

Marit Klemetsen Arneberg

The impact of wild and domestic herbivores on aboveground productivity in an East-African savannah

Master's thesis in Biology

Supervisor: Bente Jessen Graae

Co-supervisors: Stuart W. Smith, James D.M. Speed
& John Bukombe

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Photo: Per Harald Olsen

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ABSTRACT

Plant productivity in African savannahs is widely recognized to depend on temporal and spatial variations in climate, soil properties and disturbances, mainly fire and herbivory. Human driven land-use change has increased over the last few decades, and is altering the dominant herbivores in savannahs from highly mobile assemblages of wild herbivores to less mobile and typically higher densities of livestock. This shift in herbivory impact is likely to affect the temporal patterns in productivity of the savannahs.

In this study, we quantified the impacts of livestock and wildlife grazing on net aboveground productivity and herbivore consumption inside wildlife protected areas in the Serengeti National Park, Tanzania, and adjacent livestock dominated pasturelands outside protected areas. This was achieved by harvesting vegetation using moveable exclosures and paired open plots. Herbaceous biomass was destructively measured seven times over a 15 months period. Additionally we surveyed dominant and subordinate plant species consumption and determined cumulative rainfall between harvest periods using remote satellite images.

Overall we found that net aboveground primary productivity is mainly driven by rainfall and maintained at relatively high levels in both livestock dominated pastures and wildlife protected areas. Despite similar productivity between land-uses, rates of herbivore consumption was higher in livestock dominated pastures compared to wildlife protected areas, especially when rainfall and plant biomass was scarce. Over the duration of our experiment accumulated productivity did not differ between land-uses; however, the magnitude of total consumption in the livestock dominated pastures is much greater and less dependent on accumulated rainfall, compared to the wildlife protected areas. Local dominant grass species did not differ in productivity between land-uses and were equally productive as the subordinate species. Furthermore, the dominant plant species were consumed to a much lower extent than subordinate species, regardless of land-use.

Our findings demonstrate that productivity in the Serengeti Ecosystem is more driven by seasonal rainfall patterns than by land-use difference. Furthermore, in the absence of herbivores, plant species in wildlife protected areas and adjacent domestic livestock dominated pasture lands can sustain equivalent high levels of productivity in wet periods. On a short term basis there seems to be no detrimental impact of livestock grazing on the capacity of the land to produce biomass outside protected areas. However, this contrast does not account for potential illegal use of protected areas. It is necessary with further research to determine what the optimal resource ratio in these areas are and what level of stocking densities the grasslands are able to support, with a special emphasis on the interannual seasonal variability across multiple years.

Key words

Savannah, Primary productivity, Grazing, Livestock, Wildlife, Serengeti, Moveable Exclosures, Precipitation

SAMMENDRAG

Planteproduktivitet på Afrikanske savanner er allment kjent for å avhenge av tidsmessige og romlige variasjoner i klima, jordegenskaper og forstyrrelser, hovedsakelig brann og beitepress. Menneskelig drevet arealbrukendring har økt de siste tiårene, og endrer sammensetninger av beitedyr på savannen fra svært mobile samlinger av ville beitedyr til mindre mobile og høyere tetthet av husdyr. Denne forskyvningen av beitepress vil trolig påvirke de tidsmessige mønstrene i produktivitet på savanner.

I dette studiet kvantifiserte vi virkningen av husdyr- og villdyrsbeiting på netto primærproduksjon og beitepress i beskyttede områder i Serengeti National Park, Tanzania og tilstøtende husdyrdominerte beitemarker utenfor de beskyttede områdene. Dette ble oppnådd ved høsting av vegetasjon ved bruk av flyttbare bur («exclosures») og parrede åpne plott. Plantebiomasse av urteplanter ble destruktivt samlet syv ganger over en 15 måneders periode. I tillegg undersøkte vi produktivitet og beiting av dominerende og underordnede gressarter, og bestemte kumulativ nedbør mellom høstperioder ved bruk av fjernsatellittbilder.

Samlet fant vi at netto primærproduksjon hovedsakelig er drevet av nedbør og opprettholdt på relativt høye nivåer i både husdyrdominerte beiter og i beskyttede områder. Til tross for tilsvarende produktivitet mellom de to arealbrukene, var beitenivået høyere i husdyrdominerte beitemarker sammenlignet med beskyttede områder, særlig når det var lave nivåer av nedbør og plantebiomasse. I løpet av eksperimentets varighet var ikke akkumulert produktivitet forskjellig mellom arealbrukene; størrelsen på totalt forbruk i husdyrdominerte beitemarker er imidlertid mye større og mindre avhengig av akkumulert nedbør sammenlignet med beskyttede områder. Lokale dominerende gressarter varierte ikke i produktivitet mellom husdyrdominerte beskyttede områder, og var like produktive som underordnede gressarter. De dominerende gressartene ble i tillegg konsumert i mye lavere grad enn underordnede arter, uavhengig av arealbruk.

Våre funn viser at produktiviteten i Serengeti-økosystemet er mer drevet av sesongmessige nedbørmønstre enn ved arealbruksforskjeller. Videre, i fravær av beitedyr, kan plantearter i beskyttede områder og tilstøtende husdyrdominerte beiteområder opprettholde tilsvarende høye produktivitetsnivåer i våte perioder. På kort sikt er det tilsynelatende ingen skadelig innvirkning av beiting på kapasiteten for å produsere biomasse utenfor beskyttede områder. Denne kontrasten tar imidlertid ikke hensyn til potensiell ulovlig bruk av beskyttede områder. Det er nødvendig med ytterligere undersøkelser for å finne ut hva det optimale ressursforholdet i disse områdene er, og hvor stor tetthet av beitedyr gresslettene kan opprettholde, med særlig vekt på den årlige sesongvariasjonen over flere år.

