \leq 0.10$ level. Differences in forage chemical composition were tested using the Waller–Duncan multiple $k$-ratio $t$-test, with a $k$-ratio of 100.

3. Results and discussion

3.1. Chemical composition

Neutral detergent fiber concentrations of the tree legumes and of asystasia were lower than brachiaria, indicating a higher concentration of cell solubles (Table 1). Nitrogen concentrations of the tree legumes and asystasia were similar, ranging from 3.9 to 4.2%. Lignin concentrations ranged widely from 4% for brachiaria to 19% for asystasia. The

Table 1
Chemical composition of five forages: *P. falcataria*, *C. calothyrsus*, *G. sepium*, *B. brizantha* and *A. intrusa*

<table>
<thead>
<tr>
<th>Component</th>
<th><em>P. falcataria</em></th>
<th><em>C. calothyrsus</em></th>
<th><em>G. sepium</em></th>
<th><em>B. brizantha</em></th>
<th><em>A. intrusa</em></th>
<th>MSD$^a$</th>
<th>CV$^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DM (%)</td>
<td>29 b$^e$</td>
<td>36 a</td>
<td>22 c</td>
<td>24 c</td>
<td>10 d</td>
<td>2.3</td>
<td>9.0</td>
</tr>
<tr>
<td>OM (%)</td>
<td>94 b</td>
<td>95 a</td>
<td>93 c</td>
<td>88 d</td>
<td>84 e</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>NDF (%)</td>
<td>48 c,d</td>
<td>53 b</td>
<td>47 c</td>
<td>62 a</td>
<td>50 d</td>
<td>2.1</td>
<td>3.8</td>
</tr>
<tr>
<td>ADF (%)</td>
<td>29 c</td>
<td>30 c</td>
<td>25 d</td>
<td>35 b</td>
<td>39 a</td>
<td>1.8</td>
<td>5.3</td>
</tr>
<tr>
<td>LIG (%)</td>
<td>13 c</td>
<td>15 b</td>
<td>8 d</td>
<td>4 e</td>
<td>19 a</td>
<td>1.4</td>
<td>11.4</td>
</tr>
<tr>
<td>N (%)</td>
<td>3.9 a</td>
<td>4.0 a</td>
<td>4.2 a</td>
<td>1.8 b</td>
<td>4.2 a</td>
<td>0.3</td>
<td>7.8</td>
</tr>
<tr>
<td>ADF-N (%)</td>
<td>0.6 c</td>
<td>0.8 b</td>
<td>0.4 d</td>
<td>0.1 e</td>
<td>1.4 a</td>
<td>0.2</td>
<td>21.6</td>
</tr>
<tr>
<td>NDF-N (%)</td>
<td>2.4 b</td>
<td>2.8 d</td>
<td>2.2 b</td>
<td>0.4 c</td>
<td>2.9 a</td>
<td>0.3</td>
<td>14.1</td>
</tr>
<tr>
<td>IVDMD (%)</td>
<td>42 c</td>
<td>20 d</td>
<td>57 b</td>
<td>62 a</td>
<td>58 a,b</td>
<td>3.4</td>
<td>6.7</td>
</tr>
<tr>
<td>RNdFc (%)</td>
<td>38 b</td>
<td>47 a</td>
<td>28 c</td>
<td>25 c</td>
<td>34 b</td>
<td>5.8</td>
<td>8.0</td>
</tr>
<tr>
<td>SPHE$^d$ (%)</td>
<td>15 b</td>
<td>38 a</td>
<td>5 c</td>
<td>ND$^f$</td>
<td>ND</td>
<td>3.0</td>
<td>20.3</td>
</tr>
<tr>
<td>SPRO$^d$ (AU g$^{-1}$)</td>
<td>4.8 b</td>
<td>13.7 a</td>
<td>0.4 c</td>
<td>ND</td>
<td>ND</td>
<td>0.9</td>
<td>19.1</td>
</tr>
<tr>
<td>IPRO$^d$ (AU g$^{-1}$ of NDF)</td>
<td>32 b</td>
<td>32 b</td>
<td>297 a</td>
<td>ND</td>
<td>ND</td>
<td>59.1</td>
<td>60.3</td>
</tr>
</tbody>
</table>

$^a$ Minimum significant difference, Waller–Duncan $k$-ratio, $t$-test; $k$-ratio = 100.

