scientific reports

OPEN

Nutritive value and condensed tannins of tree legumes in silvopasture systems

Izabela Aline Gomes da Silva[1], José Carlos Batista Dubeux Jr.[2], Carla Giselly Souza[3], Martin Ruiz Moreno[2], Mércia Virgínia Ferreira dos Santos[4], Valéria Xavier de Oliveira Apolinário[5], Alexandre Carneiro Leão de Mello[4], Márcio Vieira da Cunha[4], James Pierre Muir[6] & Mario Andrade Lira Junior[4]✉

Introducing legumes into C4-dominated tropical pastures, may enhance their sustainability but has some pasture management constraints. One potential alternative is using arboreal legumes, but several of these species have relatively high condensed tannin (CT) concentrations, which negatively impact forage quality. There is limited knowledge, however, on how arboreal legume leaf CT content varies over the year and how this might impact forage quality. The objective of this 2 year study was to assess the seasonal variation of CT and nutritive value for ruminants of the tropical tree legumes gliricidia [*Gliricidia sepium* (Jacq.) Kunth ex. Walp.] and mimosa (*Mimosa caesalpiniifolia* Benth). The research was carried out in the sub-humid tropical region of Brazil on well-established pastures in which either legume was present with signalgrass (Urochloa decumbens Stapf.). We determined CT and nitrogen concentrations, in vitro digestible organic matter (IVDOM), and leaf δ13C and δ15N from January to October of 2017 and 2018. All parameters were affected ($P < 0.05$) by the interaction between legume species and sampling time, with generally higher leaf CT content for mimosa than gliricidia, and both were reduced at the start of the dry season, although much more drastically for mimosa. The IVDOM was strongly affected by CT content and increased at the start of the dry season, coincidentally when C4 grass forage quality typically decreased. There is a marked species effect, with CT from gliricidia impacting IVDOM more than the same CT content from mimosa. While N concentration from mimosa also increased at the start of the dry season, that for gliricidia did not vary over the year. We conclude that although these arboreal legumes have relatively high CT contents, these reduce during the dry season when CT concentrations coinciding with a reduced forage quality as the protein content for C4 grasses is usually inadequate in this season.

Keywords Digestibility, Moisture, Secondary compounds, Stable isotopes

The growing global demand for animal protein due to both human population increases and average animal protein consumption linked to greater income, coupled with societal demands for lower environmental impacts of agricultural practices, has led to a current search for sustainable pasture intensification, particularly in the tropics[1]. One of the major limitations of pasture-fed tropical animal production systems is nitrogen availability, particularly considering the high economic and ecological footprints of nitrogen fertilizers due to the large natural gas demand to produce and fossil fuel needs of distribution and application and thus high greenhouse gas effects, and the management issues linked to the establishment and maintenance of tropical grass-legume consortia, due to the higher palatability and lower growth rate of the legume in comparison to the C4 grasses which dominate tropical pastures[2–5].

One alternative for greater ruminant protein production is silvopastoral systems, in which the tree component is a legume that reduces the competition between herbaceous C_4 grasses and arboreal C_3 legumes[6–9]. In these systems, the tree component provides several ecosystem services, including biological atmospheric N_2 fixation, increased animal comfort due to shade, enhanced forage nutritional quality due to increased protein content, increased soil carbon and nitrogen storage, increased biodiversity, and further income sources[10–18].

[1]Federal University of Rondonopolis, Rondonópolis, Brazil. [2]University of Florida - North Florida Research and Education Center, Marianna, FL, USA. [3]Politechnic Institute of Santarém, Santarém, Portugal. [4]Federal Rural University of Pernambuco, Recife, Brazil. [5]Maranhão State University, São Luís, Brazil. [6]Texas Agrilife, Stephenville, TX, USA. ✉email: mario.alirajr@ufrpe.br

The nutritional value of forage depends on a wide range of characteristics. Still, some of the major ones are its digestibility, usually measured as the in vitro digestibility of the organic matter (IVDOM)[12], and its protein content, most expressed as crude protein or nitrogen content[18]. At the same time, one of the major interests in the use of forage legumes is their biological nitrogen fixation potential in symbiosis with rhizobia[16], frequently measured through the reduction in^{15}N content in relation to that present in the soil from which N would otherwise be absorbed, or its $\delta^{15}N$[8]. Under seasonally dry conditions, on the other hand, plants more efficient in water use are usually preferable, particularly when they are in a mixed pasture with C4 grasses, which are highly water-efficient, and the change in^{13}C content in relation to the atmosphere, or $\delta^{13}C$, is a good proxy for that[12,19,20].

A possible constraint to these legume trees as a forage protein source is the widespread occurrence of condensed tannins (CTs), which generally reduce digestibility and, thus, animal gain from the legume[12,21–23]. There are differences among arboreal species both for CT content, which can differentially reduce overall digestibility[3,21,24–26]. Differences in CT bioactivity might explain the weaker correlation between CT concentration and nutritional value for interspecific correlations than for intraspecific correlations[27,28].

A further point of interest is the effect of climate, season, and ontology on CT content and digestibility and how these affect the difference in CT effects on digestibility between species[29–35]. For instance, while *Lotus pedunculatus* CT contents increase with temperature, this does not occur for *L. corniculatus*[35].

Thus the objective of this 2 year study was to legumes gliricidia [*Gliricidia sepium* (Jacq.) Kunth ex. Walp.] and mimosa (*Mimosa caesalpiniifolia* Benth), since we hypothesized that the digestibility and CT content of arboreal forage legume leaves vary across species throughout the year.