Key words

Savanne, primærproduksjon, beiting, husdyr, villdyr, Serengeti, Moveable Exclosures, nedbør

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INTRODUCTION

Africa represents the largest remaining area of uncultivated land, including the most diverse and abundant mammalian fauna left on earth. Many of these areas have been protected for several decades to maintain biodiversity and preserve some of the last remaining migrating routes of large herbivores (McNaughton, 1985, Sinclair, 1995). Humans have been present alongside wild animal populations as pastoralists with nomadic livestock herds for thousands of years (Homewood et al., 2009). In recent decades, as human populations grow, the use of pastures is intensifying due to an increased demand for livestock and resultant sedentarisation of pastoralist communities (Riginos et al., 2012, Hempson et al., 2017). The effect is especially prominent at the borders of protected areas as people are being pushed from densely-settled areas closer to protective borders where arable land is still available for cultivation (Estes et al., 2012, Veldhuis et al., 2019). Human driven land-use changes in these areas have been especially high (Beale et al., 2013, Veldhuis et al., 2019). Additionally, these changes are altering the dominant herbivores in savannahs from highly mobile assemblages of wild herbivores to less mobile and typically higher densities of livestock that impose a higher grazing pressure (Hempson et al., 2017). By modification of land areas into livestock dominated areas, humans are altering the net aboveground plant productivity as well as temporal productivity patterns. Moreover, these changes in consumption dynamics may increase grassland sensitivity to climate change (Frank et al., 2017).

Studies on how grazing affects grassland plant productivity are challenging, as the productivity dynamics of the vegetation in savannah ecosystems are highly complex and may vary between different ecosystems. The topic has been the subject in numerous studies over the last decades (McNaughton, 1985, Belsky, 1990, Frank and McNaughton, 1992, Milchunas and Lauenroth, 1993, Charles et al., 2017, Anderson et al., 2006, Coughenour et al., 1985) to continuously improve an understanding of the link between herbivore impacts and the role of primary production. Well studied drivers of savannah productivity include rainfall, soil texture and nutrient availability, fire frequencies and the grazing pressure of large herbivores (Milchunas and Lauenroth, 1993, Frank et al., 1998, Anderson et al., 2006, Augustine and McNaughton, 2006, Knapp et al., 2012). Net aboveground productivity, hereafter called 'productivity' in savannah ecosystems is highly responsive to seasonal variation and the timing of rainfall (Augustine and McNaughton, 2006, Knapp et al., 2012) and may increase as the rain season initiates and progresses, but may also level off as rain season continues (Bonnet et al., 2010, Veldhuis et al., 2016). Mesic grasslands with a mean annual precipitation above 650 mm are unstable grasslands that need frequent disturbances from herbivory and fire to maintain a coexistence of trees and grasses (Sankaran et al., 2005). Grazers remove biomass and hereby decrease the available vegetation for other grazers, but they may also enhance regrowth of aboveground tissue that is more nutrient rich and has higher leaf nitrogen contents (Holland et al., 1992, Milchunas et al., 1995, Frank et al., 1998). Natural frequent fires are in a similar way to herbivory contributing to maintain a low vegetation cover that reduces light limitation and thereby increase primary productivity and species richness (Koerner et al., 2014).

McNaughton (1979) introduced this theoretically with the "grazing optimization hypothesis" suggesting that removal of herbaceous biomass by herbivores could either stimulate or

suppress aboveground productivity depending on its timing or intensity. For example, he found that moderate grazing levels could stimulate vegetation regrowth, termed overcompensation (when replaced production exceeds the amount removed). Overcompensation is mostly constricted to findings in grasslands dominated by migratory wild herbivores rather than resident herbivores, such as the productive mesic grasslands of the Serengeti-Mara Ecosystem (Frank et al., 1998). Exact compensatory growth (replacing what is removed), on the other hand, has been found to occur more generally in productive grasslands where moderate grazing removes standing dead vegetation, which in turn reduces self-shading and enhances regrowth (Knapp et al., 2012, Charles et al., 2017). Often, in productive livestock managed regions neither exact compensation nor overcompensation is found, but rather undercompensation (suppressed aboveground productivity) (Ash and McIvor, 1998).

Factors that modulate different impacts of wild and domesticated herbivores are many and diverse. Functionally, wild and domestic herbivores might be similar in terms of diets and therefore lead to similar impacts on the vegetation as they consume many of the same grass species (Kartzinel et al., 2015). However, the impact they pose on productivity may vary in space and time, i.e. cattle can enhance mean primary productivity, whereas wildlife strengthen the stability of vegetation productivity across variable climatic conditions (Charles et al., 2017). The co-evolutionary history between herbivores and plant communities also plays an important role in terms of productivity, as plants may be adapted to tolerate a certain level of grazing by specific assemblages of herbivores. The wild migrating herbivores tend to concentrate and graze intensely in areas when the grass is actively growing, and then leave when the vegetation dries out (McNaughton, 1985, Bonnet et al., 2010). Even though there is evidence that grasses in semi-arid grasslands have evolved to tolerate high grazing intensities and periodic droughts (Coughenour, 1985), they do not manage well under both conditions simultaneously. Additional drought induced by herbivores in grazing lawns can lead to reduced productivity (Veldhuis et al., 2014). Timing of herbivory relative to precipitation also plays an important role. For instance, if grazing during the growing season becomes more intense and chronic this might eventually limit the plants stored belowground reserves (Turner et al., 1993) and further lead to diminishing growth in dry periods (Ash and McIvor, 1998). Several studies have reported declining productivity rates as a result of too high intensity grazing by livestock (Milchunas et al., 1995, Ritchie, 2014, Charles et al., 2017), the latter found with stocking densities lower than in most range lands in African savannahs.