$^b$ Coefficient of variation.

$^c$ Residual neutral detergent fiber on a dry matter basis.

$^d$ SPHE, soluble phenolics; SPRO, soluble proanthocyanidins; IPRO, insoluble poanthocyanidins.

$^e$ Row means with unlike letters differ, Waller–Duncan $k$-ratio, $t$-test; $k$-ratio = 100.

$^f$ Not determined.
LIG level of asystasia may be artificially high due to the potential heat damage that could have occurred through the Maillard reaction during drying of the previously frozen samples. Upon thawing, asystasia developed a mucous-like texture, and after drying was brown, very hard and brittle. The Maillard reaction produces a substance with lignin-like properties that artificially increase LIG recovery and is enhanced by high moisture concentration (Van Soest, 1982). Lower NDF and LIG concentrations of 39.7 and 5.1%, respectively, have been found in freeze-dried asystasia from a greenhouse study (Pond, 1992). Nitrogen trapped by the Maillard reaction would also have caused inflated ADF-N and NDF-N concentrations.

Phenolic levels of 38% in calliandra and 15% in falcataria (Table 1) are higher than those found in the literature — 18% for calliandra (Ahn et al., 1989) and from 1.0 to 4.6% for falcataria (Mahyuddin et al., 1988; Ahn et al., 1989). Gliricidia phenolic levels of 5% are similar to the findings of Ahn et al. (1989). Levels of soluble proanthocyanidin were not found in the literature for these tree species. Relative ranking of these species in phenolic and condensed tannin concentration were calliandra > falcataria > gliricidia. Proanthocyanidins may bind to protein and cell wall carbohydrates, with the resulting complexes being indigestible and insoluble in neutral detergent solution (Barry et al., 1986b; Reed, 1986). Elevated NDF-N levels in the tree legumes (>2%) indicate that such reactions had occurred.

The IVDMD from calliandra (20%) and falcataria (42%) was lower than that predicted by the percentage of neutral detergent cell solubles (100 — NDF), indicating that in vitro digestion was inhibited (Table 1). Levels of RNDF, a measure of the indigestibility of a feed (Van Soest, 1982), supports this conclusion by showing indigestible levels of only 47 and 38% for calliandra and falcataria, respectively. Perera et al. (1996), testing six calliandra provenances in Sri Lanka, also reported low IVDMD ranging from 19 to 30%. The addition of tannin-containing plant extracts has been shown to decrease IVDMD in lespedeza (Cope and Burns, 1971) and temperate grasses (Burns et al., 1976), and inhibit the breakdown of leaf proteins by rumen microbes (Tanner et al., 1994).

3.2. Intake

The largest quantity of DM was consumed by the CS lambs, and was attributed to their large size (Table 2). Brachiaria had a high proportion of stem, but lambs readily consumed the leaves, resulting in refusals that were predominately stems; however, some leaves were present. This caused some difficulty in obtaining a representative, composite refusal sample.

Falcataria gave the highest intake as a percent of body weight (IBW), 3.2% (Table 2). No other estimates of its intake were found in the literature. Calliandra resulted in the lowest IBW, 2.0%, and within the range of 1.7 to 2.6% reported by Norton (1994). Gliciridia, brachiaria and asystasia gave intermediate and similar IBWs, averaging 2.6%. Sheep IBW for gliciridia has been reported ranging from 1.7 to 3.3% (Carew, 1983; Norton, 1994); however, palatability problems have been reported with gliciridia (Rangkuti, et al., 1990). Asystasia has been reported to support IBW of 2.2–4.3% (Mokhtar and Wong, 1988).

