Research Paper

How does agro-pastoralism affect forage and soil properties in western Serengeti, Tanzania?
¿Cómo afectan actividades agro-pastoriles el forraje y las características del suelo en Serengeti occidental, Tanzania?

PIUS YORAM KAVANA1,2, EPRAIM J. MTENGETI2, ANTHONY SANGEDA2, CHRISTOPHER MAHONGE3, ROBERT FYUMAGWA4 AND BUKOMBE JOHN4

1Tanzania Wildlife Research Institute, Mahale-Gombe Wildlife Research Centre, Kigoma, Tanzania. tawiri.or.tz
2Sokoine University of Agriculture, College of Agriculture, Department of Animal, Aquaculture & Range Sciences, Morogoro, Tanzania. sua.ac.tz
3Sokoine University of Agriculture, College of Social Sciences and Humanities, Department of Policy Planning and Management, Morogoro, Tanzania. sua.ac.tz
4Tanzania Wildlife Research Institute, Arusha, Tanzania. tawiri.or.tz

Abstract

The impacts of agro-pastoral activities on soil properties, plus nutritive value and residual standing biomass of herbaceous plants in areas of different land uses in western Serengeti, were evaluated. Vegetation and soil were sampled along 4,000 m transects laid across fallow land, areas grazed only by livestock, mixed grazing (livestock and wildlife) and wildlife grazing only. A total number of 123 plant species were encountered during sampling. Analyses of soil and vegetation samples were conducted at Sokoine University of Agriculture laboratories. The estimated average density of grazing animals encountered was 160 TLU/km² on transects within livestock-dominated grazing lands, 129 TLU/km² for mixed grazing and 83 TLU/km² for wildlife grazing only. Results indicated that ADF, IVDMD, IVOMD, ME and TDN in residual herbaceous forage at flowering were significantly (P<0.05) affected by land use type but CP, NDF and ADL were not affected. Soil pH, OC, CEC, C:N ratio and Ca differed significantly (P<0.05) between land use types. An overall evaluation indicated that regardless of climatic conditions, residual biomass of herbaceous plants in western Serengeti is determined by intensity of grazing, soil C:N ratio and concentrations of Ca and P in the soil. We conclude that agro-pastoral practices conducted in western Serengeti affected residual standing biomass of herbaceous plants and soil properties. We recommend that grazing pressure in communal grazing lands be reduced by either reducing number of grazing animals or duration of grazing in a particular grazing area, and specific studies be conducted to establish stocking rates appropriate for specific communal grazing lands in villages.

Keywords: Grazing pressure, land use type, nutritive value, residual standing biomass.

Resumen

En el oeste de la región de Serengeti, Tanzania, se evaluaron los impactos de diferentes actividades agropastoriles en las características del suelo, la biomasa residual y el valor nutritivo de las plantas herbáceas. Para el efecto se tomaron muestras de la vegetación y del suelo a lo largo de transectos de 4,000 m en áreas con diferentes sistemas de uso: (1) barbecho; (2) pastoreo con ganado (vacunos, caprinos y ovinos); (3) pastoreo mixto con ganado y animales silvestres; y solo (4) pastoreo por animales silvestres. En total fueron identificadas 123 especies diferentes de plantas. Los análisis de las muestras de suelo y plantas fueron realizados en los laboratorios de la University of Agriculture de Sokoine. Se encontró que la densidad promedio de animales estimada fue de 160 unidades tropicales de ganado (TLU)/km² en áreas

Correspondence: P.Y. Kavana, Tanzania Wildlife Research Institute, Mahale-Gombe Wildlife Research Centre, P.O. Box 1053, Kigoma, Tanzania. Email: pius.kavana@tawiri.or.tz, pykavana@gmail.com

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de pastoreo por solo ganado, 129 TLU/km² en áreas de pastoreo mixto, y 83 TLU/km² en áreas de pastoreo solo por animales silvestres. Los resultados mostraron que en la época de floración de la vegetación utilizada para pastoreo, la fibra detergente ácida, la digestibilidad in vitro de la materia seca, la digestibilidad in vitro de la materia orgánica, la energía metabolizable y el total de nutrientes digestibles en la biomasa herbácea residual fueron afectados (P<0.05) por el tipo de uso del suelo. Por el contrario, la proteína cruda, la fibra detergente neutra y la lignina detergente ácida no fueron afectados. El pH del suelo, la capacidad de intercambio catiónico, las concentraciones de carbono orgánico y calcio (Ca) y la relación C:N fueron diferentes (P<0.05) en los diferentes tipos de uso del suelo. Una evaluación general indicó que, independientemente de las condiciones climáticas, la biomasa residual de las plantas herbáceas en el oeste de Serengeti está determinada por la intensidad del pastoreo, la relación C:N del suelo y las concentraciones de Ca y P en el suelo. Los resultados permiten concluir que las prácticas agropastoriles en el oeste de Serengeti afectan la biomasa residual de las plantas herbáceas utilizadas por los animales en pastoreo, y las características del suelo. Los resultados sugieren (1) la necesidad de reducir la intensidad de pastoreo en las tierras comunales de la región, bien disminuyendo el número de animales en pastoreo o la duración del pastoreo en un área en particular, y (2) realizar estudios específicos para determinar ciclos de uso y cargas animal apropiadas en zonas de pastoreo comunal específicas.

**Palabras clave:** Biomasa residual, presión de pastoreo, uso de la tierra, valor nutritivo.

**Introduction**

Agro-pastoralism as a livelihood strategy involves some traditional and contemporary ‘best-bet’ practices such as deferred grazing, in Tanzania traditionally known as Ngitiri or Alalili, grass band cultivation, zay pit cultivation, traditionally known as Ngoro system, and controlled grazing. The best-bet agro-pastoral practices are considered to contribute to sustainable systems due to reduced disturbance to soil and native plants, resulting in retention of diverse plant species that contribute to high primary production. However, some agro-pastoral practices, such as keeping large herds of livestock within a small grazing area, exert high grazing pressure on plant species and soil (Veblen 2008), affecting species composition and abundance. Other practices, such as unlimited expansion of cultivated land, affect availability of herbaceous species due to land clearing, thereby reducing the feed resource base for grazing animals. Both livestock keeping and cultivation are important for the livelihood of people in western Serengeti, so good land use planning is needed to accommodate both activities.

Both land clearing and cultivation disrupt stable ecosystems (Cassman and Wood 2005) and result in changes in species composition of vegetation that consequently influence the quantity and quality of herbaceous plants available (Butt and Turner 2012). Herbaceous plants are the primary feed resource for grazing animals in western Serengeti, so any significant disturbance to herbaceous vegetation affects performance of grazing animals in the ecosystem. This suggests a need for careful consideration when allocating specific areas for either grazing or cropping as establishing cultivation within grazing lands might reduce availability of natural feed resources but availability of crop residues could offset the reduction.

