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Effect of Amazonian tree species on soil and pasture quality in silvopastoral systems

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ABSTRACT

With the expansion of livestock in the Amazon region, a high percentage of pasture areas are degraded and unproductive. Novel strategies are needed, including the use of native tree species, to simultaneously achieve economic and ecosystem benefits. This study aimed at assessing the effects of five multipurpose native tree species on soil fertility and forage quality of *Urochloa brizantha* pastures in the southern Amazon. Soil and forage samples were collected under the crown and adjacent to 25 isolated trees belonging to five species during a dry and a rainy season. The presence of native trees positively affected the level of potassium, calcium and manganese in the soil, as well as the mineral matter and crude protein of the forage, especially in the dry season, suggesting a protective effect against the seasonal drought. The tree species had variable effects on soil fertility and forage quality. Soil under *Apeiba tibourbou* had higher potassium levels, while the forage under *Handroanthus serratifolius* had higher protein and fiber content. Our results indicate that it is important to diversify silvopastoral systems in the Amazon through the use of native tree species, contributing to the design of novel silvopastoral strategies in the region. Common multipurpose tree species with widespread natural distribution could be used as a complementary aspect of pasture management to provide a protective effect against drought, contribute to enhanced nutrient cycling and even increase forage quality.

KEYWORDS: agroecosystems, soil conservation, animal nutrition, sustainable livestock, multipurpose native trees

Efeitos de espécies arbóreas amazônicas sobre o solo e qualidade da forragem em sistemas silvipastoris

RESUMO

Com a expansão da pecuária na região amazônica, um alto percentual de pastagem está degradada e improdutiva. São necessárias novas estratégias, incluindo o uso de espécies de árvores nativas, para obter simultaneamente benefícios econômicos e ecossistêmicos. Este estudo objetivou avaliar os efeitos de cinco espécies arbóreas nativas multifuncionais na fertilidade do solo e qualidade da forragem em pastagens de *Urochloa brizantha* na Amazônia Meridional. Para isso, amostras de solo e forragem foram coletadas sob a copa e áreas adjacentes de 25 árvores isoladas pertencentes a cinco espécies durante uma estação seca e uma chuvosa. A presença de árvores nativas afetou positivamente o nível de potássio, calcio e magnésio no solo, bem como aumentou a matéria mineral e proteína bruta da forragem, especialmente na estação seca, sugerindo um efeito protetivo contra a seca sazonal. As espécies arbóreas tiveram efeitos variáveis sobre a fertilidade do solo e qualidade da forragem. O solo sob *Apeiba tibourbou* apresentou aumento nos teores de potássio, enquanto a forragem sob *Handroanthus serratifolius* apresentou melhor qualidade no que se refere a proteínas e fibras. Nosso estudo indica a importância da diversificação dos sistemas silvipastoris na Amazônia por meio do uso de espécies arbóreas nativas, contribuindo para o desenho de estratégias silvipastoris inovadoras na região. Espécies arbóreas multifuncionais comuns de ampla distribuição natural podem ser utilizadas como um aspecto complementar do manejo de pastagens para fornecer um efeito protetivo contra a seca, aprimorar a ciclagem de nutrientes e aumentar a qualidade da forragem.

PALAVRAS-CHAVE: agroecossistemas, conservação do solo, nutrição animal, pecuária sustentável, espécies nativas multifuncionais

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INTRODUCTION

Agriculture-dominated landscapes cover approximately 50% of tropical biomes, with pastures being an ultimate cause of two thirds of deforested land in the neotropics (Lerner 2015). In Latin America, there is a strong link between deforestation and livestock expansion, either for establishing pastures or for producing grains for animal feed (FAO 2012). Livestock expansion throughout forested regions has brought short-term benefits, considering the sheer financial volume involved with this activity. However, livestock farming has disadvantages in the long term, especially associated with biodiversity loss, carbon emissions, and reduction or disruption of ecosystem services such as species habitat, conservation of soil and water resources, and carbon stock and sequestration (Barret *et al.* 2013). Since worldwide food demand is increasing and food production is directly linked with biodiversity and ecosystem services, it is of paramount importance to develop and consolidate novel agricultural systems that could increase productivity while mitigating climate change (IPCC 2019).

Silvopastoral systems are one of the possible solutions towards a more efficient production system, consisting of an intentional combination of various trees and livestock using different arrangements through time and space (Almeida *et al.* 2013). These systems produce extensive benefits that vary according to local traits and designs, generally including the establishment of biological corridors (Harvey *et al.* 2005; Vergne *et al.* 2016), and improvements to the biological, chemical and physical structure of the soil (Nair 2007; Pinho *et al.* 2012; Martinez *et al.* 2014;), forage quality (Bernardi *et al.* 2016), and thermal comfort of animals (West 2003; Carvalho *et al.* 2018).

Several studies on the effects of the presence of native trees in pastures, especially in the tropics, demonstrated benefits such as increased animal productivity, improved quality of forage plants and improved physical, chemical and biological parameters of the soil (Franke 1999; Delgado *et al.* 2014; Muroe and Isaac 2014; Santos *et al.* 2016; Camero-Rey and Diaz 2017; Ledesma *et al.* 2017; England *et al.* 2020; Alvarez *et al.* 2021). There is solid evidence that different tree species affect soil fertility in temperate environments by minimizing erosion and leaching while increasing nutrient inputs, as well as enhancing soil structure and biological activity (Binkley and Giarina 1998; Schroth and Sinclair 2003; Devendra 2014; Chará *et al.* 2019; Sarvade *et al.* 2019; Rozek *et al.* 2020).

These effects are related to the optimization of nutrient cycling and the establishment of a microenvironment that improves forage quality (Schroth and Sinclair 2003; Lambers *et al.* 2008; Sileshi *et al.* 2014; Bernardi *et al.* 2016; Araujo *et al.* 2020). In Brazil, the most widely recommended systems are based on the incorporation of exotic tree species such as eucalyptus (Eucalyptus spp.) and teak (*Tectona grandis* L.f.), mainly to increase financial profitability land use. However, in northern Mato Grosso state (Brazil), scattered native trees in pastures are used to provide shade and nutritional supplement (from fruits and leaves) for the herd, especially in the dry season (pers. obs. by the authors). These are usually the main reasons for farmers to keep trees in pastures (Harvey and Haber 1999; Lasco *et al.* 2016; Oliveira and Carvalhaes 2016; Olival *et al.* 2020).

As the action mechanisms of native Amazonan tree species on pastures are still little known, we assessed the forage quality and soil fertility in pasture under the influence of five native tree species during the rainy and dry season in southern Amazonia. Our hypothesis was that the presence of native trees on pastures positively influences soil fertility as well as forage quality and that these effects depend on the characteristics of the tree species and also on the pasture management.