The functional plant community response to wild and domestic herbivore grazing may reflect the response of any dominant plant species in the ecosystem. Whether or not an ecosystem is dominated by specific plant species have been found to depend on grazing regimes (Koerner et al., 2018). For instance, livestock grazing has, to a larger extent than wildlife grazing, been found to promote a more homogenous vegetation structure by opening up space for less competitive species to colonize accessible patches (Porensky et al., 2013, Charles et al., 2017, Young et al., 2018). However, livestock at high densities might also graze unselectively, and dominant less palatable species could be eaten at a larger extent, thereby leaving only a few tolerant species to dominate (Olf and Ritchie, 1998, Charles et al., 2017). Often these new dominant species have a more prostrate growth form, and are more grazing-resistant (Coughenour et al., 1985). Plants and herbivores interact in complex ways, thus it is important

to recognize the response of dominant and subordinate species in communities that are depending on many interacting factors.

The research objective of this thesis was to quantify (i) the impact of wildlife protected areas and livestock dominated pasture areas on aboveground productivity and herbivore consumption rates, (ii) the spatial and temporal effects of rainfall on productivity and consumption, (iii) the interaction effect of land-use and rainfall variability on productivity and consumption and (iv) the response of selected dominant grass species in contrast to the remaining subordinate grass species.

We hypothesised that (i) productivity would be equal to or higher in pastures compared to wildlife protected areas because more continuous grazing would facilitate regrowth and lead to higher productivity. Consumption was expected to be higher overall in pastures due to more continuous higher grazing pressure by livestock consuming all that is available in limited areas. Furthermore we hypothesised that (ii) both productivity and consumption would be strongly linked to rainfall seasonality, and expected higher productivity with higher rainfall, with a peak in the onset of the rain season followed by a saturation in productivity toward higher rainfall levels; and also that (iii) productivity would be highest in livestock dominated pastures in the onset of the wet season but also lowest in livestock dominated pastures at low rainfall due to grazing during the growing season causing reduced productivity in dry periods. Because wildlife densities vary more seasonally, consumption was expected to be closer to maximal productivity in the dry season in pastures than in the wildlife dominated areas. Lastly, we hypothesized that (iv) the dominant species in pastures would show higher productivity than subordinate species because they are adapted to tolerate the high grazing pressure in pastures. In contrast, the dominant species in the wildlife areas that are present under lower grazing pressure would show equal or lower productivity than subordinate species as they are less palatable and, hence, less grazed. Consumption of dominant species was thus expected to be higher compared to subordinate species in pastures than in wildlife protected areas.

MATERIALS AND METHODS

STUDY AREA

The study was conducted from February 2017 to May 2018 in the Serengeti-Mara Ecosystem in areas inside and outside wildlife protected areas surrounding the Serengeti National Park in Tanzania (2°27'-3°40'S, 34°02'-34°85'E). The Serengeti Ecosystem uniquely delineates the migratory route of one of the world's largest group of migratory herbivores. The original boundaries of the Serengeti National Park were set in 1959 (Sinclair, 1995). Since then the area of protection has expanded to include adjoining Ngorongoro Conservation Area, Maswa Game Reserve, Ikorongo Game reserve, Makao Wildlife Management Area and numerous other areas (Frank et al., 1998, Estes et al., 2012), all with fenceless borders. Precipitation varies spatially and temporally and ranges from 350 mm yr⁻¹ in the southeast to 1200 mm yr⁻¹ in the northwest, with a dry season from June to October and a short rain season from November to December followed by a long rain season from March to May (Norton-Griffiths, 1979). Soil types vary from fertile silty soils on the southern plains to infertile clay soils in the north-west, and typically have greater soil depth towards the north (Sinclair et al., 2007). Overstorey vegetation consists mostly of savannah woodland dominated by two tree species: *Vachellia tortilis* (formerly *Acacia tortilis*) and *Vachellia robusta* (formerly *Acacia robusta*). Herbaceous vegetation is dominated by warm-season C₄ grass species that generally respond quickly to both rainfall and defoliation; i.e. medium-height grasses, such as *Themeda triandra*, in the north-west and short-grasses, such as *Chloris pycnothrix*, in the southern plains (McNaughton, 1985). Dominant large wild herbivores include wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), elephants (*Loxodonta africana*), topi (*Damaliscus lunatus*) and numerous gazelle species in the protected areas. The dominant herbivores outside the protected areas are cattle, sheep and goat. In the protected areas wildebeest and zebra migrate in dense groups annually, stay in the northern parts of the system in the dry season, and move to stay for five months in the southern shortgrass plains in the wet season (Boone et al., 2006). The remaining wild herbivores occur at low densities. In the pasture lands, livestock are more sedentary but as borders are unfenced both wildlife and livestock can move freely across the border and there is evidence of illegal grazing into the park (Veldhuis et al., 2019). Fire is a common management tool in the protected areas and the grassy vegetation is burned regularly to prevent wood encroachment (Augustine and McNaughton, 1998), but is almost non-existent in pasture areas. The sites for this experiment were chosen due to little burning in these areas. However, during the experiment fire occurred in one of the sites, Handajega, in February-March 2018 with minimal impact on the established plots.