Both the human population and conversion of pasture lands to cropping are increasing in western Serengeti (Estes et al. 2012). However, little is known (Nortjé 2015; Lankester and Davis 2016) regarding the effects of agro-pastoralism on soil properties, livestock and wildlife performance, forage richness and diversity and biomass production. Increased human and livestock populations around the Serengeti National Park resulted in progressive livestock encroachment in the western part of the Park. Currently, no scientific study has been conducted to evaluate contradicting views between conservationists and agro-pastoralists on the effects of agro-pastoralism on conservation of wildlife in protected areas of the western part of the Serengeti ecosystem.

This work was designed to evaluate the impacts of agro-pastoral activities on soil properties plus standing biomass and quality of the herbaceous plant layer in western Serengeti. It was hypothesized that there are no variations in quantity and quality of residual standing biomass of herbaceous plants and soil properties as a result of agro-pastoral activities in fallow, livestock, mixed and wildlife-dominated land use types.

**Materials and Methods**

**Study area**

The study was conducted in western Serengeti, which is part of the Serengeti ecosystem as shown in Figure 1. Average annual rainfall ranges between 500 and 1,200 mm, declining towards the Serengeti National Park boundary and increasing towards Lake Victoria to the west (Sinclair et al. 2000). However, rainfall during the study period ranged from 400 to 900 mm. Western Serengeti is occupied by agro-pastoralists and is one of the most densely settled areas in the
Greater Serengeti ecosystem with human population growth rates exceeding those to the north, east and south of the National Park (Kideghesho 2010). The study was conducted in 4 districts by selecting villages that were adjacent to protected areas as shown in brackets, namely: Serengeti district (Park Nyigoti), Bunda district (Nyamatoke), Meatu district (Makao) and Bariadi district (Mwantimba and Matale). While the western Serengeti is considered to be unsuitable for arable agriculture, the subsistence economy depends mainly on agro-pastoralism (Emerton and Mfunda 1999), which is constrained by inadequate inputs of resources, e.g. fertilizers, and poor delivery of agricultural extension services, and people in villages practice extensive cropping and livestock keeping, which encroaches on protected areas (Mfunda and Roskaft 2011).

Figure 1. A map of Serengeti ecosystem showing the study sites and protected areas in western Serengeti. CA = Conservation Area; GCA = Game Controlled Area; GR = Game Reserve; NP = National Park; WMA = Wildlife Management Area.

Field data collection

Vegetation was sampled at the peak blooming period of herbaceous plants during April and May 2016 and 2017 to enable field identification by inflorescences. Herbaceous plants were sampled along 4,000 m transects in selected villages that were adjacent to protected areas. Transects were aligned in each village to cross different land use types in such a way that each transect started in village land and progressively traversed 0–1,000 m in lands dominated by cropping, 1,000–2,000 m in lands dominated by livestock grazing, 2,000–3,000 m crossing the boundary between village land and protected areas, where mixed grazing of livestock and wildlife occurred, and the remaining 3,000–4,000 m was in the protected areas dominated by wildlife grazing. A 0.25 m² quadrat was used to sample herbaceous plants at 100 m intervals along each transect. The sampling distance was established during a reconnaissance survey as this frequency ensured that 80–100% of the herbaceous plant species in the study areas would be encountered. Before harvesting, overall herbaceous plant ground cover in each quadrat was estimated visually and expressed as percentage cover. All plant species within quadrats were identified, clipped and weighed for determination of standing dry matter available. Species not identified in the field were taken to the National Herbarium in Arusha for identification. Samples were air-dried in the field and then re-dried to a constant weight in a vacuum oven at 50 °C for 48 hours in a laboratory. The dry samples were grounded in a Wiley mill to pass through a 1-mm screen for subsequent laboratory analyses. Following harvesting of forage, soil sampling was conducted at the central point of each quadrat to a depth of 30 cm at every 300 m along each transect.

Densities of both livestock and wildlife in the study areas were estimated based on observations made along transects during sampling periods. Livestock species commonly observed in study sites included cattle, goats and sheep, while wildlife included wildebeest, zebra, topi, impala, Grant’s gazelle, reedbuck and Thomson’s gazelle; elephant were encountered once on the border between Maswa Game Reserve and Matale village. Throughout the sampling process, all wildlife and domestic grazing animals spotted within 200 m either side of each transect were identified and counted. Animal counts were converted to tropical livestock units (TLU) based on the respective species average weights, where 1 TLU = 250 kg live weight according to LEAD/FAO (1999).

Laboratory analyses of plant samples

Laboratory analyses included neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), crude protein (CP), in vitro dry matter digestibility (IVDMD) and in vitro organic matter digestibility (IVOMD); they were performed in the laboratory at the Sokoine University of Agriculture. Standard laboratory methods were used as described by Van Soest et al. (1991) for NDF, ADF and ADL, and AOAC (1990) for CP. IVDMD was determined by the Tilley and Terry (1963) method. Total digestible nutrients and metabolizable energy were estimated according to Undersander and Moore (2004) and Spörndly (1989), respectively.
**Laboratory analysis of soil samples**

Soil samples were taken for determination of soil texture, pH, organic carbon (OC), total N, available P, Ca and CEC according to standard procedures (Okalebo et al. 2002).

**Data analysis**

Variation of residual standing biomass and nutritive value of herbaceous plants plus soil properties among different land use/grazing types were analyzed by using R statistical software version 3.5.3. Assessment of collinearity among explanatory variables was performed using stepwise variance inflation factor (VIF), whereby all predictor variables were initially included in the linear regression equation. Variables with VIF greater than 4 were eliminated from the model progressively, while the predictor variables with VIF less than 4 were retained. The resulting linear regression model was then used to assess variables that were significantly associated with the response variable standing biomass. Herbaceous plant species association was analyzed by using null model according to Griffith et al. (2016). Prominence of herbaceous plant species in different land use types was categorized into 4 groups based on the range of occurrence of all species (0–10.7%). The groups were classified as less common (0–2.7%), common (2.8–5.5%), more common (5.6–8.3%) and most common (8.4–11.1%). Analyses were performed using pooled data for respective land use type with type III sum of squares in ANOVA. Distribution of herbaceous plant species on identified soil texture classes was analyzed according to Heberle et al. (2015).