Results

Both CT and IVDOM ($P < 0.0001$ and $P = 0.0003$, respectively) interacted with species and sampling time (Fig. 1). The highest CT contents were found in July of both years for both species with an average of 48 for Gliricidia and 161 mg CT.g^{-1} for Mimosa in July, with a steady decline afterward to averages of 20 and 106 mg CT.g^{-1} in October, respectively, most likely linked to the increase in potential evapotranspiration. While the mimosa CT content was consistently greater than the gliricidia CT content, the decrease was more pronounced between July and October. The IVDOM had an almost opposite pattern, decreasing from January to July and increasing from August to October in both years.

There was a strong negative correlation between CT and IVDOM, which was different for both species (Table 1). While both species had negative correlations between CT and IVDOM, there was a steeper decline in IVDOM with increased CT contents for gliricidia than for mimosa (Fig. 2). However, the latter had a higher CT content and lower IVDOM. For the same IVDOM level, mimosa had a much greater CT content than gliricidia. This highlights the importance of assessing bioactive rather than total CT and using self-standards for each species.

Although there were ($P < 0.05$) correlations between CT and the other variables (Table 1), the difference in pattern between the species, as found for correlation with N content, indicates that this is likely mostly due to the much higher CT of Mimosa. This is particularly noticeable for $\delta^{13}C$, for which both species had negative correlations, with an overall positive correlation, and for the $\delta^{15}N$, N and C contents, for which one species had positive and the other had negative correlations.

Both species condensed tannin content and IVDOM present strong seasonal variation, with Mimosa presenting steeper differences over the year than Gliricidia (Fig. 1), with high correlation coefficients between potential evapotranspiration (PET) and CT contents ($r = ^{-}0.80$ and $^{-}0.72$ for Gliricidia and Mimosa, respectively) and digestibility ($r = 0.66$ and 0.72 for Gliricidia and Mimosa, respectively), while rainfall is also correlated for both species ($r = 0.40$ for both species), although much less so (Table 2). For both variables, there is a tendency for a reduction in CT and an increase in IVDOM with the transition to drier periods, coinciding with when the signal grass nutritive value is at its lowest.

While correlations between N contents, δ15N, and δ13C contents and rainfall and potential evapotranspiration were generally much lower than those for CT or IVOMD, they are still significant ($P < 0.05$), particularly for mimosa's (Table 2). One important difference between the species is the increased N concentration and $\delta^{15}N$ of mimosa when the season becomes drier compared to those of gliricidia, although they are still lower for the former than for the latter.

Discussion

Here, we studied a well-established system with gliricidia or mimosa as the tree components in a signalgrass pasture. One of the major characteristics of this grass is its very low N content during the dry season of the year [12,36,37]. For instance in this same experimental field, N content for pure non-N-fertilized signalgrass green fraction was *ca.* 4.18 g.kg^{-1}, when the leaf/stem proportion is taken into account[7].

While both species had high CT contents (Fig. 1), particularly compared with those of typical cool-season herbaceous legumes[4,35], for instance the 49 and 10 mg.kg^{-1} reported for high and low tannin content lines of Lotus corniculatus[38], both fall markedly when the warmer and drier season begins, typically in August in the experimental region (Fig. 1). This fluctuation in CT content was also observed for birdsfoot trefoil (*Lotus corniculatus* L.) when the ambient temperature increased[35].

As expected, a strong negative correlation existed between CT content and IVDOM, which agrees with the relevant literature[21,26,39]. Although the correlation coefficients between CT content and IVDOM were not very different between species ($^{-}0.94$ and $^{-}0.97$ for gliricidia and mimosa—Table 1), the linear regressions indicated that the digestibility of the mimosa CT was approximately one-third less than that of the gliricidia CT (Fig. 2), which agrees with the literature indicating a strong species-specific effect of CT content on nutritive value[4,22,26,31–33]. It