SITE SELECTION

Five sites were chosen based on differences in rainfall and land-use across contrasting rainfall regions (Figure 1; Table 1). Two sites were located in the north-west close to Lake Victoria, hereafter called 'wet region', one site in the center of the National Park, hereafter called 'intermediate region' and two sites in the south-east, hereafter called 'dry region'. Within the wet and the dry region, sites were located across two distinct land-uses: (1) pastureland with livestock grazing and (2) wildlife dominated grazing inside protected park areas (Figure 1).

The intermediate region was established in the core protected area (in Seronera, close to research facilities), representing only wildlife dominated grazing.

a)

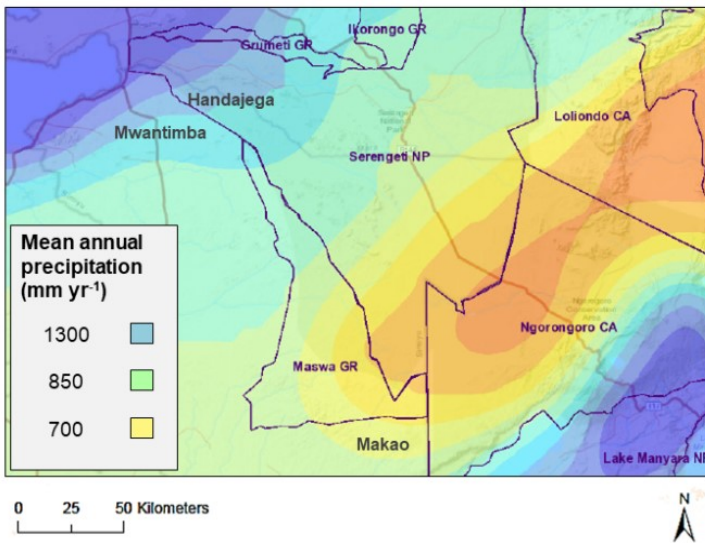
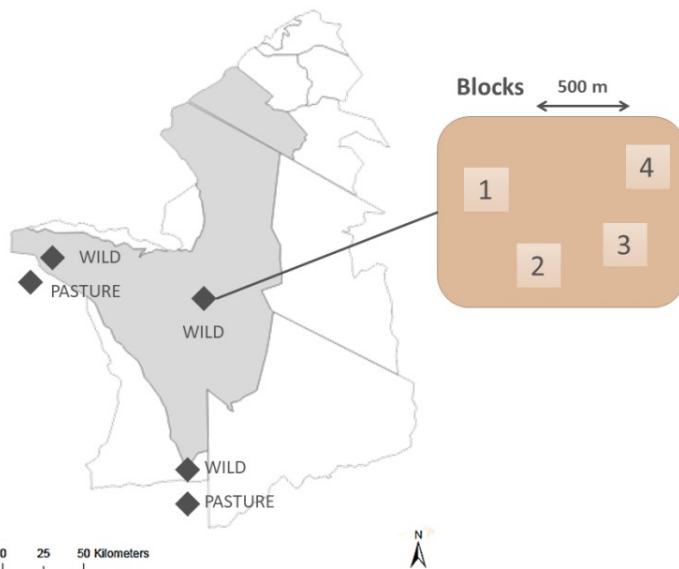


Figure 1. a) Mean annual precipitation (mm yr^{-1}) of the study system.*

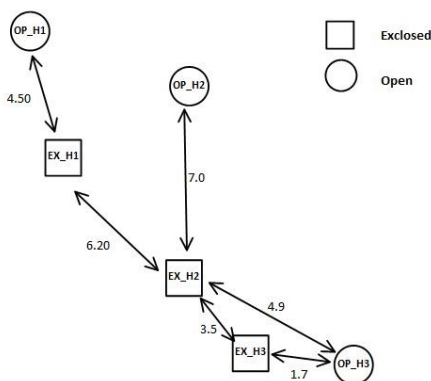
b) Experimental setup showing the five study sites in livestock dominated pastures (pasture) and wildlife protected areas (wild). Four blocks were nested within sites in a few hundred meter proximity.

c) Paired exclosures and open plots were established in each block and moved to new locations seven times between February 2017 and May 2018. Example of a hand drawn map, used for mapping previous locations.

b)



c)



*Precipitation map adapted from the Tanzanian National Bureau of Statistics [Map data: Esri, HERE, DeLorme, USGS, Intermap, INCREMENT P, NRCAN, Esri Japan, METI, Esri China (Hong Kong), Esri Korea, Esri (Thailand), MapmyIndia, NGCC, © OpenStreetMap contributors, and the GIS User Community]

Table 1. Rainfall, vegetation and soil properties at all study sites. Rainfall (MAP), dominant grass species cover \pm SE (the most dominant and second most dominant species per site), number of observations included, total vegetation cover \pm SE, mean vegetation height (cm) and soil properties (%).