**Results**

**Herbaceous plant community properties**

Average density of grazing animals observed on the various land use types was estimated as 160 TLU/km² on livestock-dominated grazing lands, 129 TLU/km² on transects dominated by mixed grazing and 83 TLU/km² on wildlife grazing areas. A total of 123 plant species (Appendix 1) were encountered during sampling; occurrence of common species is shown in Table 1.

| Species | Fallow | Livestock grazing | Mixed grazing | Wildlife grazing |
|---------|--------|-------------------|----------------|-----------------|
| Aristida kenyensis Henrard (Poaceae) | 0.3 | 2.3 | 6.3** | 0.0 |
| Bidens schimperi Sch.Bip. ex Walp. (Compositae) | 0.0 | 2.0 | 4.7* | 1.0 |
| Blepharis linatifolia Pers. (Acanthaceae) | 0.0 | 0.3 | 4.7* | 0.7 |
| Bothriochloa insculpta (A. Rich.) A. Camus (Poaceae) | 1.0 | 1.7 | 0.3 | 3.7* |
| Brachiaria semiindulata (Hochst.) Stapf (Poaceae) | 1.3 | 6.0**3 | 7.3** | 4.3* |
| Chloris pycnothrix Trin. (Poaceae) | 0.7 | 5.7** | 10.7*** | 6.0** |
| Chrysochloa orientalis (C.E. Hubb.) Swallen (Poaceae) | 0.0 | 0.7 | 0.0 | 0.7 |
| Cynodon dactylon (L.) Pers. (Poaceae) | 4.0* | 7.0** | 2.0 | 0.7 |
| Dactyloctenium aegyptium (L.) Willd. (Poaceae) | 0.7 | 4.7* | 8.0** | 0.3 |
| Digitaria macroblephara (Hack.) Paoli (Poaceae) | 0.0 | 0.3 | 0.0 | 3.7* |
| Eragrostis racemosa (Thub.) Steud. (Poaceae) | 0.3 | 0.3 | 2.3 | 1.3 |
| Eragrostis patula (Kunth) Steud. (Poaceae) | 1.0 | 1.0 | 0.0 | 0.7 |
| Euphorbia inaequalitata Sond. (Euphorbiaceae) | 0.0 | 0.7 | 1.3 | 1.7 |
| Heteropogon contortus (L.) P. Beauv. ex Roem. & Schult. (Poaceae) | 0.0 | 0.0 | 0.0 | 4.7* |
| Hyperthelia dissoluta (Nees ex Steud.) Clayton (Poaceae) | 0.0 | 0.0 | 0.0 | 4.3* |
| Indigofera hochstetteri Baker (Leguminosae) | 0.0 | 1.3 | 1.3 | 3.3 |
| Indigofera volkensii Taub. (Leguminosae) | 0.0 | 1.3 | 0.7 | 3.3 |
| Microchloa kunthii Desv. (Poaceae) | 0.0 | 1.0 | 3.7* | 3.7* |
| Panicum coloratum L. (Poaceae) | 0.0 | 1.0 | 3.7* | 3.7* |
| Portulaca quadrifida L. (Portulacaceae) | 0.7 | 0.7 | 1.0 | 0.7 |
| Sporobolus festivus Hochst. ex A. Rich. (Poaceae) | 0.0 | 0.0 | 3.7* | 5.0* |
| Sporobolus ioclados (Trin.) Nees (Poaceae) | 0.0 | 2.3 | 1.3 | 2.0 |
| Sporobolus pyramidalis P. Beauv. (Poaceae) | 0.0 | 2.3 | 1.0 | 3.3 |
| Themeda triandra Forssk. (Poaceae) | 0.0 | 0.7 | 0.3 | 8.3** |
| Tragus berteronianus Schult. (Poaceae) | 1.0 | 0.7 | 2.3 | 0.3 |

1Taxonomy according to The Plant List (theplantlist.org). ** = Common. *** = More common. **** = Most common. Values without asterisks indicate less common.
Chloris pycnothrix was the most prominent in mixed grazing land use type and was more apparent in livestock and wildlife-dominated grazing land use types. Aristida kenyensis, Bidens schimperi, Blepharis linariifolia, Microchloa kunthii, Panicum coloratum and Sporobolus festivus were common in mixed grazing land use type, while Brachiaria semiundulata was apparent in wildlife-dominated land use type and appeared more commonly in both livestock- and mixed grazing land use types. Dactyloctenium aegyptium was noticeable in livestock-dominated grazing land use type and more common in mixed grazing land use type. Digitaria macroblephara, Heteropogon contortus and Hyperthelia dissoluta were prominent in wildlife-dominated grazing land use type. Themeda triandra was more common only in wildlife-dominated land use type. Cynodon dactylon was apparent in cultivated land use type and appeared more commonly in livestock-dominated grazing land use type. Association of herbaceous plant species was analyzed using 325 species pairs combinations that provided the results presented in Figure 2.

Results from Figure 2 show that Dactyloctenium aegyptium, Cynodon dactylon, Indigofera hochstetteri and Microchloa kunthii were negatively associated with other herbaceous plant species in the community. The negative association of Cynodon dactylon with other herbaceous plant species becomes more prominent under the influence of livestock grazing, while negative association of Dactyloctenium aegyptium with other herbaceous plant species became more prominent under the influence of mixed grazing of livestock and wildlife. The negative association of Microchloa kunthii with other herbaceous plant species became noticeable under the influence of wildlife grazing. However, the negative association of Indigofera hochstetteri with other herbaceous plant species is slightly apparent under the influence of wildlife grazing.

Results shown in Table 2 indicate that standing above-ground biomass of herbaceous plants in grazing lands at flowering was significantly (P<0.05) affected by land use type. Wildlife-dominated grazing lands carried 50% more standing above-ground biomass than livestock-dominated land. While ADF, IVDMD, IVOMD, ME and total digestible nutrients were significantly (P<0.05) affected by land use type, CP, NDF and ADL were unaffected.

Soil properties

Soil samples collected in different land use types revealed that clay is a major component in all soils of western Serengeti (Figure 3).

Five soil texture classes, namely: clay, sandy clay, sandy clay loam, clay loam and sandy loam, were identified from soil samples collected in this study with the former 3 types being most common (about 95%). Distribution of herbaceous plant species in the different soil texture classes is shown in a Venn diagram (Figure 4).

Table 2. Effects of land use type on residual standing biomass and nutritive value of herbaceous plants at flowering in western Serengeti.

| Variable               | Fallow     | LG          | MG          | WG          | P value | Significance |
|------------------------|------------|-------------|-------------|-------------|---------|--------------|
| Biomass (kg DM/ha)     | 2,320b     | 2,126b      | 2,575ab     | 3,188a      | 0.02    | *            |
| CP (%)                 | 9.2        | 9.0         | 8.4         | 8.4         | 0.19    | NS           |
| NDF (%)                | 62.9       | 62.4        | 60.7        | 60.0        | 0.76    | NS           |
| ADF (%)                | 33.4b      | 33.9ab      | 35.4ab      | 36.2a       | 0.01    | **           |
| ADL (%)                | 3.7        | 3.7         | 3.9         | 3.8         | 0.96    | NS           |
| IVDMD (%)              | 47.0a      | 39.5b       | 39.5b       | 40.1b       | 0.00    | ***          |
| IVOMD (%)              | 49.0a      | 44.1ab      | 42.4b       | 42.2b       | 0.00    | ***          |
| ME (MJ/kg DM)          | 5.6a       | 4.4b        | 4.4b        | 4.5b        | 0.00    | ***          |
| TDN (%)                | 57.8a      | 57.6a       | 55.6ab      | 54.6b       | 0.00    | ***          |

Values within rows followed by different letters differ significantly (P<0.05). LG = Livestock grazing; MG = Mixed grazing; WG = Wildlife grazing.
Figure 3. Proportions of soil texture classes in western Serengeti.