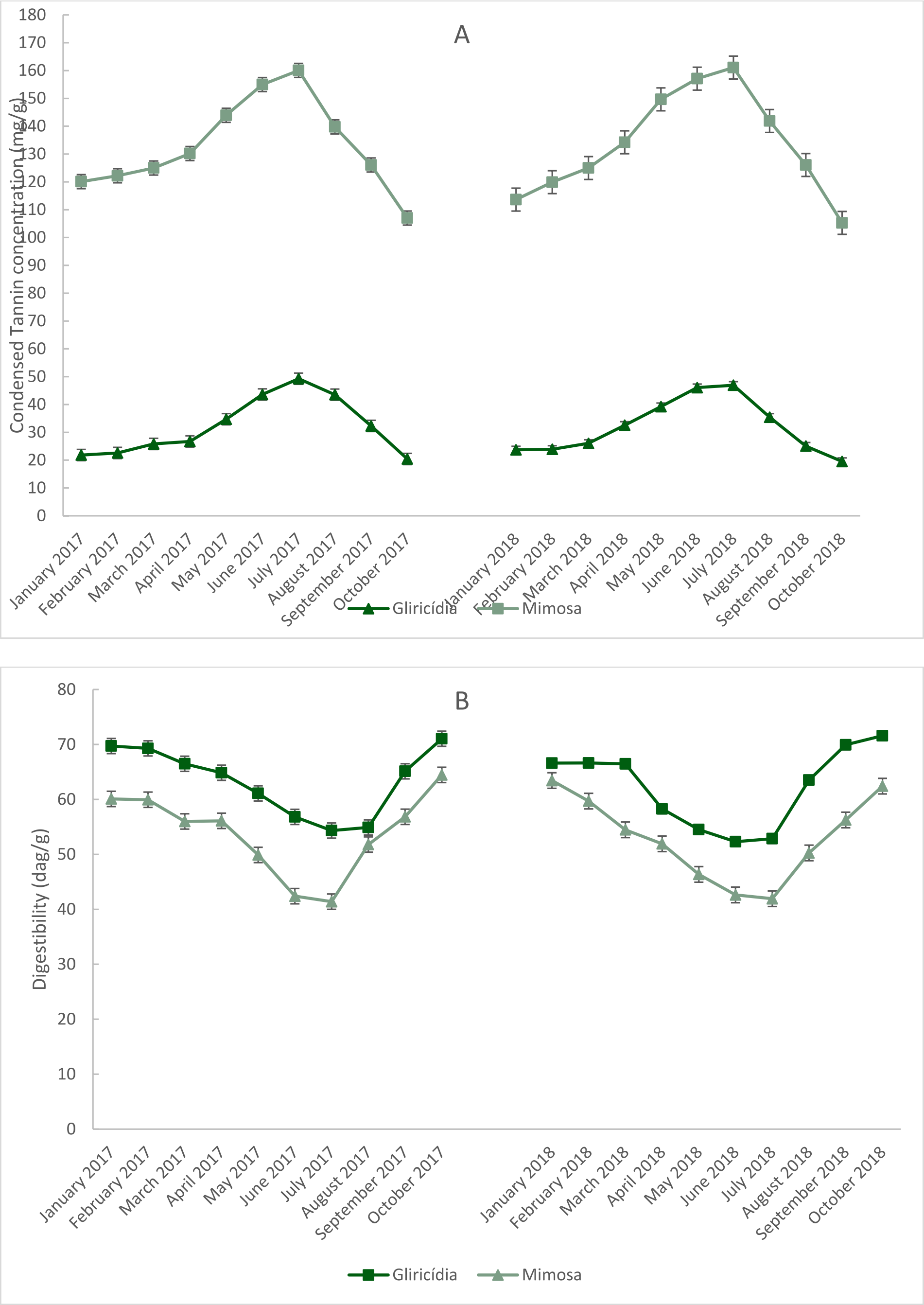

Figure 1. Evolution of condensed tannin concentration (**A**) and in vitro digestible organic matter (**B**) in Gliricidia and Mimosa leaves over two years of sampling and its relationship with rainfall and potential evapotranspiration.

	General	Gliricidia	Mimosa
Digestibility	**−0.74328**	**−0.94059**	**−0.97109**
$\delta^{15}N$	**−0.75721**	0.03158	**−0.25793**
N concentration	**−0.86954**	0.18287	**−0.33105**
$\delta^{13}C$	**0.46067**	**−0.26608**	**−0.3269**
C concentration	**0.78478**	−0.07938	**0.26692**

Table 1. Correlation coefficients between the condensed tannin concentration and the remaining plant nutrient characteristics. Significant values are in bold.

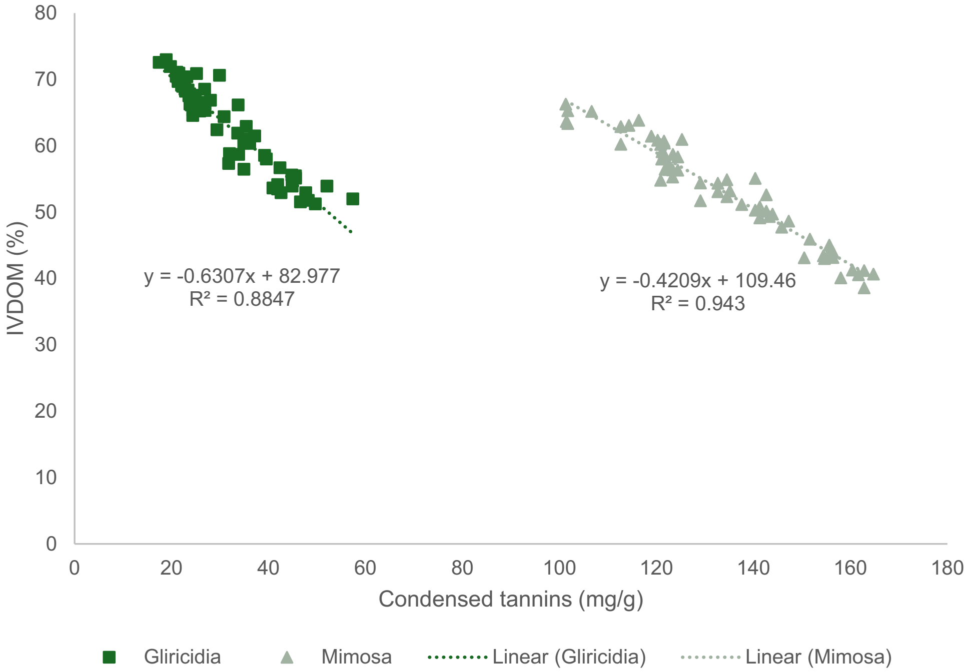

Figure 2. Variation in in vitro organic matter digestibility (IVOMD) as a function of CT content for gliricidia and mimosa over two years.