Condensed tannin in forages, such as seen with the tree legumes (Table 1), has been associated with decreased palatability and with reduced gut-wall permeability (Kumar
and Vaithiyanathan, 1990). Further, absorbed tannins and phenols can act as toxins (Robbins et al., 1987; Butler, 1989), and may cause changes in growth hormones (Barry et al., 1986a). The high concentrations of soluble phenolic compounds in calliandra are probably associated with its low IBW through either reduced palatability and/or through the formation of toxic substances.

3.3. Dry matter and fiber digestion

The digestibility of DM and NDF was highest for astasia, averaging 72 and 65%, respectively (Table 2). The high in vivo estimate of apparent DM digestibility (72%), compared with IVDMD estimates of 58% (Table 1), indicates that the Maillard reaction

<table>
<thead>
<tr>
<th>Treatment</th>
<th>DMI (grams per day)</th>
<th>BW (kg)</th>
<th>IBW</th>
<th>Digestibility</th>
<th>DE (kcal g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>DM</td>
<td>NDF</td>
</tr>
<tr>
<td>CSF</td>
<td>599</td>
<td>20.6</td>
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<tr>
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<td>16.7</td>
<td>3.4</td>
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<td>47</td>
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<tr>
<td>CSG</td>
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<td>20.2</td>
<td>2.5</td>
<td>63</td>
<td>43</td>
</tr>
<tr>
<td>SG</td>
<td>503</td>
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<td>2.8</td>
<td>63</td>
<td>43</td>
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<tr>
<td>CSC</td>
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<td>2.0</td>
<td>53</td>
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<tr>
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<td>2.8</td>
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<tr>
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<td>2.4</td>
<td>64</td>
<td>55</td>
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<td>15.1</td>
<td>2.4</td>
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<td>63</td>
</tr>
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<td>CVc</td>
<td>17.5</td>
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<td>9.2</td>
<td>3.0</td>
<td>5.6</td>
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Feed means:

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<th></th>
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<th>IBW</th>
<th>Digestibility</th>
<th>DE (kcal g⁻¹)</th>
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<td>F</td>
<td>585</td>
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<td>41</td>
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<tr>
<td>G</td>
<td>498</td>
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<td>43</td>
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<tr>
<td>C</td>
<td>317</td>
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<td>55</td>
<td>36</td>
</tr>
<tr>
<td>B</td>
<td>468</td>
<td>17.7</td>
<td>2.6</td>
<td>65</td>
<td>56</td>
</tr>
<tr>
<td>A</td>
<td>432</td>
<td>17.2</td>
<td>2.5</td>
<td>72</td>
<td>65</td>
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</table>

Contrasts:

<table>
<thead>
<tr>
<th></th>
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<th>BW (kg)</th>
<th>IBW</th>
<th>Digestibility</th>
<th>DE (kcal g⁻¹)</th>
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<tbody>
<tr>
<td>FCG vs. B</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>d</td>
<td>d</td>
</tr>
<tr>
<td>FCG vs. A</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>d</td>
<td>d</td>
</tr>
<tr>
<td>A vs. B</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>d</td>
<td>c</td>
</tr>
<tr>
<td>F vs. C</td>
<td>d</td>
<td>a</td>
<td>d</td>
<td>c</td>
<td>b</td>
</tr>
<tr>
<td>F vs. G</td>
<td>NS</td>
<td>NS</td>
<td>c</td>
<td>NS</td>
<td>NS</td>
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<tr>
<td>C vs. G</td>
<td>c</td>
<td>b</td>
<td>c</td>
<td>d</td>
<td>c</td>
</tr>
<tr>
<td>CS vs. S</td>
<td>a</td>
<td>c</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

a CS, St. Croix × Sumatra; S, Sumatra; two animals per treatment.
b F, P. falcataria; C, C. calothyrsus; G, G. sepium; A, A. intrusa; B, B. brizantha.
c Coefficient of variation.
d a, P < 0.10; b, P < 0.05; c, P < 0.01; d, P < 0.001; NS, not significant.
probably occurred during forage drying, as mentioned previously. This would reduce IVDMD estimates of dry matter digestion and would inflate the NDF concentration of the forage. In the latter case, estimates of NDF intake would also be elevated, causing a high estimate of apparent NDF digestion.