Figure 4 indicates that 12 herbaceous plant species were most common in clay soil, including: *Eragrostis tenuifolia*, *Achyranthes aspera*, *Brachiaria semiundulata*, *Commelina benghalensis*, *Digitaria milanjiana*, *Ocimum basilicum*, *Justicia exigua*, *Tragus berteronianus*, *Justicia matammensis*, *Cynodon dactylon*, *Chloris gayana* and *Lactuca capensis*. Three herbaceous plant species, i.e. *Oxygonum sinuatum*, *Sporobolus cordofanus* and *Digitaria eriantha*, were most common in sandy clay soil, while *Cynium tubulosum*, *Setaria sphacelata*, *Heteropogon contortus*, *Indigofera hochstetteri*, *Chrysochloa orientalis*, *Euphorbia inaequilatera* and *Kyllinga nervosa* occurred mainly in sandy clay loam soil. *Corchorus aestuans* grew in sandy loam soil only. The species observed in both clay and clay loam soils was *Panicum coloratum*, while *Portulaca quadrifida* occurred in sandy loam and sandy clay loam soils. *Sporobolus festivus*, *Sporobolus ioclados* and *Dactyloctenium aegyptium* were found in 4 soil texture classes, namely: clay, clay loam, sandy clay loam and sandy loam soils, while *Bothriochloa insculpta* and *Themeda triandra* occurred in clay, clay loam and sandy clay loam soils. *Aristida kenyensis*, *Bidens schimperi* and *Blepharis linariifolia* were found in clay and sandy clay soils. A universal herbaceous plant species that was growing in all 5 soil texture classes was *Microchloa kunthii*.

Table 3 shows the average values of the measured soil parameters and reveals that soil pH, soil OC, CEC, soil Ca and soil C:N ratio were significantly (P<0.05) different among land use types.

Using stepwise variance inflation factor (VIF) of distance from communal grazing land towards protected areas, herbaceous ground cover and soil variables indicated that distance, cover, soil C:N ratio and Ca and P concentrations in the soil had VIF values below the threshold that sufficed development of a linear model (Table 4) for prediction of residual standing biomass (Figure 2) in western Serengeti.

Table 3. Soil properties of different land use types in western Serengeti.

| Parameter         | Fallow | Land use type | P value | Significance |
|-------------------|--------|---------------|---------|--------------|
|                   |        | LG | MG | WG |
| pH                | 7.2b   | 7.9ab | 8.3a | 7.4ab | 0.0453 | * |
| OC (%)            | 0.78b  | 1.64a | 1.64a | 1.32a | 1.46a | ** |
| P (mg/kg)         | 1.36   | 1.26  | 1.76  | 1.63  | 0.1620 | NS |
| CEC (cmol/kg)     | 16.14b | 23.94a | 22.68a | 23.73a | 0.0008 | ** |
| Ca (cmol/kg)      | 10.52b | 12.63b | 18.10a | 13.08b | 0.0077 | ** |
| Total N (%)       | 0.10   | 0.13  | 0.12  | 0.12  | 0.5240 | NS |
| C:N ratio         | 7.74b  | 14.10a | 11.20 | 12.72a | 0.0442 | * |

Values within rows followed by different letters differ significantly (P<0.05). LG = Livestock grazing; MG = Mixed grazing; WG = Wildlife grazing; NS = Not significant.
Figure 3. Residual standing biomass prediction model validation output.

Table 4. Variables for herbaceous plant residual standing biomass prediction model.

| Variable          | Coefficient (estimate) | VIF |
|-------------------|------------------------|-----|
| Intercept         | 1,059.5                |     |
| Distance (m)      | 0.45                   | 1.44|
| Cover (%)         | 11.67                  | 1.40|
| Soil C:N ratio    | 16.70                  | 1.25|
| Soil Ca (cmol/kg) | 1.10                   | 1.08|
| Soil P (mg/kg)    | 8.64                   | 1.07|

Model: Residual Standing Biomass = 0.45 Distance + 11.67 Cover + 16.70 C:N + 1.10 Ca + 8.64 P + 1059.54.

Discussion

Effects of agro-pastoralism on residual standing biomass

This study showed that grazing areas under high density of animals and continuous livestock grazing had lower residual standing biomass than areas with low animal density and intermittent animal grazing, e.g. in protected areas. This result was not surprising, given the different densities of animals grazing the different areas and hence grazing pressure applied. Low residual standing biomass levels on heavily grazed areas observed in this study are consistent with observations by Ngatia et al. (2015) in Kenya and Mbatha and Ward (2010) in South Africa. However, other studies on effects of grazing on standing biomass showed that the effect is site-specific, influenced by environmental conditions and grazing history (Osem et al., 2002; Jia et al., 2018). Livestock at high density tend to graze herbaceous plants to ground level without strong plant selection (Adler et al., 2001; Hayes and Holl, 2003), which reduces the ability of livestock to graze out more desirable species. However, pastures need periodic rest periods to allow species to recover and it is up to herders to control these grazing patterns. In village lands, high density of domestic animals occurs during the rainy season and extends until late dry season, when communal grazing lands become bare. Herders shift groups of animals to more remote areas in search of pastures, including trespassing in protected areas based on independent decisions of livestock owners. As a result grazing pressure on the village lands is reduced at this time. Wildlife, in contrast, move freely on grazing areas to select nutritious herbaceous plants depending on their mouth width and body weight (Fynn, 2012; Bukombe et al., 2017) but at much lower grazing pressures. These differences in grazing pressure and duration of grazing on specific areas for livestock and wildlife obviously contributed to the big differences in residual standing biomass observed between livestock- and wildlife-dominated grazing lands. Cultivation resulted in low standing biomass of herbaceous plants due to removal of herbaceous plants in crop farms as they are viewed as weeds in the crops.

Effects of agro-pastoralism on nutritive value of herbaceous plants

While some significant differences in nutritive parameters for forage from the different land use types were recorded, the magnitude of most differences was scarcely significant from an overall perspective.

IVDMD and IVOMD were highest in herbaceous plants found in cultivated lands as compared with other land use types, which is possibly a function of release of nutrients.
from the soil during plowing/hoeing etc. plus plants not having been grazed and the more digestible components still being present. Energy is an important indicator of the nutritive value of feeds and considerably more nutrient is required to maintain normal energy metabolism than for all other purposes combined (Dietz 1970). The most common nutritional deficiency affecting range animals is lack of available energy in feeds, digestible energy or both (Michalk and Savile 1978; Corbett and Ball 2002). Results from this study showed that herbaceous plants found in cultivated lands and lands grazed by livestock had highest metabolizable energy and total digestible nutrients.

Effects of agro-pastoralism on soil properties

Clay formed the major texture component of soils of the study area in western Serengeti with a range from straight clay to sandy loams. As would be expected, different herbaceous plant species were found on the different soil types, which produced a mosaic pattern of herbaceous plants in the Serengeti ecosystem. The aggregation of herbaceous plants according to soil texture classes supports findings reported by Kavana et al. (2019), which showed soil texture as an important input variable in herbaceous plant ground cover models. Microchloa kunthii was the only herbaceous species present in all soil texture classes, highlighting the versatility of this species and its ability to compete with other herbaceous plant species by exhibiting negative association as shown in Figure 2.