MATERIAL AND METHODS

Study area

The study was carried out in two farms in the municipality of Nova Canaã do Norte (10°36’42.840”S, 55°2’35.880”W; 10°48’59.654”S, 55°41’54.350”W) and two farms in Nova Guarita (10°12’21.030”S, 55°14’49.369”W; 10°13’8.279”S, 55°23’18.122”W), in northern Mato Grosso state, Brazil, all within the watershed of the Teles Pires River, a major tributary of the Tapajós River in the Amazon basin. Local landscapes are characterized by large expanses of pasture interspersed with soy and cotton crops and native vegetation, mainly represented by open tropical forest fragments (IBGE 2012). Soil is dystrophic red-yellow podzolic (Mato Grosso 2000). The climate is tropical monsoon (type Am by the Köppen system), with total annual precipitation around 3000 mm, mainly from November to March, and average annual temperature above 26 °C (Alvarez *et al.* 2013).

The areas are located in the “arc of deforestation” of the Amazon region, where large areas of forest have been transformed into pastures over the last 30 years. In many pastures, remnant trees persist or are allowed to grow, especially in family farms, which account for more than 80% of rural properties in northern Mato Grosso (IBGE 2019). The four rural properties sampled in the study participate in forest-restoration and agroforestry projects since 2010 in partnership with local organizations.

Species selection

For the selection of trees to test the effect on soil fertility and nutritional properties of the forage, we mapped all trees scattered across 237.9 ha in pastures of 39 family farms across the study area. Based on this survey, three workshops were held with the farm owners to decide, based on their perception, which of the naturally occurring tree species on their lands had the highest potential to bring benefits for their productive systems. The main benefits identified by the farmers were the provision of thermal comfort to livestock through shade and the improvement of soil conditions.

We selected five tree species considered by the farmers as having the highest potential to bring benefits: *Apeiba tibourbou* Aubl. (Malvaceae), *Handroanthus serratifolius* (Vahl.) S. Grose (Bignoniaceae), *Maclura tinctoria* (L.) D.Don ex Steud (Moraceae), *Platymiscium floribundum* Vogel (Fabaceae) and *Samanea tubulosa* (Benth.) Barneby & J.W.Grimes (Fabaceae). These are multipurpose species with a widespread natural occurrence in Brazil and adjacent countries, with spontaneous colonization and persistence in local pastures. All provide high quality timber, *H. serratifolius* being currently the most valued Brazilian timber species (Brancalion *et al.* 2018). *Platymiscium floribundum* and *S. tubulosa* are N-fixing species (de Souza 2010). Leaves of *A. tibourbou* and *M. tinctoria*, and fruits of *S. tubulosa* provide alternative forage for cattle, as indicated by the farmers and by Carvalho (2007). See Supplementary Material (Table S1) for further information on functional and silvicultural characteristics of the species.

Sampling design

For each selected tree species, we identified one pasture containing five isolated individuals in the same paddock. Trees had to be mature, older than 10 years and isolated from other trees by at least 50 m, in order to avoid confusing the effects of focal trees with those of neighboring trees. Out of the 39 mapped farms, only four met all these criteria. Three contained sets of one species each, and one contained sets of two species (*H. serratifolius* and *S. tubulosa*). The pastures in all four farms were of palisade grass (*Urochloa brizantha* (A. Rich) R.D.Webster), the most common forage grass used in the southern Amazon.

Pastures containing *H. serratifolius* and *S. tubulosa* covered 3.41 ha and had 4.7% of total tree cover, including trees of other species, and the highest cattle-stocking rate (6.3 AU ha^{-1}), with 14 paddocks for rotational grazing and grass-fed supplementation during the dry season. The pasture containing *A. tibourbou* covered 5.29 ha with 13.1% tree cover. This was the only pasture where cattle received no feed supplementation in the dry season, and had the lowest cattle-stocking rate (0.6 AU ha^{-1}) and grazing divided in 11 paddocks. The pasture containing *M. tinctoria* covered 8.17 ha with 9.8% tree cover, a cattle-stocking rate of 1.32 AU ha^{-1}, 23 paddocks and grass supplementation in the dry season. The pasture containing *P. floribundum* covered 1.93 ha, with the highest proportion of tree cover (31.6%), cattle-stocking rate of 0.97 AU ha^{-1}, and five paddocks. Resting time of the pastures varied around 30 days, except for the A. tibourbou pasture, which rested for 45 days in the rainy season, and 120 days in the dry season.

For each tree, we measured diameter at breast height (DBH) and crown area by measuring eight crown-radius lengths (distance from trunk to crown projection limits using measuring tapes) in order to form eight triangles. The crown area was then calculated from the sum of the triangle areas (Gomes *et al.* 2003) (Supplementary Material, Table S2). We collected forage and soil samples in the crown area of each tree (considered to be directly influenced by the tree presence) and in areas 5 m outside the crown area, considered not to be influenced by the trees, asthe benefits of trees on soil decrease with increasing distance from the tree (Oliveira et al. 2012). Thus, although there were other trees in the pastures, each focal tree was assumed to be isolated from the effect of other trees of the same or other species. Forage and soil samples were collected during one dry (August 2017) and one rainy season (January 2018). In each season, we randomly collected four forage and five soil samples within the crown area of each focal tree, and four and five samples, respectively, outside the crown area. For each forage sample, we placed a hollow square (1 m^2) and collected the forage mass (cut at 2/3 of blade height) inside the square area. The soil samples were collected at 0-10 cm depth. The samples for each tree and season were pooled to form one composite sample of forage and one of soil under the canopy (within the crown area), and one sample each off the canopy (outside the crown area). Therefore, we had five replicates per species and season for each treatment (presence or absence of the tree).

The fresh mass of the forage samples was weighed in the field and then transported to the laboratory, where they were oven dried at 65°C for 72 h to obtain the dry mass. The percentage of mineral materials (MM), ethereal extract (EE) and crude protein (CP) were quantified according to AOAC (2012). Neutral detergent fiber (NDF), acid detergent fiber (ADF) and lignin content (LC) were determined following Van Soest *et al.* (1991). The soil samples were analyzed for organic matter (OM), calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P) following Embrapa (2009). Forage samples were analyzed at the Laboratory of Animal Nutrition of Universidade Federal de São Carlos, and soil samples were analyzed at the Laboratory of Soil and Leaf Analysis of Universidade so Estado de Mato Grosso.