	Monthly rainfall	Potential evapotranspiration
Overall		
Condensed tannin	0.10304	**−0.19501**
Digestibility	**−0.35141**	**0.57593**
$\delta^{15}N$	**−0.19449**	−0.14069
N concentration	−0.10014	−0.05343
$\delta^{13}C$	**−0.44248**	**−0.20857**
C concentration	−0.00764	0.08596
Gliricidia		
Condensed tannin	**0.39929**	**−0.79806**
Digestibility	**−0.44777**	**0.65689**
$\delta^{15}N$	−0.06135	−0.11549
N concentration	0.20839	0.07053
$\delta^{13}C$	**−0.53805**	−0.23416
C concentration	**−0.41471**	−0.03098
Mimosa		
Condensed tannin	**0.39579**	**−0.72503**
Digestibility	**−0.40039**	**0.72361**
$\delta^{15}N$	**−0.41239**	**−0.27835**
N concentration	**−0.51303**	−0.24473
$\delta^{13}C$	**−0.52354**	**−0.27225**
C concentration	**0.40852**	**0.32092**

Table 2. Correlations between rainfall, potential evapotranspiration, rain deficit, and gliricidia and mimosa leaf nutrients. Values in bold are significant ($P \leq 0.05$).

also reemphasizes the need to assay bioreactive CT rather than simple total CT[40], since a given CT content on gliricidia would decrease IVDOM more than if the same content in mimosa.

Although there was an overall strong correlation between CT and N content (Table 1), the difference between species indicates that this difference is likely due to the difference between the species for both CT and N contents and, thus, a species effect rather than a CT effect. On the other hand, while the N content of the gliricidia was either maintained or decreased (depending on the year) at the start of the dry season, that of the mimosa increased by more than 50% in both years. This coincides with a decrease in CT and an increase in overall digestibility, both of which indicate that this is a valuable source of protein for cattle and small ruminants during the dry season.

One possible reason for this discrepancy between legume species is Mimosa's characteristic leaf loss at the beginning of the dry season[8]. This might have led to N redistribution from discarded leaves to the attached new ones, which could affect the sampling conducted exclusively on attached leaves.

This difference between legume species has yet to be observed in studies evaluating animal performance in the same experimental field[10]. We hypothesize that the animal performance of gliricidia is superior to that of mimosa. However, the former is reportedly among the least palatable arboreal forage legumes when fed to cattle or small ruminants alongside other legumes, perhaps because of its CT, although these papers did not include mimosa with its higher CT content[41,42]. We likewise hypothesize that the Gliricidia silvopasture system will achieve greater animal performance than the singlegrass monoculture. This is likely due to the reduction in signalgrass herbage accumulation under mimosa, likely because of competition for water and light[43] between mimosa and signalgrass, which needs to be considered when establishing such a silvopastoral system.

A possible approach, which has yet to be studied in our system, would include increasing interrow spacing for mimosa to reduce its effect on signalgrass or rotating harvests in rows to allow cattle to browse the regrowth leaves while reducing competition. However, this would reduce the economic potential of Mimosa wood products[11].

Other results of interest include δ^{13}C, whose similarity indicates that although both species have similar behaviors, overall, mimosa is likely to be slightly more water efficient than gliricidia due to its usually lower enrichment[19,20,44], although it is still much less efficient than C_4 grasses, as expected[12].

At the same time, while the δ^{15}N of gliricidia was relatively stable throughout both years (even if more variable in the second year), the δ15 N of mimosa was usually more depleted, particularly during the wetter season, which may indicate a higher biological atmospheric N_2 fixation rate since it indicates a higher proportion of atmospheric nitrogen with its lower15N proportion in plant tissue than observed for gliricidia..

Materials and methods

The study was conducted at the Experimental Station of Itambé (7°23′S and 35° 10′W and 190 m above sea), Agronomic Institute of Pernambuco-IPA, in which the predominant soil class is dystrophic Ultisol according to the Brazilian Soil Classification System[45], approximately corresponding to the Ferric Luvisolon World Reference Database[46]. The average annual rainfall is 1200 mm, of which *ca.* 75 from March to August and the remaining from September to February although subject to high year to year variability, and the annual average temperature is 25 ℃ ranging from 23 to 26 ℃ through the year. The relative annual average air humidity is 80%, and the local climate is defined as an As warm-humid rainy tropical climate with a dry summer. The monthly rainfall during the experimental period and the thirty-year average potential evapotranspiration in the region[47] are shown in Fig. 3.

Treatments, experimental design, establishment, and management

The treatments consisted of two silvopasture systems: 1. Signalgrass (*Urochloa decumbens* Stapf) + mimosa [*Mimosa caesalpiniifolia* Benth]; 2. Signalgrass (*Urochloa decumbens* Stapf) + *Gliricidia sepium* (Jacq.) Kunth ex. Walp.], in 1 ha experimental units, in a randomized complete block design, with three blocks to exclude soil differences. Although more details can be found in[7], we include some information here.

Neither legume species has recognized cultivars, and seeds were obtained from trees from the experimental station. Cultivar Basilisk signalgrass seeds were obtained from local commerce. The experiment followed institutional guidelines, and since there were no seed collection from the wild, and the species are not under environmental or biodiversity protection, there is no Brazilian legislation requiring permission to conduct the experiment.

In July 2011, tree legume seedlings were planted in 14 double rows in 1-ha paddocks for a population of 2500 trees ha^{-1}. Signalgrass was established in one of the blocks in 1969, while the same signalgrass cultivar was established along with the tree legumes in the other two blocks. Seeds were planted 5 cm deep, in rows spaced 1.0 × 0.5 m, using 10 kg of commercial seeds ha^{-1} with 40% pure live seeds. Pastures were fully established by the end of the 2011 rainy season.