While in general wildlife distribute their faeces and urine at random, except for camping areas where there is some accumulation of faeces, livestock deposit much of their faeces in specific areas such as kraals and other resting areas, where they are generally held at night. Returning of this manure to cultivated areas would help counteract the rundown of nutrients on fallow where lowest CEC and equally lowest soil OC, Ca, P, C:N ratio and pH were measured. Juo et al. (1995) in Nigeria and Lian et al. (2013) in China reported a decline in fertility on cultivated areas in the absence of fertilizer inputs.

Broader implications of agro-pastoralism on grazing land systems

In addition to weather conditions, residual standing biomass production in western Serengeti relies on a range of variables that affect the complex soil and plant systems. The finding that distance from the protected areas, ground cover, C:N ratio, soil Ca and P were key factors in determining amount of standing biomass was of interest. Distance from protected areas was possibly merely a reflection of the grazing pressure applied to the relevant areas as was ground cover. The C:N ratio indicates whether or not mineralization of N is taking place in the soil and the amount available to plants and is significantly correlated (Appendix 2) with CEC (r = 0.51), so is important. Soil Ca is important as building blocks for herbaceous plant cells as Ca has a structural role in the cell wall membranes and as a counter cation for inorganic and organic anions in the cell vacuole (Marschner 1995). The importance of P for fundamental processes of photosynthesis, flowering, fruiting (including seed production) and maturation of herbaceous plants is well understood (Weil and Brady 2017).

Conclusion

This study contributes to the understanding of the ecological effects of agro-pastoralism on the herbaceous vegetation and soil properties in Western Serengeti. The results indicate that decrease in residue standing biomass and soil properties as a result of agro-pastoral activities is significant, highlighting the need for sustainable agro-pastoralism. It was shown that persistence and successful production of herbaceous plants in western Serengeti requires consideration of agro-pastoral activities that are not detrimental to adequate C:N ratio, and Ca and P concentrations in soil. Grazing pressure appeared to affect seriously residual standing biomass in communal grazing lands that requires reduction in order to allow recovery of herbaceous plants. Grazing pressure should be reduced by either reducing number of animals or duration of grazing on these lands. Specific studies should be conducted by respective local government authorities to establish appropriate stocking rates and grazing patterns for specific communal grazing lands in villages. Based on the findings, appropriate grazing strategies can be developed. Manure accumulated in kraals should be returned to at least cultivated areas to reduce soil run-down.

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### Appendix 1. Herbaceous plant species occurrence (%) in different land use types (taxonomy according to The Plant List; theplantlist.org).

| No. | Species (Family) | Fallow | Livestock | Mixed | Wildlife | Overall |
|-----|------------------|--------|-----------|-------|----------|---------|
| 1.  | *Abutilon mauritianum* (Jacq.) Medik. (Malvaceae) | 0 | 0.283 | 0.243 | 0 | 0.189 |
| 2.  | *Achyranthes aspera* L. (Amaranthaceae) | 0 | 0.283 | 0.973 | 0 | 0.472 |
| 3.  | *Aeschynomene indica* L. (Leguminosae) | 1.136 | 0 | 0 | 0 | 0 |
| 4.  | *Albuca kirkii* (Baker) Brenan (Asparagaceae) | 0 | 0 | 0.243 | 0 | 0.094 |
| 5.  | *Alternanthera pungens* Kunth (Amaranthaceae) | 0 | 0 | 0 | 0.678 | 0.189 |
| 6.  | *Amaranthus graecizans* L. (Amaranthaceae) | 0 | 0 | 0.243 | 0 | 0.094 |
| 7.  | *Andropogon greenwayi* Napper (Poaceae) | 0.85 | 0.243 | 0 | 0.378 |
| 8.  | *Aristida adoensis* Hochst. ex A. Rich. (Poaceae) | 0 | 0 | 0.243 | 0.339 | 0.189 |
| 9.  | *Aristida kenyensis* Henrard (Poaceae) | 2.273 | 1.983 | 4.623 | 0 | 2.455 |
| 10. | *Asparagus africanus* Lam. (Asparagaceae) | 0 | 0.567 | 0.487 | 0.339 | 0.472 |
| 11. | *Aspilia mossambicensis* (L.) Lam. (Compositae) | 0 | 0 | 0 | 1.356 | 0.378 |
| 12. | *Bidens schimperi* Sch.Bip. ex Walp. (Compositae) | 2.273 | 1.7 | 3.406 | 1.017 | 2.172 |
| 13. | *Blepharis linariafolia* Pers. (Acanthaceae) | 0 | 0.283 | 3.406 | 0.678 | 1.605 |
| 14. | *Blepharis maderaspatensis* (L.) Heyne ex Roth (Acanthaceae) | 0 | 0 | 0.486 | 1.695 | 1.699 |
| 15. | *Bothriochloa insculpta* (A. Rich.) A. Camus (Poaceae) | 4.545 | 3.966 | 2.676 | 3.729 | 3.399 |
| 16. | *Brachiaria brizantha* (A. Rich.) Stapf (Poaceae) | 0 | 2.833 | 1.46 | 1.017 | 1.794 |
| 17. | *Brachiaria jubata* (Fig. & De Not.) Stapf (Poaceae) | 0 | 0.567 | 0 | 0.678 | 0.378 |
| 18. | *Brachiaria semiundulata* (Hochst.) Stapf (Poaceae) | 4.545 | 5.099 | 5.353 | 4.407 | 5.005 |
| 19. | *Brachiaria serrata* (Thunb.) Stapf (Poaceae) | 0 | 0.85 | 0.73 | 0 | 0.567 |
| 20. | *Cenchrus ciliaris* L. (Poaceae) | 0 | 0.283 | 3.406 | 0.678 | 1.605 |
| 21. | *Centropalus pauciflorus* (Willd.) H. Rob. (Compositae) | 1.136 | 0 | 0 | 0.339 | 0.094 |
| 22. | *Chamaecrista mimosoides* (L.) Greene (Leguminosae) | 1.136 | 0 | 0 | 0 | 0 |
| 23. | *Chloris gayana* Kunth (Poaceae) | 2.273 | 0 | 0.73 | 1.356 | 0.661 |
| 24. | *Chloris pychnothrix* Thrin. (Poaceae) | 4.545 | 5.949 | 8.029 | 6.102 | 6.799 |
| 25. | *Chloris virgata* Sw. (Poaceae) | 0 | 0 | 0.243 | 0 | 0.094 |
| 26. | *Chrysochloa orientalis* (C.E. Hubb.) Swallen (Poaceae) | 0 | 1.416 | 0.487 | 0.678 | 0.85 |
| 27. | *Cleome monophylla* L. (Cleomaceae) | 2.273 | 0 | 0 | 0 | 0 |
| 28. | *Clitoria ternatea* L. (Leguminosae) | 0 | 0.283 | 0 | 0 | 0.094 |
| 29. | *Commelina africana* L. (Commelinaceae) | 0 | 0.567 | 0.243 | 0.339 | 0.378 |
| 30. | *Commelina aspera* G. Don ex Bent. (Commelinaceae) | 0 | 0 | 0.243 | 0 | 0.094 |
| 31. | *Commelina benghalensis* L. (Commelinaceae) | 2.273 | 0.567 | 0.487 | 0.678 | 0.567 |
| 32. | *Corchorus aestuans* L. (Malvaceae) | 0 | 0.283 | 0.243 | 0 | 0.189 |
| 33. | *Corchorus trilocularis* L. (Malvaceae) | 1.136 | 0 | 0 | 0 | 0 |
| 34. | *Craterostigma plantagineum* Hochst. (Linderniaceae) | 0 | 0.85 | 0.487 | 0.339 | 0.567 |
| 35. | *Crotalaria spinosa* Benth. (Leguminosae) | 0 | 1.416 | 0.243 | 0.339 | 0.661 |
| 36. | *Cynodon dactylon* (L.) Pers. (Poaceae) | 13.636 | 7.082 | 1.946 | 0.678 | 3.305 |
| 37. | *Cynodon plectostachyus* (K. Schum.) Pilg. (Poaceae) | 0 | 0 | 0 | 0.339 | 0.094 |