The DM digestion estimates for gliricidia, 63%, are above the range of 43 to 55% reported in the literature (Smith and van Houtert, 1987; Norton, 1994). This discrepancy may, in part, be associated with differences in environmental conditions and age at harvest. The low apparent DM digestibility for calliandra is within the range of 47 to 59% reported by Tangendjaja et al. (1992).

The reduced DM and NDF digestibilities noted for the legume trees are associated, in part, with the presence of SPHE, SPRO and IPRO which are not found in either brachiaria or asystasia (Table 2). Calliandra had highest concentrations of SPHE, averaging 38%, compound to 15% in falcataaria and 5% in gliricidia (Table 1). Further, calliandra also had highest concentrations of SPRO, with gliricidia having the lowest. The occurrence of phenolics and condensed tannins has been reported to decrease DM and cell wall digestibility through binding to cell wall carbohydrates, forming indigestible complexes (Mueller-Harvey, 1989; Woodward and Reed, 1989) or through bacteriostatic or bacteriocidal effects (Kumar and Vaithiyathan, 1990). Chiquette et al. (1988) found that rumen bacteria adherent on high tannin trefoil did not penetrate plant tissue as well as those on low tannin strains.

The legume trees also contained higher concentrations of LIG than brachiaria, with calliandra highest at 15% and gliricidia lowest at 8% (Table 1). Lignin has also been shown to negatively influence DM digestion (Van Soest, 1982). In a study with 24 tropical browse species, Bamualim et al. (1980) reported lower in sacco DM digestion than predicted by the percentage of neutral detergent solubles and a correlation of $\sim 0.92$ was obtained between lignin concentration and in sacco DM digestibility.

It is not clear from these data what specific role SPHE, SPRO, IPRO and LIG had in altering in vivo digestion of DM and NDF of legume trees. Highest concentrations of these constituents, however, were present in calliandra, which had the lowest DM and NDF digestion coefficients (Table 2).

### 3.4. In vivo and in vitro digestibility

A large discrepancy occurred between in vivo estimates of apparent DM digestion (Table 2) and IVDMD of the tree legumes (Table 1) and raises questions about the use of laboratory procedures to estimate the digestibility of tanniferous feedstuffs. The widest difference of 35 digestion units occurred with calliandra, which had the highest concentration of SPHE and SPRO. Falcataaria showed a difference of 19 percentage units and had second highest concentration of SPHE and SPRO.

The presence of anti-quality compounds in forage tissues appears to have a greater negative effect on in vitro estimates of digestion than on in vivo estimates and has been addressed by Burns and Cope (1976) and warrants caution. Phenolic compounds may form complexes with protein or carbohydrates, thereby contaminating fiber fractions in feed or feces (Reed, 1986). Sample preparation may affect the degree of complex formation as freeze-dried samples of tree legume leaves have recorded lower fiber and
higher IVDMD than identical oven-dried samples (Merkel et al., 1994). The residual NDF procedure which allows calculation of in vitro true dry matter digestibility (Van Soest, 1982) is also useful in ranking the digestibility of tanniferous browse (Conklin, 1994), and may be a better indicator of in vivo digestibility.

3.5. Energy

Gliricidia had the highest DE at 3.0 kcal g\(^{-1}\), while calliandra (2.6 kcal g\(^{-1}\)) and falcataria (2.7 kcal g\(^{-1}\)) were similar (Table 2). Reed (1986) noted, however, that energy values of browse may be overestimated due to the presence of phenolic compounds which are absorbed into the body and are not metabolized, but are excreted in urine. Brachiaria (2.6 kcal g\(^{-1}\)) and asystasia (2.7 kcal g\(^{-1}\)) recorded similar DE levels. Values of 1.5 to 3.3 kcal g\(^{-1}\) have been reported for asystasia hays (Mokhtar and Wong, 1988).