All farms showed some sign of pasture degradation, mainly due to management problems. We found a high incidence of invasive plants and sudden-death syndrome, as well as signs of poor quality of forage plants, especially in the dry season. Forage yield was not the focus of this study, but, for the sake of charcterization, we observed that average forage availability varied from around 300 kg dry mass ha^{-1} off the canopy of *M. tinctoria* in the dry season to almost 5,000 kg ha^{-1} off the canopy of *H. serratifolius* in the rainy season. There was a two to three-fold reduction in pasture dry mass in the dry season, when yield varied from 300 to almost 2,000 kg ha^{-1}. In the rainy season it varied from 2,000 to almost 5,000 kg ha^{-1}. Average yield difference between forage grown under and off canopy varied from less than 20 kg in the dry season *A. tibourbou* pasture to almost 1,000 kg ha^{-1} in the *M. tinctoria* pasture.

Data analysis

As forage quality proxies, we used the proportion of MM, CP, NDF, ADF and LC, and as proxies for soil fertility we used P, K, Ca, Mg and OM. The adherence of the variables to different theoretical distribution functions was tested through skewness and kustosis comparisons using graphical analysis of the package 'fitdistrplus' (Delignette-Muller and Dutang 2015), in the R environment (R Core Team 2019). Then we used the information-theoretic approach for model selection (Burnhan and Anderson 2002) by fitting generalized linear mixed models (GLMM) to the data of each of the above dependent variables and using tree presence/absence, season and species as categorical fixed effects. To account for repeated measures of individual trees, we fitted random intercept models, with varying intercept among individuals. The beta distribution family with a *logit* link was used to fit forage quality models, while the gamma family with a *log* link was used to fit soil fertility models. The models were fitted with the aid of 'glmmTMB' and 'lme4' packages (Bates *et al.* 2015; Brooks *et al.* 2017). Summary statistics such as the coefficient of determination (R^2) and intra-class correlation coefficients (ICC) were computed according to Nakagawa *et al.* (2017). Finally, Wald Type II chi-square tests on the fixed effects and Tukey *post hoc* tests were performed for every selected model (Fox and Weisberg 2019). Confidence intervals for model estimates were derived from Wald approximation.

RESULTS

The best-fitting GLMM models for soil fertility included a significant effect of tree presence for all variables (except P) as well as variation between seasons and among species (Supplementary Material, Table S3). There was a general tendency of decrease in soil fertility in the dry season (Figure 1). The selected models explained between 65% (P) and 90% (K) of the observed variance in soil fertility, as indicated by the conditional coefficient of determination ($R^2_{GLMM(c)}$) (Table 1). The presence of trees accounted for 10 to 28% of observed variation, as indicated by the adjusted ICC values (Table 1).

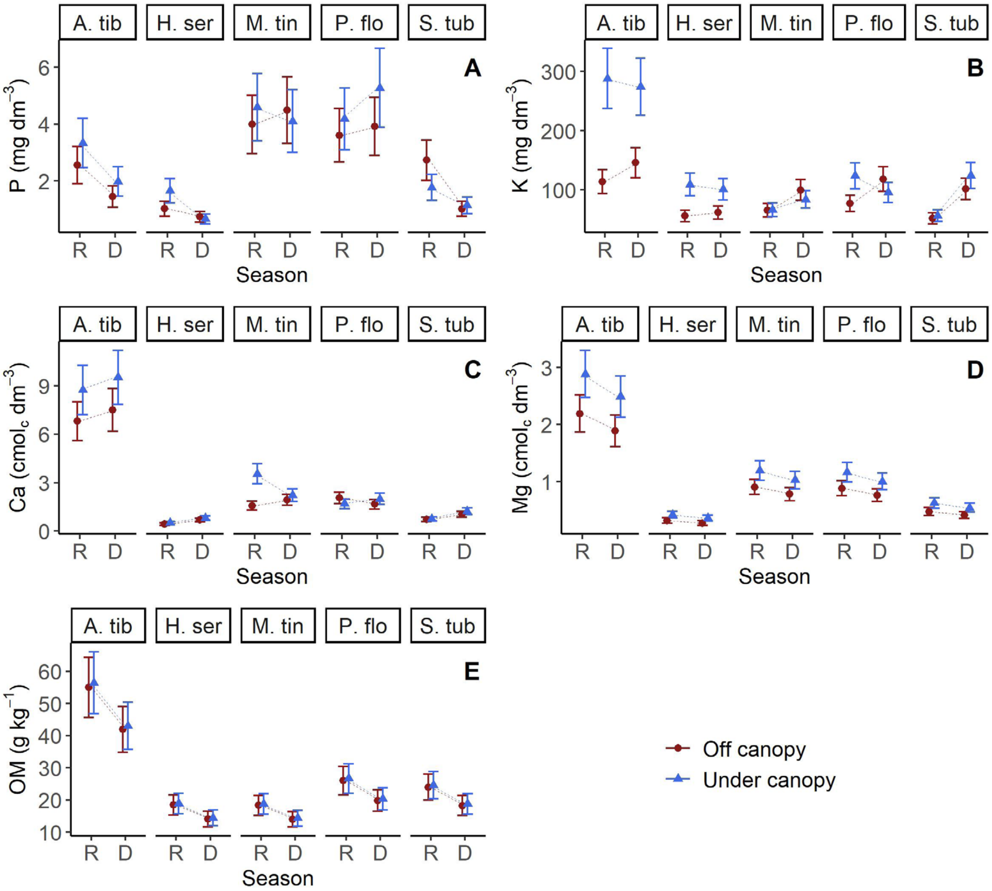

Figure 1. Estimated marginal means and standard errors of models selected to explain the variance in parameters of soil inside and outside the crown area of isolated trees of five native species in four pastures in the dry and rainy season in northwestern Mato Grosso State, Brazil. A – phosphorus (P); B – potassium (K); C – calcium (Ca); D – magnesium (Mg); E – organic matter (OM). A. tib = *Apeiba tibourbou*; H. ser = *Handroanthus serratifolius*; M. tin = *Maclura tinctoria*; P. flo = *Platymiscium floribundum*; S. tub = *Samanea tubulosa*. Season: R = rainy; D = dry. This figure is in color in the electronic version.

Incidence ratios of tree presence from our soil models indicated significantly higher levels of K [153% (95% CI: 84 – 249%)], Ca [28% (10 – 82%)] and Mg [32% (11 – 55%)] under canopy than off canopy, when keeping all other variables constant (Supplementary Material, Figure S1). K content was significantly higher in both seasons under *A. tibourbou* (rainy: *z ratio* = -5.672, $p < 0.001$; dry: *z ratio* = -3.849, $p = 0.0001$) and (almost twice as high under the trees), *H. serratifolius* (rainy: *z ratio* = -4.024, $p = 0.0001$; dry: *z ratio* = -2.972, $p = 0.0030$), and *P. floribundum* in the rainy season (*z ratio* = -2.892, $p = 0.0038$) (Figure 1b).

The best-fitting models for forage quality (except for LC) included the interaction effects of tree presence, season and species (Table 1; Supplementary Material, Table S4). Contrary to the soil fertily models, there was no significant influence of random effects of individual trees on forage-quality attributes (Supplementary Material, Figure S1b and S2b). The best-fitting LC model included seasonality and species (a proxy for sampling sites) (Figure 2e), but not tree presence (Supplementary Material, Table S4).