Continued
| No. | Species (Family) | Fallow | Livestock | Mixed | Wildlife | Overall |
|-----|-----------------|--------|-----------|-------|----------|---------|
| 40  | *Cyperus pulchellus* R.Br. (Cyperaceae) | 1.136  | 1.216     | 0.73  | 0.017    | 1.138   |
| 41  | *Cyphostemma serpens* (Hochst. ex A. Rich.) Desc. (Vitaceae) | 0      | 0         | 0.243 | 0        | 0.094   |
| 42  | *Dactyloctenium aegyptium* (L.) Willd. (Poaceae) | 5.682  | 4.816     | 6.083 | 0.339    | 4.06    |
| 43  | *Desmodium tortuosum* (Sw.) DC. (Leguminosae) | 0      | 0.283     | 0     | 0        | 0.094   |
| 44  | *Digitaria abyssinica* (A.Rich.) Stapf (Poaceae) | 0      | 0         | 0.243 | 0        | 0.094   |
| 45  | *Digitaria bicornis* (Lam.) Roem. & Schult. (Poaceae) | 0      | 0         | 0.243 | 0        | 0.094   |
| 46  | *Digitaria eriantha* Steud. (Poaceae) | 0      | 0         | 0.243 | 0        | 0.094   |
| 47  | *Digitaria longiflora* (Retz.) Pers. (Poaceae) | 2.273  | 0.85      | 0.73  | 0        | 0.567   |
| 48  | *Digitaria macrocephala* (Hack.) Paoli (Poaceae) | 0      | 0.283     | 2.676 | 3.729    | 2.172   |
| 49  | *Digitaria milanjiana* (Rendle) Stapf (Poaceae) | 1.136  | 0.567     | 1.703 | 0        | 0.85    |
| 50  | *Digitaria ternata* (A. Rich.) Stapf (Poaceae) | 0      | 2.266     | 0.243 | 0.339    | 0.944   |
| 51  | *Dyschoriste radicans* (Hochst. ex A. Rich.) Nees (Acanthaceae) | 0      | 0.567     | 0.487 | 0.678    | 0.567   |
| 52  | *Echinochloa pyramidalis* (Lam.) Hitchc. & Chase (Poaceae) | 0      | 0.283     | 0     | 1.356    | 0.472   |
| 53  | *Eleusine indica* (L.) Gaertn. (Poaceae) | 0      | 0.283     | 0.243 | 0        | 0.189   |
| 54  | *Eragrostis aspera* (Jacq.) Nees (Poaceae) | 1.136  | 0.283     | 0.243 | 0        | 0.189   |
| 55  | *Eragrostis ciliaris* (All.) Janch. (Poaceae) | 1.136  | 0         | 0.243 | 0        | 0.094   |
| 56  | *Eragrostis patula* (Kunth) Steud. (Poaceae) | 3.409  | 2.266     | 0     | 0.678    | 0.944   |
| 57  | *Eragrostis racemosa* (Thunb.) Steud. (Poaceae) | 1.136  | 1.416     | 2.92  | 1.356    | 1.983   |
| 58  | *Euphorbia inaequalata* Sond. (Euphorbiaceae) | 0      | 2.266     | 0.973 | 1.695    | 1.605   |
| 59  | *Eustachys paspaloides* (Vahl) Lanza & Mattei (Poaceae) | 0      | 0         | 0.243 | 0.339    | 0.189   |
| 60  | *Gomphrena globosa* L. (Amaranthaceae) | 3.409  | 1.133     | 0.243 | 0        | 0.472   |
| 61  | *Gutbergenia cordifolia* Benth. ex Oliv. (Compositae) | 0      | 0.283     | 0.973 | 0.339    | 0.567   |
| 62  | *Gutbergenia petersii Steetz* (Compositae) | 1.136  | 0         | 0     | 1.017    | 0.283   |
| 63  | *Harpaceae schimperi* A. Rich. (Poaceae) | 0      | 0.567     | 0.73  | 1.017    | 0.755   |
| 64  | *Heliotropium nelsonii* C.H. Wright (Boraginaceae) | 0      | 0.567     | 0     | 0        | 0.189   |
| 65  | *Heliotropium steudneri* vatke (Boraginaceae) | 0      | 0.567     | 0     | 0        | 0.189   |
| 66  | *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult. (Poaceae) | 1.136  | 0         | 2.19  | 4.746    | 2.172   |
| 67  | *Hygrophila auriculata* (Schumach.) Heine (Acanthaceae) | 0      | 0.85      | 0     | 0.678    | 0.472   |
| 68  | *Hyparrhenia hirta* (L.) Stapf (Poaceae) | 0      | 0         | 0     | 0.678    | 0.189   |
| 69  | *Hyperthelia dissolata* (Nees ex Steud.) Clayton (Poaceae) | 1.136  | 0         | 0.73  | 4.407    | 1.511   |
| 70  | *Hypoixis hirsuta* (L.) Coville (Hypoxidaceae) | 0      | 0         | 0.243 | 0        | 0.094   |
| 71  | *Indigofera basiliflora* J.B. Gillett (Leguminosae) | 2.273  | 0         | 0.243 | 0        | 0.094   |
| 72  | *Indigofera hochstetteri* Baker (Leguminosae) | 0      | 2.55      | 0.973 | 3.39     | 2.172   |
| 73  | *Indigofera scapata* Forssk. (Leguminosae) | 1.136  | 1.133     | 0     | 0        | 0.378   |
| 74  | *Indigofera volkensii* Taub. (Leguminosae) | 0      | 1.983     | 1.703 | 3.39     | 2.266   |
| 75  | *Ipomoea nephila* vatke (Convolvulaceae) | 0      | 0         | 0     | 0.678    | 0.189   |
| 76  | *Justicia betonica* L. (Acanthaceae) | 0      | 0.85      | 0.73  | 0.339    | 0.661   |
| 77  | *Justicia exigua* S. Moore (Acanthaceae) | 0      | 0         | 0.73  | 0.339    | 0.378   |
| 78  | *Justicia glabra* K.D. Koenig ex Roxb. (Acanthaceae) | 0      | 0         | 0.243 | 0        | 0.094   |
| 79  | *Justicia matamensis* (Schweinf.) Oliv. (Acanthaceae) | 0      | 0.283     | 0.73  | 0        | 0.378   |
| 80  | *Kyllinga nervosa* Steud. (Cyperaceae) | 1.136  | 1.983     | 0.73  | 0.678    | 1.133   |
| 81  | *Lactuca virosa* Habl. (Compositae) | 1.272  | 0.283     | 0     | 0        | 0.094   |