3.6. Nitrogen

3.6.1. Nitrogen intake and excretion

Of the three tree species, falcataria had the highest \((P < 0.05)\) N intake, followed by gliricidia and calliandra (1.33, 1.10 and 0.89 g kg\(^{-1}\) BW/day, respectively) (Table 3). Asystasia N intake of 0.99 g kg\(^{-1}\) BW/day was greater \((P < 0.01)\) than that of brachiaria, 0.67 g kg\(^{-1}\) BW/day. Whereas forage NDF-N concentrations in falcataria (Table 1) were lower than in calliandra, higher DMI led to higher \((P < 0.05)\) NDF-N intakes than for either calliandra- or gliricidia-fed lambs \((P > 0.10)\). Tree legumes had higher \((P \leq 0.01)\) excretions of fecal N and fecal NDF-N than either asystasia or brachiaria. Calliandra had the lowest fecal metabolic N excretion of 0.055 g kg\(^{-1}\) BW/day.

Dietary tannins have been found to increase fecal N excretion (Woodward and Reed, 1989) because forage proteins bound by proanthocyanidins are recovered along with the undigested feed nitrogen in the fecal NDF-N fraction (Mason, 1969). Fecal metabolic N is related to animal nutritional status, diet quality and intake levels as well as hindgut fermentation (Van Soest, 1982). The low quantity of fecal metabolic N excreted from calliandra-fed lambs is largely due to the low dry matter intake, resulting in low fecal output.

Urinary N excretion was higher for falcataria-, gliricidia- and asystasia-fed lambs than for brachiaria- or calliandra-fed lambs. High urinary N indicates high protein or inorganic nitrogen intake and rapid ruminal digestion, resulting in ammonia production in excess of microbial needs. Ammonia in excess of recycling needs is absorbed into the bloodstream, converted to urea in the liver and excreted in the urine. Condensed tannins have been shown to reduce rumen ammonia and urinary N excretion (Barry et al., 1986b; Waghorn et al., 1987; Reed et al., 1990).

3.6.2. Nitrogen retention and digestibility

Of the three tree legumes, falcataria had the highest retained N of 0.697 g kg\(^{-1}\) BW/day, followed by gliricidia and asystasia at 0.546 and 0.543 g kg\(^{-1}\) BW/day, respectively (Table 4). Calliandra-fed lambs had the lowest N retention of 0.347 g kg\(^{-1}\) BW/day.
True and apparent N digestibilities followed similar patterns, with tree legumes having lower digestibilities than either asystasia or brachiaria. Brachiaria, however, had the highest apparent and true digestibilities, averaging 76 and 93%. In contrast, calliandra resulted in lowest apparent N (51%) and true N (57%) digestibilities, being lower than falcataria and gliricidia, which were similar. Asystasia had higher NDF-N digestibility than brachiaria (77 versus 66%), and both had higher NDF-N digestibility than the tree legumes (43–60%).

True N digestibility was calculated by replacing fecal N with fecal NDF-N in the digestibility calculations. Approximately 20% of the fecal N excreted by lambs fed calliandra was fecal NDF-N, indicating considerable proanthocyanadin-protein complexing, leading to low true N digestibility. Conversely, only one-third of fecal N from lambs fed calliandra was fecal NDF-N, indicating considerable proanthocyanadin-protein complexing, leading to low true N digestibility.
fed brachiaria was composed of NDF-N, which, along with a higher N digestibility, led to a true N digestibility of 93%. Apparent N digestibility in asystasia was higher than the 60.2% reported by Wong et al. (1990) using Malin sheep. The NDF-N digestibility of asystasia was artificially high, due, in part, to the drying problems experienced with samples of asystasia, as described earlier.