As expected, MM and CP content in the forage decreased in the dry season in all cases, while fiber content increased in most cases (Figure 2). Tree presence tended to increase MM and CP in forage, with positive effects of varying magnitude in all species (Figure 2). MM was significantly higher under *A. tibourbou* in the dry season (*t ratio* = -4.787, $p < 0.0001$), *M. tinctoria* in both seasons (dry: *t ratio* = -2.335, $p = 0.0221$; rainy: *t ratio* = -4.969, $p < 0.0001$), and *P. floribundum* in the rainy season (*t ratio* = -2.347, $p = 0.0215$) (Figure 2a). CP was significantly higher under *H. serratifolius* in both the dry (*t ratio* = -3579, $p = 0.0006$) and rainy season (*t ratio* = -2.593, $p = 0.0114$), and *S. tubulosa* in the rainy season (*t ratio* = -2.060, $p = 0.0428$).

Tree presence did not significantly affect NDF content in forage, but did affect ADF (*chi-squared* = 13.219, $p = 0.0002$). Forage under *H serratifolius* had significantly lower ADF content then off the canopy in the dry season (*t ratio* = 2.437,

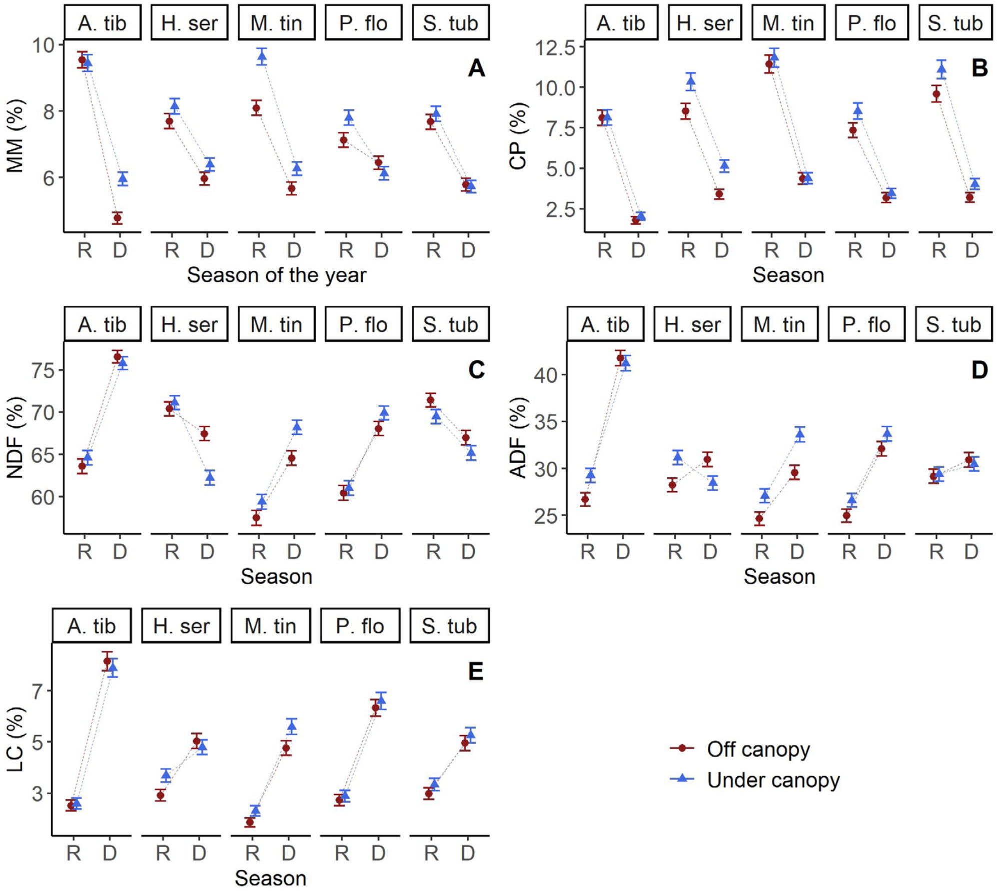

Figure 2. Estimated marginal means and standard errors of models selected to explain the variance in nutritional properties of palisade grass (*Urochloa brizantha*) inside and outside the crown cover of isolated trees of five native species in four pastures in the dry and rainy season in northwestern Mato Grosso State, Brazil. A – mineral matter (MM); B –crude protein (CP); C – neutral detergent fiber (NDF); D – acid detergent fiber (ADF); E – lignin content (LC). A. tib = *Apeiba tibourbou*; H. ser = *Handroanthus serratifolius*; M. tin = *Maclura tinctoria*; P. flo = *Platymiscium floribundum*; S. tub = *Samanea tubulosa*. Season: R = rainy; D = dry. This figure is in color in the electronic version.

Table 1. Summary statistics of selected GLMM models for additive (+) or interactive (*) effects of tree presence, season and species on soil and forage attributes in northern Mato Grosso state, Brazil. GLMM adapted coefficient of determination (R^2) of marginal (*m*) and conditional (*c*) terms and adjusted intra-class correlation (ICC_{adj}) are shown. Model calculation for NDF and lignin was not possible due to some variance components being equal to zero.

Selected models	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$	ICC_{adj}
Soil			
Phosphorus ~ season*species	0.56	0.649	0.202
Potassium ~ tree*season*species	0.654	0.751	0.282
Calcium ~ tree*season*species	0.87	0.901	0.239
Magnesium ~ tree+season+species	0.703	0.733	0.101
Organic matter ~ tree+season+species	0.564	0.685	0.277
Forage			
Mineral matter ~ tree*season*species	0.925	0.91	0.168
Crude protein ~ tree*season*species	0.951	0.948	0.057
NDF ~ tree*season*species	–	–	–
ADF ~ tree*season*species	0.962	0.954	0.17
Lignin ~ season*species	–	–	–

p= 0.0171) and higher in the rainy season (*t ratio* = -2.462, *p*= 0.0061). Significantly higher ADF was also observed under *A. tibourbou* in the rainy season (t ratio = -2.541, p = 0.0130) and *M. tinctoria* in both seasons (dry: t ratio = -3.839, p = 0.0002; rainy = -2.462, p = 0.0160, Figure 2d).

DISCUSSION

Our results showed that native Amazonian tree species can have neutral or positive eefects on forage quality and soil fertility in agricultural landscapes that interact with seasonal and site-specific effects. Quantitative and qualitative responses of forage depend on the architecture of forage plants, the density and shading of tree canopies, and environmental factors such as soil fertility and moisture, (Jose *et al.* 2019). Several studies have demonstrated the benefits of natural or artificial shade for forage yield and quality (Andrade *et al.* 2004; Sousa *et al.* 2010; Pang *et al.* 2019a; Pang *et al.* 2019b; Pezzopane *et al.* 2019). Some forage species, including grasses and legumes commonly used in pastures across the Amazon basin, are shade tolerant, usually adjusting to decreased sunlight influx by devoting more primary production to leaf area than root matter (Andrade *et al.* 2004).