The legume seeds were planted in a greenhouse, and both species were inoculated, each with its own specific rhizobium strains[48] supplied by the soil Microbiology Laboratory at the Federal Rural University of Pernambuco. In July 2011, all paddocks were fertilized with 44 kg P ha-1 (as ordinary superphosphate) and 100 kg K ha-1 (as potassium chloride) throughout the entire area. Legume plants were transplanted to the field in June 2011 at a height of approximately 30 cm and planted in 20 cm deep furrows.

From 2011 until 2018, each paddock contained at least two crossbred Holstein x Zebu (193 ± 70 kg) steers to graze under a continuous, variable stocking rate. The stocking rate was calculated based on the metabolic weight of the tester animals and "put and take" animals. The experiment followed the relevant guidelines of both Universidade Federal Rural de Pernambuco and Instituto Agronômico de Pernambuco, for animal and plant experiments.

Nutritive value and isotopic composition determination

Approximately 300 g of leaves from the same three legume trees from each experimental plot were collected monthly from January to October in 2017 and 2018, totaling 360 samples. CT was determined on the individual samples, and the remaining variables were bulked for each experimental plot, for a total of 120 samples. The samples were analyzed for total N, $\boldsymbol{\delta}^{13}$C, and $\boldsymbol{\delta}^{15}$N at the University of Florida Forage Laboratory—North Florida

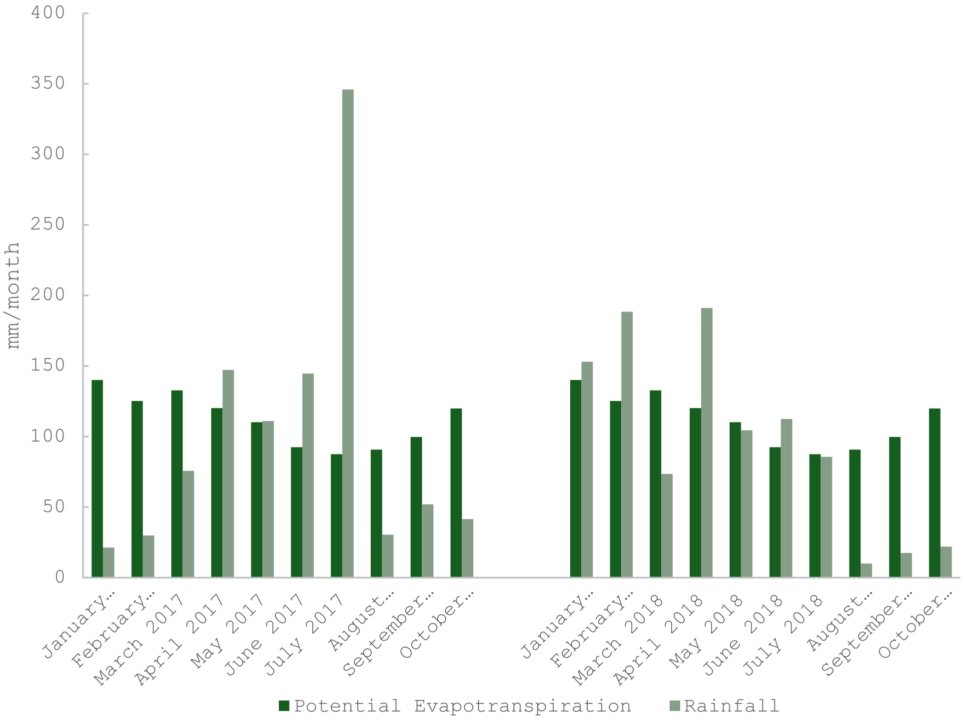

Figure 3. Rainfall during the experimental period in Itambe-PE, Brazil, 40- and 30 year average potential evapotranspiration in the microregion[47].

Research and Education Center, Marianna, Florida. The samples were dried in a circulation oven at 55 ℃ to constant weight and ground to pass through a 1 mm screen using a Wiley Mill (Model 4, Thomas-Wiley Laboratory Mill, Thomas Scientific, Swedesboro, NJ, USA). Subsamples were taken and ball-milled in a Mixer Mill MM 400 (Retsch, Newton, PA, USA) at 25 Hz for 9 min. Ball-milled samples were analyzed for total C and N contents and $\delta^{13}C$ and $\delta^{15}N$ using a CHNS analyzer and the Dumas dry combustion method (Vario Micro Cube; Elementar, Hanau, Germany) coupled to an isotope ratio mass spectrometer (IsoPrime 100, IsoPrime, Manchester, UK).

Samples ground to 1 mm were also used to determine in vitro digestible organic matter (OM). digestibility (IVDOM) as described by Moore and Mott (1974)[49] and determined according to the following equation:

$$Digestibility(\%) = \left(Substrate\ OM\ incubated - \left(\frac{Substrate\ OM\ remains}{Blank\ OM\ remains}\right)\right) \times 100$$

Condensed tannin determination

Sampling was conducted as described earlier and CT determined[50]. Briefly, we used 10 mg aliquots in duplicate to extract soluble CT using a mixture of 2.5 mL of 70% aqueous acetone with 0.1% ascorbic acid and 2.5 mL of diethyl ether. After removing the solvents by evaporation, the extract was adjusted to 5 mL with distilled water, centrifuged, and separated from the solid residue. Then, 1.8 mL of 5% butanol-HCL was added to 0.3 mL aliquots of the extract and placed in a water bath at 95 ℃ for 70 min. In both cases, the absorbance was read on a 550 nm spectrophotometer (Fento 600-Plus), and the result was converted to percent CT in legumes, based on a standard curve determined using the butanol-HCL method, using purified CT from each legume species[51]. The total CT concentration included soluble fractions and CT bound to the residue[52].