### Table 4

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Ret N (g kg(^{-1}) BW/day)</th>
<th>Digestibilities (%)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>App N</td>
<td>True N</td>
</tr>
<tr>
<td>CSF</td>
<td>0.601</td>
<td>63</td>
<td>72</td>
</tr>
<tr>
<td>SF</td>
<td>0.793</td>
<td>69</td>
<td>77</td>
</tr>
<tr>
<td>CSG</td>
<td>0.506</td>
<td>67</td>
<td>76</td>
</tr>
<tr>
<td>SG</td>
<td>0.585</td>
<td>66</td>
<td>75</td>
</tr>
<tr>
<td>CSC</td>
<td>0.348</td>
<td>50</td>
<td>56</td>
</tr>
<tr>
<td>SC</td>
<td>0.347</td>
<td>51</td>
<td>58</td>
</tr>
<tr>
<td>CSB</td>
<td>0.461</td>
<td>77</td>
<td>93</td>
</tr>
<tr>
<td>SB</td>
<td>0.378</td>
<td>75</td>
<td>92</td>
</tr>
<tr>
<td>CSA</td>
<td>0.594</td>
<td>76</td>
<td>85</td>
</tr>
<tr>
<td>SA</td>
<td>0.474</td>
<td>71</td>
<td>82</td>
</tr>
<tr>
<td>CV(^c)</td>
<td>12.4</td>
<td>2.9</td>
<td>2.0</td>
</tr>
</tbody>
</table>

Feed means:

- **F**: 0.697 (66 | 75 | 60)
- **G**: 0.546 (67 | 76 | 57)
- **C**: 0.347 (51 | 57 | 43)
- **B**: 0.419 (76 | 93 | 67)
- **A**: 0.534 (73 | 84 | 77)

Contrasts:

- **FCG vs. B**: b d d d
- **FCG vs. A**: NS d d d
- **A vs. B**: b a d c
- **F vs. C**: d d d d
- **F vs. G**: c NS NS NS
- **C vs. G**: c d d d
- **CS vs. S**: NS NS NS NS

---

\(^a\) CS, St. Croix × Sumatra; S, Sumatra; two animals per treatment.


\(^c\) Coefficient of variation.

\(^d\) a, \(P < 0.10\); b, \(P < 0.05\); c, \(P < 0.01\); d, \(P < 0.001\); NS, not significant.

#### 3.6.3. Ruminal N degradation and tannin effects

Low urinary N in calliandra-fed lambs was likely due to decreased ruminal protein degradation and digestion. As previously discussed, calliandra had the lowest N digestibility and highest tannin content of the forages fed. Other studies using the in sacco technique have found low digestibility and rates of ruminal protein degradation in
calliandra. Jones et al. (1992) reported that 91% of initial calliandra N remained after 48 h ruminal incubation, whereas Perera et al. (1996) found 50–83% of N remaining in six calliandra genotypes after 72 h ruminal incubation. The latter study also reported a rapidly digested portion ranging from 1 to 16%, with a potential degradable portion of only 2–48%. Conversely, approximately 70% of glicidicia N has been reported to disappear after only 24 h rumen incubation (Ash, 1990).

Lower N digestibility leads to greater amounts on N flowing to the small intestine, where effects of tannins are uncertain. Jones and Mangan (1977) reported that tannin–protein complexes, stable in the pH ranges typically found in the rumen, dissociated on encountering lower or higher pH environments, such as those found in the abomasum or proximal small intestine. Waghorn et al. (1994) list three mechanisms by which tannins may affect intestinal N digestion and absorption: binding with enzymes rendering them inactive; binding with digesta protein; and associating with intestinal mucosa decreasing ability for amino acid transport and absorption. Perez-Maldonado and Norton (1996) stated that increased fecal N found in sheep fed calliandra or Desmodium intortum was due to an increased total flow of N to the small intestine rather than reduced protein digestion and absorption post-ruminally. These authors postulated that all tannin–protein complexes dissociated in the lower digestive tract. If true, the higher fecal NDF-N found when feeding tanniferous diets would result from tannins binding proteins in the intestines, as postulated by Waghorn et al. (1994), and may not represent bound feed protein.