Our results suggest that the presence of native tree species could potentially mitigate forage quality decline in the dry season, as evidenced by the significantly higher contents of MM and CP in dry season forage under *A. tibourbou* and *M. tinctoria*. *Handroanthus serratifolius* in particular stood out as the forage under its canopy had higher levels of CP in both seasons, in addition to a reduced fiber content in the dry season, and overall higher K levels in the soil under the canopy, which was also found for *A. tibourbou*. Direct effects of trees on the microclimatic and edaphic factors depends primarily on the tree`s ability of shading, which means covering a large area and allowing enough light simultaneously (Andrade *et al.* 2012). Therefore, allowing some level of tree shading in pastures as a drought mitigation practice, and also as a key source of protective shade, is widely desirable for sustainable tropical livestock systems (Chará *et al.* 2019; Gomes *et al.* 2019; Olival *et al.* 2020).

Overall, our best-fitting models suggested that most soil and forage variables responded to some extent to tree presence and seasonality, and also varied among the species. Yet, although we were able to observe some effects of tree presence on soil fertility and forage quality within species, our sampling design did not allow the identification of interspecific effects. All pastures were located in the same microregion, and were subject to the same climate, overall soil type and stocking rate, yet, as all focal trees of each species were aggregated in different pastures, the species effect was confounded with site effects such as different management practices, stocking rates and herd productivity, as well as soil and terrain specificities. Thus the differencial occurrence and magnitude of the effects of these native tree species on pastures should be elucidated in further studies using an appropriately replicated sampling design.

Species-specific traits generate distinct root exudation, microenvironments and litter quality that strongly influence the soil nutrient supply (Lambers *et al.* 2008). Higher contents of polyphenols can have a strong effect on litter quality (Lambers *et al.* 2008), which may be the case with *A. tibourbou*, as its leaves have high content of rosmarinic acid (Souza *et al.* 2012) and it had the largest effect on soil fertility, especially on K content. *Apeiba tibourbou* is commonly found in secondary forests across the Amazon, and probably prefers soils with higher fertility (Tavares *et al.* 2019). Hence, because of its nutrient requirement, it may recycle nutrients from deeper layers (Sileshi *et al.* 2014).

The effect of tree presence on forage quality may vary depending not only on tree characteristics but also on the forage species. Many grasses, such as *Urochloa* spp., can tolerate a reduction in light intensity up to 30 or 40% without affecting dry matter production (Xavier *et al.* 2014; Ledesma *et al.* 2017), which may explain the either neutral or positive effects of the trees on forage quality. The shade tolerance of different forage species is associated with adaptive mechanisms such as leaf area increase, allowing shaded pastures to sustain productivity at levels equivalent to pastures without shade (Araujo *et al.* 2020; Gomes *et al.* 2020). It is important to emphasize that all tree species were selected by farmers based on their experience and perception of non-negative influence on forage species.

Forage under *M. tinctoria* was the only with MM significantly higher than off canopy in both seasons. Litter from this species has an accelerated decomposition time and high potential for rapid nutrient incorporation into the soil, especially N, P, K, Ca and Mg (Silva 2016). Constant and abundant leaf production leads to greater nutrient cycling, offering optimal conditions for forage development, making pioneer species such as *M. tinctoria* good candidates for further studies on the strengthening of ecological processes for the improvement of silvopastoral systems (Parsons and Congdon 2008). The presence of *H. serratifolius* and *S. tubulosa* was associated with significantly higher CP in forage in both seasonsand the rainy season, respectively. Trees of *Samanea*, particularly *S. saman* and *S. tubulosa*, provide protective shade in pastures, produce palatable pods that are suitable as a dry-season feed supplementation and enhance grass production beneath their crown (Durr 2001; Andrade *et al.* 2012). We showed that forage under *S. tubulosa* has higher CP content, possibly due to higher nitrogen content in the ryzosphere and litter fall, because of its ability to symbiotically fix atmospheric nitrogen or unlock mineral nutrients through enhanced microbiome activities (Epihov *et al.* 2021).

The higher CP content in forage under *H. serratifolius* and *S. tubulosa* could be related to the larger size of forage-leaf cells and the higher amount of intracellular nutrients, including proteins, resulting from the greater cell volume as a response to higher moisture, stable temperature and light reduction (Sousa *et al.* 2010; Moreira *et al.* 2013). Also, forage plants under trees may be physiologically younger, since they have a higher proportion of green leaves, thereby extending the juvenile vegetative state and allowing the maintenance of higher metabolic levels for a longer period (Sousa *et al.* 2010). In addition, nitrogen-rich organic matter from litter of N-fixing species, such as *S. tubulosa*, could explain a higher content of CP in forage under these trees (Ledesma *et al.* 2017). It is noteworthy, however, that, although forage CP under *H. serratifolius* and *S. tubulosa* was higher than off the canopy, the protein levels were still less than the minimum required for cattle (Valente *et al.* 2013), pointing to the importance of complementary measures to manage the livestock system.

The seasonality observed in some positive effects of the presence tree was probably related to the intensity and frequency of rainfall, as the effect of trees on forage quality and soil depends mainly on the weather conditions, which influence the decomposer biota and the quality of the organic matter offered by the trees, such as the C/N ratio and lignin content (Prause and Lopes 2012; Machado *et al.* 2017). Deciduousness patterns of trees along the year may also affect forage quality and yield during dry seasons, which is a major challenge for the sustainability of livestock systems, as it implies supplementing animal diet at a high cost in order to spare pasture. The long-term effect of native tree species in minimizing forage loss during the dry season, as well as providers of supplemental fodder from their leaves and fruits is a promising line for further studies.

Tree and crown size might be an important factor determining forage and soil characteristics beneath canopies (Treydte *et al.* 2009) and also the chemical composition of leaves (Binkley and Giardina 1998). Considering the wide spectrum of tree functional traits, such as leaf lifespan, leaf composition, crown dimensions, vegetative and reproductive phenological patterns, further studies should also address diversified set of tree species in the pasture environment for functional complementarity.