*Continued*
| No. | Species (Family)                                           | Fallow | Livestock | Mixed | Wildlife | Overall |
|-----|-----------------------------------------------------------|--------|-----------|-------|----------|---------|
| 82  | *Lepidagathis scabra* C.B. Clarke (Acanthaceae)           | 0      | 0.567     | 0     | 0        | 0.189   |
| 83  | *Leucas aspera* (Willd.) Link (Lamiaceae)                 | 0      | 0         | 0.243 | 0.678    | 0.283   |
| 84  | *Leucas deflexa* Hook.f. (Lamiaceae)                      | 3.409  | 0         | 0.243 | 0        | 0.094   |
| 85  | *Leucas martinicensis* (Jacq.) R.Br. (Lamiaceae)          | 1.136  | 0         | 0     | 0        | 0       |
| 86  | *Macroptilium atropurpureum* (DC.) Urb. (Leguminosae)     | 0      | 0         | 0     | 0.339    | 0.094   |
| 87  | *Melania ovata* Spreng. (Malvaceae)                       | 1.136  | 0         | 0     | 0        | 0       |
| 88  | *Microchloa kunthii* Desv. (Poaceae)                      | 0      | 4.249     | 5.839 | 3.729    | 4.721   |
| 89  | *Mollugo nudicaulis* Lam. (Molluginaceae)                 | 0      | 0.283     | 0     | 0        | 0.094   |
| 90  | *Ocimum basilicum* L. (Lamiaceae)                         | 1.136  | 0.283     | 0.487 | 0.339    | 0.378   |
| 91  | *Ocimum gratissimum* L. (Lamiaceae)                       | 0      | 0         | 0     | 0.339    | 0.094   |
| 92  | *Ormocarpum kiriki* S. Moore (Leguminosae)                | 0      | 0         | 0.243 | 0        | 0.094   |
| 93  | *Ormocarpum trichocarpum* (Taub.) Engl. (Leguminosae)     | 0      | 0         | 0     | 0.339    | 0.094   |
| 94  | *Oxygonum sinuatum* (Hochst. & Steud. ex Meisn.) Dammer (Polygonaceae) | 1.136  | 0.283     | 0.487 | 0        | 0.283   |
| 95  | *Panicum coloratum* L. (Poaceae)                          | 0      | 1.133     | 1.46  | 3.729    | 1.983   |
| 96  | *Panicum maximum* Jacq. (Poaceae)                         | 0      | 0         | 0.243 | 1.356    | 0.472   |
| 97  | *Pennisetum meziunum* Lekee (Poaceae)                     | 0      | 0.283     | 0.973 | 1.695    | 0.944   |
| 98  | *Portulaca oleracea* L. (Portulacaceae)                   | 0      | 0.283     | 0     | 0.339    | 0.189   |
| 99  | *Portulaca quadrifida* L. (Portulacaceae)                  | 2.273  | 2.266     | 0.73  | 0.678    | 1.228   |
| 100 | *Rhynchosia minima* (L.) DC. (Leguminosae)                 | 0      | 0         | 0.243 | 0        | 0.094   |
| 101 | *Senna occidentalis* (L.) Link (Leguminosae)               | 0      | 0.283     | 0     | 0.339    | 0.189   |
| 102 | *Sesbania sesban* (L.) Merr. (Leguminosae)                 | 0      | 0.567     | 0     | 0        | 0.189   |
| 103 | *Setaria pumila* (Poir.) Roem. & Schult. (Poaceae)        | 1.136  | 1.7       | 0     | 0        | 0.567   |
| 104 | *Setaria sphenelata* (Schumach.) Stapf & C.E. Hubb. ex Moss (Poaceae) | 1.136  | 0.283     | 0.487 | 1.356    | 0.661   |
| 105 | *Setaria verticillata* (L.) P. Beauv. (Poaceae)            | 2.273  | 0.283     | 0.243 | 0        | 0.189   |
| 106 | *Sida acuta* Burm.f. (Malvaceae)                          | 0      | 0.283     | 0     | 0        | 0.094   |
| 107 | *Solanum incanum* L. (Solanaceae)                         | 1.136  | 0.283     | 0.487 | 0.678    | 0.472   |
| 108 | *Sphaeranthus suaveolens* (Forssk.) DC. (Compositae)      | 0      | 2.266     | 0.243 | 0        | 0.85    |
| 109 | *Sporobolus africanus* (Poir.) Robyns & Tournay (Poaceae) | 0      | 0         | 0.243 | 0.678    | 0.283   |
| 110 | *Sporobolus cordifolius* (Hochst. ex Steud.) Hérincq ex Coss. (Poaceae) | 0      | 0.283     | 0     | 0.339    | 0.189   |
| 111 | *Sporobolus festivus* Hochst. ex A. Rich. (Poaceae)       | 0      | 0.567     | 6.569 | 5.085    | 4.155   |
| 112 | *Sporobolus isolados* (Trin.) Nees (Poaceae)               | 0      | 5.382     | 0.973 | 2.034    | 2.738   |
| 113 | *Sporobolus kentrophyllum* (K. Schum.) Clayton (Poaceae)  | 0      | 0.567     | 0.73  | 0        | 0.472   |
| 114 | *Sporobolus pyramidalis* P. Beauv. (Poaceae)               | 0      | 2.266     | 1.946 | 3.39     | 2.455   |
| 115 | *Tagetes minuta* L. (Compositae)                          | 2.273  | 0         | 0     | 0        | 0       |
| 116 | *Talinum portulacifolium* (Forssk.) Asch. ex Schweinf. (Talinaceae) | 0      | 0         | 0     | 0.339    | 0.094   |
| 117 | *Tephrosia pumila* (Lam.) Pers. (Leguminosae)              | 0      | 0.567     | 1.46  | 1.356    | 1.133   |
| 118 | *Thineda triandra* Forssk. (Poaceae)                      | 1.136  | 3.966     | 5.596 | 8.475    | 5.855   |
| 119 | *Tragus berteronianus* Schult. (Poaceae)                   | 3.409  | 0.85      | 1.703 | 0.339    | 1.039   |
| 120 | *Tribulus terrestris* L. (Zygophyllaceae)                  | 0      | 0.567     | 0.243 | 0        | 0.283   |
| 121 | *Triumfetta rhomboidea* Jacq. (Malvaceae)                  | 0      | 0         | 0     | 0.339    | 0.094   |
| 122 | *Urochloa brachyura* (Hack.) Stapf (Poaceae)               | 0      | 0.283     | 0     | 0        | 0.094   |
| 123 | *Xanthium strumarium* L. (Compositae)                     | 0      | 0.283     | 0     | 0        | 0.094   |

1Taxonomy according to Global Plants (JSTOR); [plants.jstor.org](http://plants.jstor.org). 2Taxonomy according to African Plants data base ([vilege.ch/musinfo/bd/cjb/africa](http://vilege.ch/musinfo/bd/cjb/africa)).