Statistical analyses

The data were subjected to statistical analyses via SAS on demand for academics mixed procedure[53]. Initially, plants were considered fixed effects to evaluate CT interplant variability. Subsequently, since there were no significant differences between plants, the average CT content of the three plants per paddock was utilized. The fixed effects included legume species and evaluation date, considered repeated measures, while block was considered a random effect. Linear correlation coefficients were calculated between CT concentration and IVDOM, C and N content, and $\delta^{13}C$ and $\delta^{15}N$, as well as between CT concentration and rainfall and potential evapotranspiration[47]. Statistical effects were considered significant when $P \leq 0.05$.

Conclusions

The forage CT content strongly predicts digestibility in the rumen, but the strong interspecific difference does not allow it to be used as an indicator by itself. On the other hand, the absence of differences between plants indicates that there is likely no need to follow individual plants over time and forage plant ontogeny, simplifying data collection.

Both arboreal legumes reduced the CT content and increased the digestibility of the arboreal legume at the beginning of the dry season, when the nutritive value of the C4 forage species was the lowest, indicating that these legumes may have important functions as protein sources for cattle. This could be particularly impactful for mimosa, considering the increased leaf N concentration at this time of year. Differences in the bioreactivity of CT between these arboreal legumes merit further research as possible explanations for differences in IVDOM and palatability for ruminants.

Data availability

Data will be provided by J. C. B. Dubeux Junior or M. A. Lira Junior upon request.

Received: 15 March 2024; Accepted: 25 July 2024

References

1. Dubeux Junior, J. C. B. *et al.* Sustainable intensification of lifestock production on pastures. *Archivos Latinoamericanos Prod. Anim.* **25**, 97–111 (2017).
2. Sollenberger, L. E. & Dubeux Junior, J. C. B. Warm-climate, legume-grass forage mixtures versus grass-only swards: An ecosystem services comparison. *Rev. Bras. Zootec.* https://doi.org/10.37496/RBZ5120210198 (2022).
3. Williams, A. R., Fryganas, C., Ramsay, A., Mueller-Harvey, I. & Thamsborg, S. M. Direct anthelmintic effects of condensed tannins from diverse plant sources against Ascaris suum. *PLoS ONE* https://doi.org/10.1371/journal.pone.0097053 (2014).
4. Min, B. R., Barry, T. N., Attwood, G. T. & McNabb, W. C. The effect of condensed tannins on the nutrition and health of ruminants fed fresh temperate forages: A review. *Anim. Feed Sci. Technol.* **106**, 3–19. https://doi.org/10.1016/S0377-8401(03)00041-5 (2003).
5. Kronberg, S. L., Provenza, F. D., van Vliet, S. & Young, S. N. Review: Closing nutrient cycles for animal production—Current and future agroecological and socio-economic issues. *Animal* https://doi.org/10.1016/j.animal.2021.100285 (2021).
6. Dubeux Junior, J. C. B. *et al.* Tree legumes: An underexploited resource in warm-climate silvopastures. *R. Bras. Zootec.* **46**, 689–703. https://doi.org/10.1590/S1806-92902017000800010 (2017).
7. Gomes da Silva, I. A. *et al.* Tree legume enhances livestock performance in a silvopasture system. *Agronomy J.* **113**, 358–369. https://doi.org/10.1002/agj2.20491 (2021).
8. Herrera, A. M. *et al.* Potential of *Gliricidia sepium* (jacq.) Kunth ex Walp. and Mimosa caesalpiniifolia Benth silvopastoral systems intercropped with signalgrass. *Agroforestry Systems* https://doi.org/10.1007/s10457-021-00625-7 (2021).
9. Muir, J. P., Pitman, W. D. & Foster, J. L. Sustainable, low-input, warm-season, grass-legume grassland mixtures: Mission (nearly) impossible?. *Grass Forage Sci.* **66**, 301–315. https://doi.org/10.1111/j.1365-2494.2011.00806.x (2011).
10. dos Santos, A. M. G. *et al.* Animal performance in grass monoculture or silvopastures using tree legumes. *Agroforest. Syst.* **94**, 615–626. https://doi.org/10.1007/s10457-019-00431-2 (2020).