Site	Location	Land-use	MAP (mm yr ⁻¹) 2015- 2017	MAP (mm yr ⁻¹) May 2017- May 2018	Dominant grass species cover (%)	Number of observations	Total veg. cover (%)	Mean veg. height (cm)	Soil properties*			
									Soil N (%)	Soil organic carbon (%)	Sand (%)	Soil type
Handajega	2.27° S 34.03° E	Wildlife protected area	1279	1531	<i>The_tri</i> (22 \pm 1.58), <i>Spo_fes</i> (5 \pm 0.93)	28	49.98 \pm 0.20	14.25	0.11	1.42	60.49	Vertisol/ Planosol
Mwantimba	2.35° S 34.05° E	Pasture	1295	1523	<i>Chr_ori</i> (35 \pm 3.44), <i>Chl_pyc</i> (5 \pm 1.39)	24	53.63 \pm 0.34	3.8	0.14	1.38	47.69	Arenosol
Seronera	2.44° S 34.85° E	Wildlife protected area	856	1207	<i>Dig_mac</i> (17 \pm 1.32), <i>Pan_col</i> (10 \pm 1.49)	34	47.21 \pm 0.17	9.68	0.13	1.40	61.76	Solonchacks
Maswa GR	3.30° S 34.85° E	Wildlife protected area	717	951	<i>Cyn_dac</i> (11 \pm 0.68), <i>Tri_ter</i> (8 \pm 1.31)	35	28.86 \pm 0.15	3.15	0.25	2.16	20.57	Leptosol
Makao	3.40° S 34.85° E	Pasture	672	894	<i>Chl_pyc</i> (13 \pm 1.83), <i>Dac_aeg</i> (6 \pm 1.36)	22	38.30 \pm 0.28	3.97	0.14	1.41	61.28	Leptosol

*The soil samples were recorded per block for all sites in December 2018. Data included soil properties such as soil texture classified by soil sand %, soil nitrogen % and soil organic carbon %. Soil texture analyses were done with the pipette method and estimated by the particle size distribution (Krogstad et al., 2018) and a Vario Micro Cube (Elementar) analyser was used to get SOC and N estimates.

EXPERIMENTAL DESIGN

Productivity and consumption of the herbaceous vegetation were quantified using moveable exclosures. With this approach, as opposed to long-term exclosures, it is possible to measure productivity under the influence of grazing and to determine temporal variation in grazing intensity. The method is frequently used in grazed grasslands and savannahs (Frank and McNaughton, 1992, Turner et al., 1993, McNaughton et al., 1996, Knapp et al., 2012, Veldhuis et al., 2016, Frank et al., 2017). Four replicate blocks were established in each site (Figure 1b) approximately 500 m apart. All established blocks were located in open grass swards >1.5m away from tree canopies (Treydte et al., 2010). In each block we established two plots (0.6 × 0.6 m) at the beginning of the experiment. Barbed wire fences (0.8 × 0.8 m) was built around one of the plots using wooden poles pounded into the ground and three to four rounds of barbed wire (approximately up to 1m above ground level) to prevent access for grazers >5kg (Figure S1). Within each land-use, blocks were chosen based on shared dominant species to minimize the influence of species composition on herbaceous biomass estimates through time when moving exclosures and open plots. The dominant species were *Themeda triandra* and *Chrysochloa orientalis* in wildlife and pasture sites in the wet region, *Cynodon dactylon* and *Chloris pycnothrix* in wildlife and pasture sites in the dry region as well as *Digitaria macroblephara* in the wildlife site in the intermediate region (Table 1). Exclosures and open plots were moved within 30 m of previous plots (Figure 2b) to comparable areas based on the dominant species.

PLANT ABOVEGROUND BIOMASS AND COVER

Plant aboveground biomass and plant species composition were surveyed regularly between February 2017 and May 2018. This time-period encompassed two long rain seasons, one short rain season and one dry season. Paired exclosures and open plots were moved every 21 to 87 days, resulting in a total of seven harvests over 15 months. For each setup and harvest, vegetation height (cm) and vegetation covers were all recorded. Total vegetation cover, dominant species and subordinate species with >5% cover were visually estimated and assigned a cover value (percentage of the area) within a 0.6 × 0.6 m quadrat. Aboveground biomass (including green herbaceous material and standing dead herbaceous material) was clipped to soil surface in both open and exclosed plots. All clipped biomass was collected in labelled paper bags with the dominant species in one bag and other subordinate species in another. All plant biomass was solar air-dried for several weeks until reaching a stable weight, then weighed (± 0.01 g). Total productivity was calculated as the difference in dry weight biomass inside the exclosure at the end of a sample period and the initial dry weight biomass of an adjacent open plot at the start of the period (equation 1). For subsequent sample periods biomass clipped in the open plot was used as the initial biomass estimate for the next period. Herbivore consumption was calculated as the difference in dry weight biomass inside the exclosure and the paired open plot at the end of each sample period (equation 2). The measures of both productivity and consumption were converted to daily rates ($\text{g m}^{-2} \text{day}^{-1}$) to account for differences in length of the harvest intervals (Frank et al., 2017).

$$Productivity (g m^{-2} day^{-1}) = \frac{\frac{Dry\ biomass\ Ex_{t1}(g)}{0.36\ m^2}}{harvest\ period\ (days)} - \frac{\frac{Dry\ biomass\ Op_{t0}(g)}{0.36\ m^2}}{harvest\ period\ (days)} \quad (1)$$

$$Consumption (g m^{-2} day^{-1}) = \frac{\frac{Dry\ biomass\ Ex_{t1}(g)}{0.36\ m^2}}{harvest\ period\ (days)} - \frac{\frac{Dry\ biomass\ Op_{t1}(g)}{0.36\ m^2}}{harvest\ period\ (days)} \quad (2)$$

Due to variability between covers in exclosures and open plots, sometimes biomass of the exclosed treatment would be less than the open treatment, and so the data also includes negative productivity values, also demonstrated by e.g. Charles et al. (2017). To account for the even larger heterogeneity of dominant species cover between plots (ranging from 0-92%) the dominant species estimates of productivity and consumption were weighted by their estimated proportional dominant species covers in each plot (Equation 3 and 4).