Fig. 1. Retained N (Ret N), fecal NDF-N, fecal metabolic N (Fec Met N) and urinary N (Ur N) as percent of total intake.

<table>
<thead>
<tr>
<th>Contrasts:</th>
<th>Ret N</th>
<th>Fec NDF-N</th>
<th>Fec Met N</th>
<th>Urinary N</th>
</tr>
</thead>
<tbody>
<tr>
<td>FCG v B</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>NS</td>
</tr>
<tr>
<td>FCG v A</td>
<td>**</td>
<td>**</td>
<td>*</td>
<td>**</td>
</tr>
<tr>
<td>A v B</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>F v C</td>
<td>**</td>
<td>**</td>
<td>*</td>
<td>†</td>
</tr>
<tr>
<td>F v G</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>*</td>
</tr>
<tr>
<td>C v G</td>
<td>**</td>
<td>**</td>
<td>*</td>
<td>NS</td>
</tr>
<tr>
<td>CS v S</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

1 CS=St. Croix v Sumatra, S=Sumatra; two animals per treatment.

F= P. falcata, C=C. calothyrsus, G=G. sepium, B=B. brizantha, A=A. intrusa.
† P<0.10; * P<0.05; ** P<0.01; NS, not significant.

Fig. 1. Retained N (Ret N), fecal NDF-N, fecal metabolic N (Fec Met N) and urinary N (Ur N) as percent of total intake.
3.7. Nitrogen retention and excretion as percent of intake nitrogen

Animals consuming brachiaria showed highest efficiency of N utilization by retaining 63% of N consumed, with a loss of only 7% as fecal NDF-N (Fig. 1). Low N digestibility of calliandra resulted in only 39% retention of intake N, with the major loss occurring through fecal NDF-N (43% of total N intake). Falcataria and gliricidia gave similar percentages of retained N, fecal NDF-N and fecal metabolic N. However, gliricidia resulted in a higher percentage loss of urinary N, likely due to a rapid ruminal protein digestion rate, as discussed above.

Urinary N in asystasia accounted for a higher percentage loss of N than fecal NDF-N. Asystasia has been found to contain high quantities of nitrate. Concentrations from 0.8 to 3.7% of leaf dry matter and from 5.9 to 13.8% of stem dry matter have been found in asystasia grown under differing light and fertilizer regimes in a greenhouse study (J.C. Burns, unpublished data). The high urinary nitrogen loss in asystasia was likely due to a combination of nitrate conversion to ammonia in the rumen (Van Soest, 1982) and rapid ruminal digestion of protein, leading to increased levels of rumen ammonia.

4. Conclusions

Intake, digestibility, and energy values for these five forages when fed alone were established. Proanthocyanidins in tree legumes apparently bound protein, rendering it less available for digestion, as seen by increased fecal N, largely due to fecal NDF-N, and reduced nitrogen digestibilities. Calliandra, with the highest levels of soluble phenolics and soluble proanthocyanidins, was most affected. However, the assumption that all fecal NDF-N represents bound feed protein may not be valid if tannins are liberated from tannin–protein complexes in the abomasum or small intestine and later bind with other digesta, enzymatic or mucosal proteins.

In practical feeding systems, tree legumes would be incorporated at supplementary levels. Consequently, further testing is needed to ascertain if the negative effects reported here are mitigated by feeding the tree leaves as a smaller proportion of the diet. Where asystasia is established, it can be an important feed source for grazing animals or as a cut-and-carry feed. Further, it may have a more important role in plantation cropping where shade restricts the growth of most grasses. Its invasive growth habit and its tendency to crowd out other forage plants, however, requires that careful thought be given before it is introduced for cultivation in new areas.

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References