11. Apolinário, V. X. O. *et al.* Tree legumes provide marketable wood and add nitrogen in warm-climate silvopasture systems. *Agronomy J.* **107**, 1915–1921. https://doi.org/10.2134/agronj14.0624 (2015).
12. Costa, S. B. D. M. *et al.* Proportion and digestibility of tree legumes in diets of grazing cattle in a tropical silvopastoral system. *Livestock Sci.* https://doi.org/10.1016/j.livsci.2021.104689 (2021).
13. Lima, I. M. A., Araújo, M. C. & Barbosa, R. S. Avaliação das propriedades físicas do solo em sistemas silvipastoris, região centro-norte, estado do Piauí. *Agropecuária Científica no Semi-Árido* **9** (2013).
14. Lira Junior, M. A., Fracetto, F. J. C., Ferreira, J. S., Silva, M. B. & Fracetto, G. G. M. Legume-based silvopastoral systems drive C and N soil stocks in a subhumid tropical environment. *Catena* **189**, 104508. https://doi.org/10.1016/j.catena.2020.104508 (2020).
15. Lira Junior, M. A., Fracetto, F. J. C., Ferreira, J. D. S., Silva, M. B. & Fracetto, G. G. M. Legume silvopastoral systems enhance soil organic matter quality in a subhumid tropical environment. *Soil Sci. Soc. Am. J.* **84**, 1209–1218. https://doi.org/10.1002/saj2.20106 (2020).
16. Schultze-Kraft, R. *et al.* Tropical forage legumes for environmental benefits: An overview. *Trop. Grassl.Forrajes Trop.* **6**, 1–14. https://doi.org/10.1713/TGFT(6)1-14 (2018).
17. Dablin, L., Lewis, S. L., Milliken, W., Monro, A. & Lee, M. A. Browse from three tree legumes increases forage production for cattle in a silvopastoral system in the southwest Amazon. *Animals* https://doi.org/10.3390/ani11123585 (2021).
18. Rubanza, C. D. K., Shem, M. N., Otsyina, R., Ichinohe, T. & Fujihara, T. Nutritive evaluation of some browse tree Legume Foliages native to semi-arid areas in Western Tanzania. *Asian Australas J. Anim. Sci.* **16**, 1429–1437. https://doi.org/10.5713/ajas.2003.1429 (2003).
19. Fischer, P. M. & du Toit, B. Use of δ13C as water stress indicator and potential silvicultural decision support tool in Pinus radiata stand management in South Africa. *iFor. Biogeosci. For.* **12**, 51–60. https://doi.org/10.3832/ifor2628-011 (2019).
20. Farquhar, G. D., Hubick, K. T., Condon, A. G. & Richards, R. A. *Stable Isotopes in Ecological Research* 21–40 (Springer, 1989).
21. Gemeda, B. S. & Hassen, A. Effect of tannin and species variation on in vitro digestibility, gas, and methane production of tropical browse plants Asian-Australas. *J Anim Sci* **28**(188), 199. https://doi.org/10.5713/ajas.14.0325 (2015).
22. Pereira, T. P. *et al.* Characterization and biological activity of condensed tannins from tropical forage legumes. *Pesq. Agropec. Bras.* **53**, 1070–1077. https://doi.org/10.1590/s0100-204x2018000900011 (2018).
23. Muir, J. P. *et al.* Value of endemic legumes for livestock production on Caatinga rangelands. *Braz. J. Agric. Sci.* **14**, 1–12. https://doi.org/10.5039/agraria.v14i2a5648 (2019).
24. García-González, R., González, J. S. & López, S. Decrease of ruminal methane production in Rusitec fermenters through the addition of plant material from rhubarb (Rheum spp.) and alder buckthorn (*Frangula alnus*). *J. Dairy Sci.* **93**, 3755–3763. https://doi.org/10.3168/jds.2010-3107 (2010).
25. García-González, R., López, S., Fernández, M., Bodas, R. & González, J. S. Screening the activity of plants and spices for decreasing ruminal methane production in vitro. *Anim. Feed Sci. Technol.* **147**, 36–52. https://doi.org/10.1016/j.anifeedsci.2007.09.008 (2008).
26. McAllister, T. A. *et al.* Characterization of condensed tannins purified from legume forages: Chromophore production, protein precipitation, and inhibitory effects on cellulose digestion. *J. Chem. Ecol.* **31**, 2049–2068. https://doi.org/10.1007/s10886-005-6077-4 (2005).
27. Abdulrazak, S. A., Fujihara, T., Ondiek, J. K. & Ørskov, E. R. Nutritive evaluation of some Acacia tree leaves from Kenya. *Anim. Feed Sci. Technol.* **85**, 89–98. https://doi.org/10.1016/s0377-8401(00)00133-4 (2000).