The absence of significantly negative effects of the presence of trees in almost all cases is noteworthy, since cutting trees is a culturally widespread practice among cattle ranchers across the Amazon, which has increased the negative impacts of livestock, especially on soil fertility (Machado *et al.* 2017; Steingraber *et al.* 2018). The history of recent colonization of agricultural frontiers at the fringes of the Amazon biome is marked by high deforestation encouraged by governments and colonization companies, followed by livestock occupation (Godar *et al.* 2012). The extensive livestock systems have been established on the basis of slash and burn practices, and subsequent pasture degradation and mismanagement lead to productivity reduction and, eventually, to abandonment of the land. This is a very common condition in Brazil, where more than half of livestock production takes place on degraded pastures (Silva *et al.* 2017). Reintroducing the tree element in pastures in Brazil's arc of deforestation has the potential to contribute as a sustainable practice to restoring degraded pastures and improving soil quality and the quality and amount of forage, in addition to the adjustment of stocking rates to the actual carrying capacity of the pasture (Boval and Dixon 2012). The implementation of these types of silvopastoral systems is advancing across the Amazon region and can potentially support livestock intensification while benefitting ecosystem services (Gomes *et al.* 2020).

CONCLUSIONS

Our study complements the empirical knowledge of cattle farmers in the southwestern Brazilian Amazon about the silvopastoral benefits of five native Amazonian tree species.

We observed some effects of the presence of common multipurpose tree species widely used in pastures in our study area regarding protecton against drought effects, enhancement of nutrient cycling and improvement of forage quality through higher mineral and protein content, as well as lower fiber content. The species with more significant positive effects were *Apeiba tibourbou*, *Handroanthus serratifolius* and *Maclura tinctoria*. Our results suggest that tree cover is a beneficial complementary strategy of pasture management. Contrary to cultural beliefs, our results showed practically no signs that the presence of trees impairs forage quality. Further studies using larger samples and site-independent designs should further assess the influence of the presence of these species on the pasture environment and their benefits for sustainable silvopastoral systems.

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SUPPLEMENTARY MATERIAL (only available in the electronic version)

Olival *et al*. Effect of Amazonian tree species on soil and pasture quality in silvopastoral systems

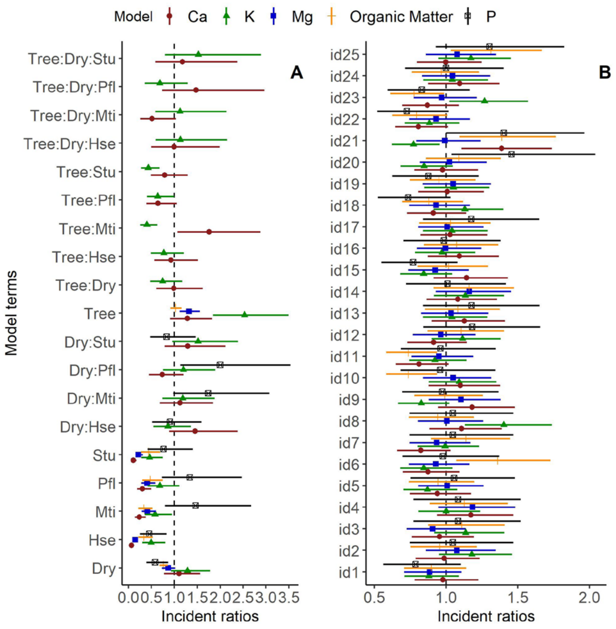

Figure S1. Estimates and 95% confidence intervals of fixed (A) and random (B) terms of all selected models of soil fertility responses to tree presence in silvopastoral systems in northern Mato Grosso, Brazil. The vertical dashed line represents the intercept term, which is the sampling outside the crown area for *Apeiba tibourbou* (id16:id20) in the rainy season for A, and the average intercept of all individual trees sampled for B. Hse = *Handroanthus serratifolius* (id6:id10); Mti = *Maclura tinctoria* (id21:id25); Pfl = *Platymiscium floribundum* (id1:id5); Stu = *Samanea tubulosa* (id11:id15).

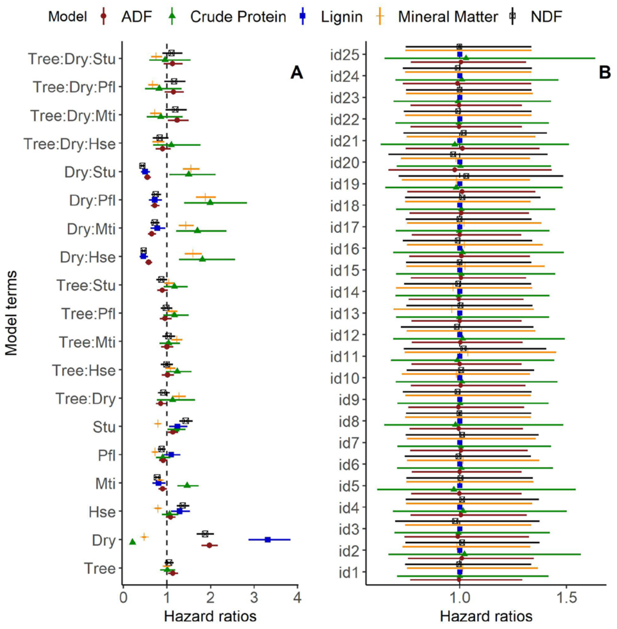

Figure S2. Estimates and 95% confidence intervals of fixed (a) and random (b) terms of all selected models of forage quality responses to tree presence in silvopastoral systems in northern Mato Grosso, Brazil. The vertical dashed line represents the intercept term, which is the sampling outside the crown area for *Apeiba tibourbou* (id16:id20) in the rainy season for A, and the average intercept of all individual trees sampled for B. Hse = *Handroanthus serratifolius* (id6:id10); Mti = *Maclura tinctoria* (id21:id25); Pfl = *Platymiscium floribundum* (id1:id5); Stu = *Samanea tubulosa* (id11:id15).

Table S1. Functional and silvicultural information on the targeted tree species for soil and forage analysis in the north region of Mato Grosso state, Brazil. N-fixing = legume species able to symbiotically fix nitrogen.

Species	N-fixing	Deciduousness	Growth	Total adult height (m)	Canopy shape	Canopy density
Apeiba tibourbou	No	Evergreen	Fast	10 - 20	Flabeliform	Low
Handroanthus serratifolius	No	Deciduous	Medium	> 20	Cylindrical	Low
Maclura tinctoria	No	Semideciduous	Fast	10 - 20	Horizontally elliptical	Very low
Platymiscium floribundum	Yes	Evergreen	Slow	> 20	Cylindrical	Low
Samanea tubulosa	Yes	Deciduous	Medium	10 - 20	Flabeliform	Low

Source: Adapted from Carvalho (2003).

Table S2. Height, diameter at breast height (DBH) and canopy area of five native species targeted for forage and soil analysis in pastures in northern Mato Grosso state, Brazil. Values are the mean and standard deviation of five trees per species.