$$Productivity\ weighted (g m^{-2} day^{-1}) = \frac{\frac{Dry\ biomass\ Ex_{t1}(g)}{(0.36\ m^2 \times cover)}}{harvest\ period\ (days)} - \frac{\frac{Dry\ biomass\ Op_{t0}(g)}{(0.36\ m^2 \times cover)}}{harvest\ period\ (days)} \quad (3)$$

$$Consumption\ weighted (g m^{-2} day^{-1}) = \frac{\frac{Dry\ biomass\ Ex_{t1}(g)}{(0.36\ m^2 \times cover)}}{harvest\ period\ (days)} - \frac{\frac{Dry\ biomass\ Op_{t1}(g)}{(0.36\ m^2 \times cover)}}{harvest\ period\ (days)} \quad (4)$$

Due to occasional mismatch between the ground cover estimates and the dry biomass weights, some productivity measures were extreme negatives. The most extreme values were considered unreliable; therefore estimates that subsided below $-10\ g\ m^{-2}\ day^{-1}$ were removed from the dataset (four observations).

ACCUMULATED PRODUCTIVITY AND CONSUMPTION

Accumulated productivity and consumption were estimated for the entire 15 months experiment period; averaged per block per harvest period, and then summarized from the first to the last harvest. Due to missing plots from toppling or missing markers the productivity estimates of some blocks were estimated as averages of the remaining blocks within a land-use during the same harvest period. These missing values included; Makao harvest 1 (block 3) and harvest 5 (block 3 and 4) and Maswa harvest 2 (block 1 and 3). This was done to be able to obtain accumulated values for each block for the entire experiment period. The total percentage of the production that was consumed was calculated using the accumulated consumption and accumulated productivity estimates.

DAILY PRECIPITATION ESTIMATES

Daily precipitation data for the duration of the experiment was obtained using satellite-based daily rainfall from NASA's Goddard Earth Sciences Data and Information Services Center (Huffmann, 2017) and half-hourly measurements of cloud cover were taken using multi-satellite microwave data at $10 \times 10\ km$ spatial resolution. The data was used to calculate daily average rainfall (mm) for each harvest interval and cumulative rainfall (mm) for the entire 15

months. Mean annual rainfall at the study sites ranged from 672 to 1531 mm between 2015 and 2018 (Table 1).

STATISTICAL ANALYSIS

Linear mixed effect models were used to determine the influence of different land-use and precipitation regimes on seasonal productivity and consumption for both total plant community and dominant plant species. Land-use (wildlife protected area versus livestock pasture), daily average rainfall per harvest period and the two-way interaction (land-use \times rainfall) were used as fixed effects for the seasonal total community models. In addition to a linear term, a quadratic term was added for rainfall, as effect size was expected to saturate at higher levels of rainfall. For the consumption models, fixed effects also included productivity, and species (dominant species versus subordinate species) was additionally included as fixed effect in the models that investigated dominant species in relation to subordinate species. To account for non-independence due to the nested structure of the data we used block nested within site as a random effect structure. Because the experimental setup has repeated measures we used a temporal auto-correlation.

Accumulated total productivity, consumption and percentage production consumed was analyzed using linear mixed models similarly as the seasonal data, but with site only as a random effect, as accumulated productivity and consumption rates were averaged per block per time period. Fixed effects included land-use (wildlife protected area versus livestock pasture), accumulated total rainfall per block (and accumulated productivity for the consumption models) in addition to a two-way interaction.

Productivity observations from the last harvest in the wildlife protected area in the wet region were exceptionally high, and were therefore considered outliers within the dataset. For this reason, analyses were done both with and without these values. Additionally, rain region was not included as a fixed term because the patterns over the regions were more similar than we had expected from the start; most of the variation was within sites (96%) compared to between sites (4%). We therefore chose to exclude the rainfall region in this study to simplify the analyses and to focus more on the temporal patterns across land-uses.

All analyses started with full models using backwards stepwise removal of non-significant terms with the `drop1` function to obtain final models using the likelihood ratio test (LRT) and Akaike Information Criterion (AIC) selection of the most parsimonious model. The reduced models were contrasted with and without the fixed factors using the `update` function to generate p-values (Zuur et al., 2009). The mixed model analyses were run using the `lme` function of the `nlme` package (Pinheiro et al., 2007). All analyses were done in R version 3.5.1 (R Core Team, 2018).

RESULTS

SEASONAL PRIMARY PRODUCTION

Seasonal primary plant biomass production was overall strongly dependent on daily rainfall. However, differences in productivity between land-uses (livestock dominated pastures and wildlife protected areas) were marginal (Table 3; Figure 2). Mean productivity across the entire experiment was marginally lower in pastures, averaging $1.17 (\pm \text{SD } 1.82) \text{ g m}^{-2} \text{ day}^{-1}$ compared to $1.27 (\pm 2.07) \text{ g m}^{-2} \text{ day}^{-1}$ in wildlife protected areas (Table 3). Although land-use was not influencing productivity alone, it modulated the effect of rainfall on productivity, with a more positive effect in wildlife protected areas (Table 3; Figure 2). In harvest periods with average daily rainfall above 2 mm day^{-1} , productivity in pastures were equal or higher than productivity in protected areas ($1.18 \pm 1.25 \text{ g m}^{-2} \text{ day}^{-1}$ and $0.94 \pm 1.95 \text{ g m}^{-2} \text{ day}^{-1}$, respectively). However, during the last harvest period that experienced a high level of rainfall, productivity levelled off in pastures as opposed to a continuous increase in the wildlife protected area (Figure 2 and Figure 3).