28. Animut, G. *et al.* Methane emission by goats consuming diets with different levels of condensed tannins from lespedeza. *Anim. Feed Sci. Technol.* **144**, 212–227. https://doi.org/10.1016/j.anifeedsci.2007.10.014 (2008).
29. Silva, M. J. D. S. *et al.* Influence of the period of year on the chemical composition and digestibility of pasture and fodder selected by goats in caatinga. *Rev. Bras. Saúde Prod. Anim.* **18**, 402–416. https://doi.org/10.1590/s1519-99402017000300001 (2017).
30. Azevêdo, T. K. B. D., Paes, J. B., Calegari, L. & Santana, G. M. Teor de taninos condensados presente na casca de Jurema-Preta (*Mimosa tenuiflora*) em função das fenofases. *Florest. Ambient.* https://doi.org/10.1590/2179-8087.026613 (2017).
31. Muir, J. P. *et al.* in *45th Annual Meeting Caribbean Food Crops Society.* 46–50 (Caribbean Food Crops Society).
32. Vitti, D. M. S. S. *et al.* Do all tannins have similar nutritional effects? A comparison of three Brazilian fodder legumes. *Anim. Feed Sci. Technol.* **119**, 345–361. https://doi.org/10.1016/j.anifeedsci.2004.06.004 (2005).
33. Oliveira, O. F. D. *et al.* Condensed tannins bioactivity and nutritional value of *Bauhinia cheilantha* (Bong) Steud. under sheep grazing and different forage allowances. *Biochem. Syst. Ecol.* https://doi.org/10.1016/j.bse.2021.104359 (2022).
34. Kapp-Bitter, A. N., Dickhoefer, U., Kreuzer, M. & Leiber, F. Mature herbs as supplements to ruminant diets: effects on in vitro ruminal fermentation and ammonia production. *Anim. Prod. Sci.* **61**, 470. https://doi.org/10.1071/an20323 (2021).
35. Morris, P. *et al.* Responses of Lotus corniculatus to environmental change 3: The sensitivity of phenolic accumulation to growth temperature and light intensity and effects on tissue digestibility. *Planta* https://doi.org/10.1007/s00425-020-03524-w (2021).
36. Santos, M. E. R., da Fonseca, D. M., Balbino, E. M., da Silva, S. P. & Monnerat, J. P. I. S. Nutritive value of tillers and morphological components on deferred and nitrogen fertilized pastures of Brachiaria decumbens cv. *Basilisk. R. Bras. Zootec.* **39**, 1919–1927. https://doi.org/10.1590/S1516-35982010000900009 (2010).
37. Teixeira, F. A. *et al.* Annual production and quality of Brachiaria decumbens pastures deferred and strategies nitrogen fertilization. *Acta Scientiarum – Anim. Sci.* **33**, 241–248. https://doi.org/10.4025/actascianimsci.v33i3.10194 (2011).
38. Chiquette, J., Cheng, K. J., Costerton, J. W. & Milligan, L. P. EFFECT of tannins on the digestibility of two isosynthetic strains of birdsfoot trefoil (Lotus corniculatus L.) using in \ttro and in sacco techniques. *Can. J. Anim. Sci.* **68**, 751–760 (1988).
39. Huang, X. D. *et al.* Molecular weight and protein binding affinity of Leucaena condensed tannins and their effects on in vitro fermentation parameters. *Anim. Feed Sci. Technol.* **159**, 81–87. https://doi.org/10.1016/j.anifeedsci.2010.05.008 (2010).
40. Muir, J. P. *et al.* in *4th International Legume Conference.* 167–169 (4th International Legume Conference).
41. Karda, I. W., Dryden, G. M. & Gutteridge, R. C. Oven-dried gliricidia leaf (*Gliricidia sepium*) is unpalatable to sheep and goats. *Anim. Prod. Aust.* **22**, 366 (1998).
42. Pérez, A. N., Ibrahim, M., Villanueva, C., Skarpe, C. & Guerin, H. Uso de la diversidad forrajera tropical en combinaciones pareadas de leñosas forrajeras como indicador de preferencia para su inclusión en el diseño de sistemas silvopastoriles en zonas secas. *Revista Corpoica - Ciencia y Tecnología Agropecuaria* **13**, 79–88 (2012).
43. Da Silva, I. A. G. *et al.* Tree canopy management affects dynamics of herbaceous vegetation and soil moisture in silvopasture systems using *Arboreal legumes*. *Agronomy* **11**, 1509. https://doi.org/10.3390/agronomy11081509 (2021).
44. Goldstein, G. *et al. Tropical Forest Plant Ecophysiology* 244–267 (Springer, 1996).
45. Solos, E. Sistema brasileiro de classificação de solos. *Centro Nacional de Pesquisa de Solos: Rio de Janeiro*, 353 (2013).
46. FAO. *The Soil*, <http://www.fao.org/docrep/u8480e/U8480E0b.htm> (2017).
47. Moura, G. B. A., Melo, J. S. P., Giongo, P. R., Medeiros, S. R. R. & Silva, A. P. N. in *XV Congresso Brasileiro de Agrometeorologia.* CD ROM (XV Congresso Brasileiro de Agrometeorologia).
48. Brasil, S. d. D. A.-M. d. A. P. e. A. in *Diário Oficial da União - Seção 1* Vol. 58, 25 de março de 2011 3–7 (Imprensa Nacional, Brasília, 2011).
49. Moore, J. E. & Mott, G. O. Recovery of residual organic matter from in vitro digestion of forages. *J. Dairy Sci.* **57**, 1258–1259 (1974).
50. Hagerman, A. E. & Butler, L. G. Protein precipitation method for the quantitative determination of tannins. *J. Agric. Food Chem.* **26**, 809–812. https://doi.org/10.1021/jf60218a027 (1978).
51. Wolfe, R. M., Terrill, T. H. & Muir, J. P. Drying method and origin of standard affect condensed tannin (CT) concentrations in perennial herbaceous legumes using simplified butanol-HCl CT analysis. *J. Sci. Food Agric.* **88**, 1060–1067. https://doi.org/10.1002/jsfa.3188 (2008).
52. Mupangwa, J. F., Acamovic, T., Topps, J. H., Ngongoni, N. T. & Hamudikuwanda, H. Content of soluble and bound condensed tannins of three tropical herbaceous forage legumes. *Anim. Feed Sci. Technol.* **83**, 139–144 (2000).
53. SAS On Demand For Academics (SAS Institute, 2023).

Acknowledgements

The authors wish to acknowledge and deeply thank the research staff of the Itambé Experimental Station of the Pernambuco Agronomic Institute (IPA), without whom this research would not be possible. We are also thankful for the research funding and grants provided for several of the authors by the Coordination of Superior Level Staff Improvement—CAPES (fellowships and Finance Code 1), the National Council for Scientific and Technological Development – CNPq (both fellowships and research grants), and the Pernambuco Research Foundation – FACEPE (both fellowships and research grants). Grammarly and Curie were used for language review.

Author contributions

Conceptualization – IAGS, Data curation IAGS, Formal Analysis IAGS, MALJ, Funding acquisition JBCDJ, MVFS, ACLM, MVC, Investigation of IAGS, CGS, MRM, and VXOA, Methodology IAGS, JCBDJ, MVFS, VXAO, ACLM, MVC, Project administration JCBDJ, MVFS, VXOA, ACLM, MVC, Supervision JCBDJ, MVFS, ACLM, MVC, Visualization IAGS, MALJ, Writing – original draft – IAGS, Writing – review & editing – IAGS, JCBDJ, MVFS, ACLM, MVC, JPM, MALJ

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to M.A.L.J.