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**Appendix 2. Correlation analysis for soil and plant properties in western Serengeti.**

| Distance | Biomass | Soil pH | Clay | Silt | Sand | Soil N | Soil OC | Soil C:N | Soil P | Soil C:P | Soil N:P | CEC | Soil Ca | Forage CP | NDF | ADF | ADFL IVDMD | IVOMD | TDN | ME |
|----------|---------|---------|------|------|------|--------|---------|---------|--------|---------|---------|-----|--------|----------|-----|-----|----------|-------|-----|-----|
| Distance | 1.00 |       |      |      |      |        |         |         |        |         |         |     |        |          |     |     |          |       |     |     |
| Biomass  | 0.68*** | 1.00 |      |      |      |        |         |         |        |         |         |     |        |          |     |     |          |       |     |     |
| Soil pH  | 0.10 | 0.06  | 1.00 |      |      |        |         |         |        |         |         |     |        |          |     |     |          |       |     |     |
| Clay     | 0.18 | 0.03  | 0.24 | 1.00 |      |        |         |         |        |         |         |     |        |          |     |     |          |       |     |     |
| Silt     | 0.06 | 0.13  | -0.59*** | -0.06 | 1.00 |        |         |         |        |         |         |     |        |          |     |     |          |       |     |     |
| Sand     | -0.18 | -0.08 | 0.03 | -0.91*** | 0.37 | 1.00 |        |         |        |         |         |     |        |          |     |     |          |       |     |     |
| Soil N   | 0.20 | -0.18 | -0.07 | 0.37 | 0.05 | -0.36 | 1.00 |        |        |         |         |     |        |          |     |     |          |       |     |     |
| Soil OC  | 0.13 | -0.09 | 0.04 | 0.59*** | 0.15 | -0.61*** | 0.58*** | 1.00 |        |         |         |     |        |          |     |     |          |       |     |     |
| Soil C:N | -0.04 | 0.03 | 0.04 | 0.38 | 0.15 | -0.42* | -0.10 | 0.73*** | 1.00 |        |         |     |        |          |     |     |          |       |     |     |
| Soil P   | 0.04 | -0.05 | -0.17 | -0.35 | 0.06 | 0.31 | 0.18 | -0.23 | -0.43 | 1.00 |        |     |        |          |     |     |          |       |     |     |
| Soil C:P | 0.19 | -0.07 | 0.01 | 0.59*** | 0.13 | -0.60*** | 0.67*** | 0.97*** | 0.61*** | -0.18 | 1.00 |        |     |        |          |     |     |          |       |     |     |
| Soil N:P | 0.07 | -0.07 | 0.14 | 0.61*** | 0.01 | -0.57*** | 0.53*** | 0.61*** | 0.30 | -0.67*** | 0.63*** | 1.00 |        |          |     |     |          |       |     |     |
| CEC      | 0.08 | 0.01 | 0.46* | 0.90*** | -0.18 | -0.76*** | 0.27 | 0.63*** | 0.51** | -0.44* | 0.59*** | 0.64*** | 1.00 |        |          |     |     |          |       |     |     |
| Soil Ca  | 0.12 | 0.05 | 0.73*** | 0.63*** | -0.49** | -0.38 | 0.24 | 0.36 | 0.17 | -0.32 | 0.26 | 0.49*** | 0.81*** | 1.00 |        |          |     |     |          |       |     |     |
| Forage CP | -0.28 | -0.12 | -0.10 | 0.05 | 0.18 | -0.13 | -0.27 | 0.20 | 0.52** | -0.19 | -0.02 | 0.00 | 0.17 | -0.05 | 1.00 |        |          |     |     |          |       |     |     |
| NDF      | -0.15 | -0.15 | -0.15 | 0.00 | 0.12 | -0.05 | 0.30 | -0.07 | -0.38 | 0.14 | -0.04 | 0.15 | -0.02 | 0.08 | -0.11 | 1.00 |        |          |     |     |          |       |     |     |
| ADF      | 0.27 | 0.20 | 0.02 | -0.11 | 0.01 | 0.11 | 0.02 | -0.22 | -0.33 | 0.05 | -0.10 | -0.09 | 0.20 | 0.03 | -0.51 | 0.20 | 1.00 |        |          |     |     |          |       |     |     |
| ADFL     | 0.07 | 0.18 | 0.19 | 0.32 | 0.20 | -0.38 | 0.13 | 0.05 | -0.10 | -0.03 | 0.11 | 0.18 | 0.24 | 0.15 | -0.24 | 0.06 | 0.18 | 1.00 |        |          |     |     |          |       |     |     |
| IVDMD    | 0.03 | -0.02 | 0.05 | 0.06 | 0.27 | -0.17 | 0.23 | 0.32 | 0.20 | 0.21 | 0.25 | 0.10 | 0.12 | 0.01 | 0.34 | 0.08 | -0.66*** | 0.11 | 1.00 |        |          |     |     |          |       |     |     |
| IVOMD    | 0.17 | 0.12 | -0.07 | 0.28 | 0.12 | -0.31 | 0.16 | 0.13 | 0.00 | 0.01 | 0.15 | 0.18 | 0.18 | 0.09 | 0.05 | 0.19 | -0.40 | 0.09 | 0.60*** | 1.00 |        |          |     |     |          |       |     |     |
| TDN      | -0.27 | -0.20 | -0.02 | 0.11 | -0.01 | -0.11 | -0.02 | 0.22 | 0.33 | -0.05 | 0.10 | 0.09 | 0.20 | -0.03 | 0.51** | -0.20 | -1.00*** | -0.18 | 0.66*** | 0.40* | 1.00 |        |          |     |     |          |       |     |     |
| ME       | 0.17 | 0.12 | -0.07 | 0.28 | 0.12 | -0.31 | 0.16 | 0.13 | -0.01 | 0.01 | 0.15 | 0.18 | 0.18 | 0.08 | 0.05 | 0.19 | -0.40 | 0.09 | 0.60*** | 1.00** | 0.40* | 1.00 |        |          |     |     |          |       |     |     |

Values with asterisks indicate significant correlation (* = P<0.05; ** = P<0.01; *** = P<0.001).

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