Species	Total height (m)	DBH (cm)	Canopy area (m^2)
Handroanthus serratifolius	26.8 ± 3.9	34.5 ± 12.0	58.8 ± 25.9
Samanea tubulosa	18.4 ± 1.6	17.5 ± 2.7	48.8 ± 17.7
Apeiba tibourbou	22.6 ± 6.0	74.9 ± 18.3	144.3 ± 37.4
Maclura tinctoria	18.7 ± 2.6	65.9 ± 8.9	133.9 ± 79.0
Platymiscium floribundum	22.2 ± 5.2	40.4 ± 28.0	100.3 ± 66.7

Table S3. Akaike`s Information Criterion (AIC) parameters for predictors of forage quality under and off the canopy of native species in northern Mato Grosso, Brazil. Generalized linear mixed models (GLMM) fitted using the gamma distribution family, with link log, and random intercept structure of individual grouping. + = additive term; * = interaction term.

Dependent variable / Model specification	df	AIC	ΔAIC	Weight	Likelihood	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
Phosphorus (mg dm^{-3})							
tree + season + species	9	334.4	7.0	2.81E-02	3.04E-02	0.49	0.59
tree + season	5	348.5	21.0	2.48E-05	2.69E-05	0.05	0.46
tree + species	8	344.0	16.6	2.33E-04	2.52E-04	0.43	0.52
season + species	8	333.5	6.1	4.48E-02	4.85E-02	0.49	0.58
species	7	343.2	15.7	3.57E-04	3.87E-04	0.42	0.51
tree*season*species	22	338.4	11.0	3.86E-03	4.19E-03	0.59	0.68
tree*season	6	350.5	23.0	9.14E-06	9.91E-06	0.05	0.46
tree*species	12	348.4	21.0	2.56E-05	2.78E-05	0.46	0.55
season*species	**12**	**327.4**	**0.0**	**9.23E-01**	**1.00E+00**	**0.56**	**0.65**
tree	4	357.9	30.4	2.26E-07	2.45E-07	0.00	0.40
season	4	347.4	20.0	4.26E-05	4.61E-05	0.04	0.46
Intercept only	3	356.9	29.5	3.71E-07	4.02E-07	0.00	0.39
Potassium (mg dm^{-3})							
tree + season + species	9	1028.2	27.8	9.23E-07	9.23E-07	0.47	056
tree + season	5	1036.7	36..3	1.30E-08	1.30E-08	0.13	0.45
tree + species	8	1037.4	37.0	9.12E-09	9.12E-09	0..42	0.50
season + species	8	1043.8	43.4	3.85E-10	3.85E-10	0.42	0.50
species	7	1049.8	49.4	1.92E-11	1.92E-11	0.38	0.45
tree*season*species	**22**	**1000.4**	**0.0**	**1.00E+00**	**1.00E+00**	**0.65**	**0.75**
tree*season	6	1034.3	33.9	4.34E-08	4.34E-08	0.15	0.47
tree*species	12	1025.2	24.7	4.24E-06	4.24E-06	0.51	0.60
season*species	12	1038.8	38.4	4.62E-09	4.62E-09	0.49	0.57
tree	4	1046.1	45.6	1.23E-10	1.23E-10	0.08	0.39
season	4	1054.2	53.7	2.15E-12	2.15E-12	0.04	0.36
Intercept only	3	1060.1	59.7	1.09E-13	1.09E-13	0.00	0.32
Calcium (cmol$_c$ dm^{-3})							
tree + season + species	9	214.5	5.0	6.91E-02	8.14E-02	0.83	0.86
tree + season	5	249.0	39.5	2.21E-09	2.60E-09	0.03	0.66
tree + species	8	217.4	7.9	1.61E-02	1.89E-02	0.82	0.85
season + species	8	220.9	11.4	2.82E-03	3.33E-03	0.81	0.84
species	7	223.2	13.7	8.77E-04	1.03E-03	0.81	0.84
tree*season*species	**22**	**209.5**	**0.0**	**8.49E-01**	**1.00E+00**	**0.87**	**0.90**
tree*season	6	250.9	41.4	8.70E-10	1.03E-09	0.03	0.66
tree*species	12	219.1	9.6	7.08E-03	8.34E-03	0.83	0.86
season*species	12	215.0	5.5	5.54E-02	6.53E-02	0.84	0.87
tree	4	251.7	42.2	5.93E-10	6.99E-10	0.02	0.65
season	4	256.1	46.6	6.59E-11	7.77E-11	0.01	0.64
Intercept only	3	258.1	48.6	2.41E-11	2.84E-11	0.00	0.63
Magnesium (cmol$_c$ dm^{-3})							
tree + season + species	**9**	**88.6**	**0.0**	**6.01E-01**	**1.00E+00**	**0.70**	**0.73**
tree + season	5	115.4	26.8	8.94E-07	1.49E-06	0.05	0.53
tree + species	8	89.6	1.0	3.62E-01	6.03E-01	0.70	0.73
season + species	8	96.4	7.8	1.19E-02	1.97E-02	0.68	0.70
species	7	97.6	9.0	6.57E-03	1.09E-02	0.66	0.69
tree*season*species	22	104.0	15.4	2.72E-04	4.53E-04	0.74	0.77
tree*season	6	116.0	27.4	6.58E-07	1.09E-06	0.06	0.53
tree*species	12	96.0	7.4	1.49E-02	2.47E-02	0.70	0.73
season*species	12	101.5	12.9	9.34E-04	1.56E-03	0.68	0.71
tree	5	99.5	10.9	2.57E-03	4.27E-03	0.06	0.44
season	4	125.3	36.7	6.34E-09	1.06E-08	0.01	0.48
Intercept only	3	126.5	37.9	3.54E-09	5.90E-09	0.00	0.47

Table S3. Continued

Dependent variable / Model specification	df	AIC	ΔAIC	Weight	Likelihood	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
			Organic matter (g kg^{-1})				
tree + season + species	**9**	**713.2**	**1.8**	**2.67E-01**	**3.99E-01**	**0.56**	**0.68**
tree + season	5	721.3	10.0	4.58E-03	6.87E-03	0.08	0.51
tree + species	8	729.0	17.6	1.00E-04	1.50E-04	0.51	0.63
season + species	8	711.4	0.0	6.68E-01	1.00E+00	0.56	0.68
species	7	727.1	15.7	2.55E-04	3.82E-04	0.51	0.62
tree*season*species	22	720.1	8.7	8.46E-03	1.27E-02	0.61	0.74
tree*season	6	723.3	11.9	1.71E-03	2.57E-03	0.08	0.51
tree*species	12	725.3	13.9	6.38E-04	9.56E-04	0.56	0.67
season*species	12	717.1	5.7	3.83E-02	5.74E-02	0.57	0.69
tree	4	737.7	26.3	1.31E-06	1.96E-06	0.00	0.44
season	4	719.5	8.1	1.17E-02	1.76E-02	0.08	0.51
Intercept only	3	735.7	24.4	3.40E-06	5.09E-06	0.00	0.44

The rows in bold indicate the best-fitting models with the lowest AIC value or ΔAIC < 2. df = degrees of freedom; AIC: = Akaike's Information Criterion; ΔAIC = difference in AIC between the given model and the model with the lowest AIC score; Weight = Akaike weight showing the relative support for each model; Likelihood = the likelihood of the model, an indicator of fit; $R^2_{GLMM(m)}$ = marginal coefficient of determination; $R^2_{GLMM(c)}$ = conditional coefficient of determination.