In relation to daily rainfall, productivity increased towards periods that averaged 4 mm day^{-1} for livestock pastures and then levelled off at higher rainfall levels. Meanwhile, productivity in wildlife protected areas increased without saturating at higher daily rainfall levels, reaching productivity levels that were 70% higher than in livestock pastures at daily rainfall levels above 6 mm day^{-1} (Figure 3). However, the four high productivity observations from the wildlife protected area in the wet region of the last harvest in May 2018 differentiated from the rest of the observations and were potentially due to a fire accelerating herbaceous regrowth. When omitting these observations, productivity was only dependent on rainfall and there was no longer any modulating effect of land-use (Table 3). During the driest harvest periods of July and September with daily average rainfall levels below 2 mm day^{-1} overall productivity decreased dramatically in both livestock pastures and wildlife protected areas, averaging $-0.27 (\pm 0.73) \text{ g m}^{-2} \text{ day}^{-1}$ and $-0.11 (\pm 0.70) \text{ g m}^{-2} \text{ day}^{-1}$, respectively.

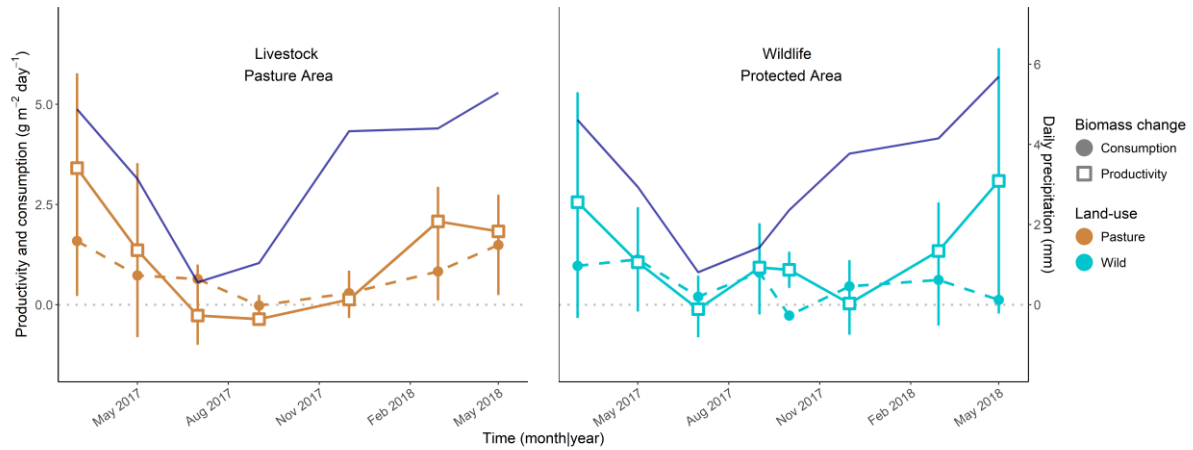


Figure 2. Daily productivity (squares) and consumption (circles) for each sampling interval in livestock dominated pasture lands (left, brown) and wildlife dominated protected areas (right, turquoise). Each point represents the mean of eight and twelve replicates in livestock pastures and wildlife protected areas, respectively. Error bars are \pm SD. Daily average rainfall (mm) for each harvest period is averaged across the rainfall regions and represented by the dark blue line.

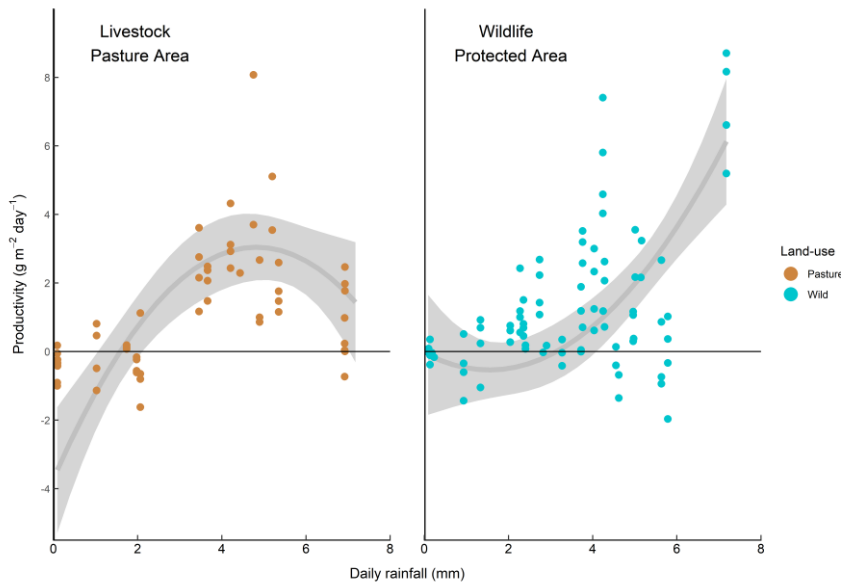


Figure 3. Daily productivity ($\text{g m}^{-2} \text{day}^{-1}$) in relation to daily rainfall (mm) for livestock pasture (left, brown) and wildlife protected (right, turquoise) areas. Predicted line of best fit using a linear mixed model is shown in grey. Error margin \pm SE.