Table S4. Akaike`s Information Criterion (AIC) parameters for predictors of forage quality under and off the canopy of native species in northern Mato Grosso, Brazil. Generalized linear mixed models (GLMM) fitted using beta distribution family, with link logit, and random intercept structure of individual grouping.

Response variable/ Model specification	df	AIC	ΔAIC	Weight	Likelihood	Pseudo R^2
			Mineral matter (%)			
tree + season + species	9	-684.2	62.6	2.55E-14	2.55E-14	0.75
tree + season	5	-680.0	66.9	3.04E-15	3.04E-15	0.70
tree + species	8	-555.0	191.9	2.19E-42	2.19E-42	0.06
season + species	8	-675.8	71.0	3.80E-16	3.80E-16	0.73
species	7	-554.2	192.7	1.45E-42	1.45E-42	0.03
tree*season*species	**22**	**-746.8**	**0.0**	**1.00E+00**	**1.00E+00**	**0.92**
tree*season	6	-678.0	68.8	1.12E-15	1.12E-15	0.70
tree*species	12	-548.5	198.4	8.35E-44	8.35E-44	0.07
season*species	12	-719.5	27.3	1.17E-06	1.17E-06	0.84
tree	4	-560.8	186.0	4.03E-41	4.03E-41	0.03
season	4	-673.1	73.7	9.73E-17	9.73E-17	0.68
Intercept only	3	-560.1	186.7	2.90E-41	2.90E-41	0.07
			Crude protein (%)			
tree + season + species	9	-606.7	12.4	1.99E-03	2.04E-03	0.88
tree + season	5	-572.4	46.7	7.13E-11	7.34E-11	0.91
tree + species	8	-400.5	218.5	3.45E-48	3.55E-48	0.10
season + species	8	-597.2	21.9	1.71E-05	1.75E-05	0.87
species	7	-400.9	218.1	4.19E-48	4.31E-48	0.09
tree*season*species	**22**	**-619.1**	**0.0**	**9.72E-01**	**1.00E+00**	**0.92**
tree*season	6	-570.8	48.2	3.26E-11	3.36E-11	0.91
tree*species	12	-393.5	225.6	1.01E-49	1.04E-49	0.11
season*species	12	-611.8	7.3	2.57E-02	2.65E-02	0.89
tree	4	-396.3	222.8	4.12E-49	4.24E-49	0.01
season	4	-564.0	55.0	1.08E-12	1.12E-12	0.89
Intercept only	3	-396.9	222.1	5.72E-49	5.88E-49	0.10
			Neutral detegernt fiber (%)			
tree + season + species	9	-328.8	140.0	4.06E-31	4.06E-31	0.37
tree + season	5	-303.6	165.2	1.37E-36	1.37E-36	0.31
tree + species	8	-314.5	154.2	3.23E-34	3.23E-34	0.26
season + species	8	-330.8	138.0	1.10E-30	1.10E-30	0.37

Table S4. Continued

Response variable/ Model specification	df	AIC	ΔAIC	Weight	Likelihood	Pseudo R^2
species	7	-316.5	152.2	8.76E-34	8.77E-34	0.26
tree*season*species	**22**	**-468.7**	**0.0**	**9.99E-01**	**1.00E+00**	**0.90**
tree*season	6	-301.8	167.0	5.51E-37	5.52E-37	0.32
tree*species	12	-310.6	158.2	4.45E-35	4.46E-35	0.29
season*species	12	-454.3	14.4	7.37E-04	7.38E-04	0.83
tree	4	-292.8	176.0	6.19E-39	6.19E-39	0.29
season	4	-305.6	163.2	3.71E-36	3.72E-36	0.31
Intercept only	3	-294.8	174.0	1.68E-38	1.68E-38	0.29
Acid detergent fiber (%)						
tree + season + species	9	-400.1	89.2	4.20E-20	4.20E-20	0.59
tree + season	5	-372.8	116.5	4.95E-26	4.95E-26	0.56
tree + species	8	-340.2	149.1	4.15E-33	4.15E-33	0.23
season + species	8	-398.3	91.1	1.68E-20	1.68E-20	0.58
species	7	-340.0	149.3	3.72E-33	3.72E-33	0.21
tree*season*species	**22**	**-489.3**	**0.0**	**1.00E+00**	**1.00E+00**	**0.89**
tree*season	6	-372.5	116.9	4.20E-26	4.20E-26	0.57
tree*species	12	-334.4	155.0	2.24E-34	2.24E-34	0.25
season*species	12	-472.3	17.0	2.01E-04	2.02E-04	0.82
tree	4	-326.4	163.0	4.12E-36	4.12E-36	0.02
season	4	-371.6	117.7	2.74E-26	2.74E-26	0.54
Intercept only	3	-326.5	162.8	4.49E-36	4.49E-36	0.25
Lignin (%)						
tree + season + species	9	-658.8	49.0	2.21E-11	2.32E-11	0.80
tree + season	5	-634.6	73.2	1.22E-16	1.28E-16	0.74
tree + species	8	-511.4	196.4	2.09E-43	2.20E-43	0.08
season + species	8	-658.6	49.2	1.94E-11	2.04E-11	0.80
species	7	-512.6	195.2	3.88E-43	4.08E-43	0.07
tree*season*species	22	-701.8	6.0	4.79E-02	5.03E-02	0.89
tree*season	6	-633.5	74.3	6.94E-17	7.29E-17	0.75
tree*species	12	-503.8	204.0	4.84E-45	5.08E-45	0.08
season*species	**12**	**-707.8**	**0.0**	**9.52E-01**	**1.00E+00**	**0.88**
tree	4	-513.6	194.3	6.26E-43	6.58E-43	0.01
season	4	-634.5	73.3	1.15E-16	1.21E-16	0.74
Intercept only	3	-514.7	193.1	1.13E-42	1.18E-42	0.08

The rows in bold indicate the best-fitting models with the lowest AIC value. df = degrees of freedom; AIC = Akaike's Information Criterion; ΔAIC = difference in AIC between the given model and the model with the lowest AIC score; Weight = Akaike weight showing the relative support for each model; Likelihood = the likelihood of the model, an indicator of fit; Pseudo R^2 = a generalized measure of the model coefficient of determination.