DOMINANT SPECIES

Each of the targeted species represented on average between 11% and 35% of the total vegetation cover in each of the five sites across livestock pastures and wildlife protected areas and all were the most dominant species in their respective sites (Table 1). We found that, when weighted by their respective coverage, seasonal productivity of dominant species did not vary from subordinate species (Table 1; Figure 4). Furthermore, dominant species followed the overall same seasonal productivity patterns as the total community (Figures 2 and 4). Despite large variability (Table 2), the most productive of the dominant species throughout the experiment period was *Themeda triandra* in the wildlife protected wet region,

averaging $1.73 (\pm 2.29) \text{ g m}^{-2} \text{ day}^{-1}$. However, when considering peak productivity per harvest period, *Chloris pycnotherix* in the livestock pasture in the dry region reached the highest maximum productivity in February 2017 during the wet season. However, it should be noted that the model used to investigate productivity of the dominant species only had a low marginal effect ($R^2=0.13$ compared to $R^2=0.32$ in the plant community model, Table 3).

Table 2. Mean productivity of the dominant species (Productivity mean) and their standard deviation (SD) across harvest periods, and maximum productivity per species per harvest period (Productivity max) and standard deviations.

Dominant species	Productivity mean ($\text{g m}^{-2} \text{ day}^{-1}$)	SD (harvest)	Productivity max ($\text{g m}^{-2} \text{ day}^{-1}$)	SD (block)
<i>Themeda triandra</i>	1.73	2.29	2.90 (May 2018)	4.46
<i>Chloris pycnotherix</i>	1.22	3.07	6.60 (Feb 2017)	0.42
<i>Cynodon dactylon</i>	1.02	2.62	4.62 (May 2018)	1.26
<i>Chrysochloa orientalis</i>	1.12	2.42	2.83 (Mar 2018)	1.38
<i>Digitaria macroblephara</i>	0.48	3.27	3.92 (Mar 2018)	2.31

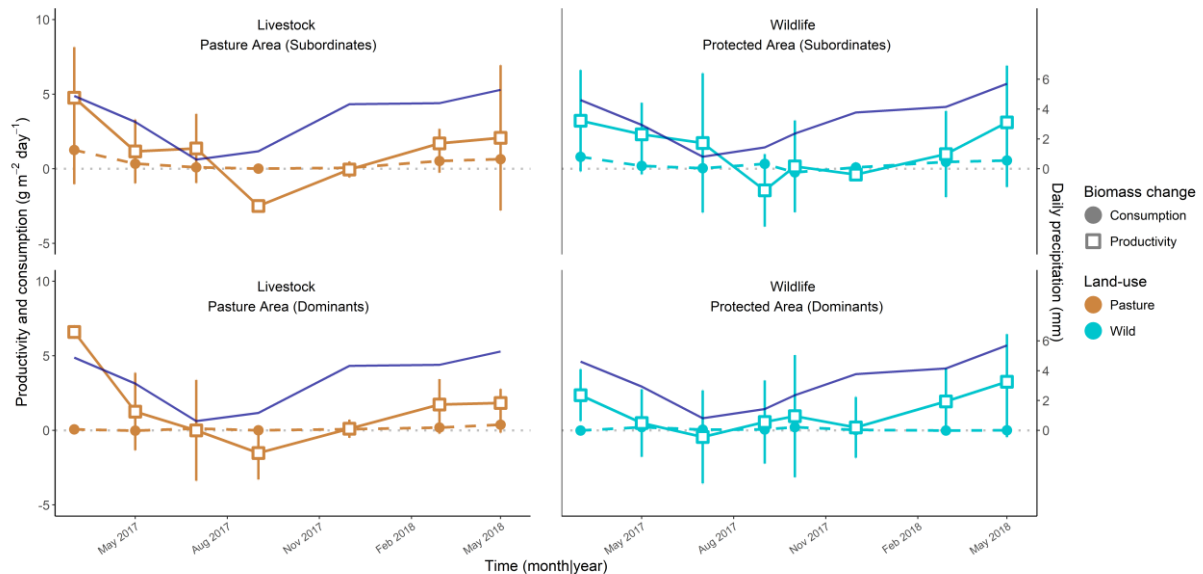


Figure 4. Daily productivity (squares) and consumption (circles) for subordinate species (upper) and dominant species (lower) for each sampling interval in livestock dominated pasture lands (left, brown) and wildlife dominated protected areas (right, turquoise). Each point represents the mean of eight and twelve replicates in livestock pastures and wildlife protected areas, respectively. Error bars are \pm SD. Daily average rainfall (mm) for each harvest period is averaged across the rainfall regions and represented by the dark blue line.

Table 3. Linear mixed model results for the seasonal productivity and consumption, showing all response variables and the fixed factors that are included in the final models. Conditional R^2 (Con R^2) and marginal R^2 (Mar R^2) are given for all models, and represents the explained proportion of variance by both fixed and random effects and fixed effects only, respectively. The corresponding degrees of freedom (df), parameter estimates of each fixed factor (Estimates), standard errors (SE), F-statistics (F) and the corresponding p-values (P) from likelihood ratio test are given.

Response variable	Explanatory variables	Con R^2	Mar R^2	df	Estimate	SE	F	P
Periodic productivity		0.35	0.32					
	Intercept			116	1.32	0.33		
	Land-use			3	0.01	0.42	0.04	NS
	Periodic daily rainfall			116	10.39	2.43	36.50	<.001
	Periodic daily rainfall ²			116	-8.30	2.43		
	Land-use × Periodic daily rainfall			116	2.83	3.38	17.17	<.001
	Land-use × Periodic daily rainfall ²			116	14.30	3.36		
Periodic productivity (without plots from Handajega)*		0.31	0.25					
	Intercept			114	1.30	0.37		
	Land-use			3	-0.44	0.48	1.33	NS
	Periodic daily rainfall			114	7.94	1.50	39.11	<.001
	Periodic daily rainfall ²			114	-6.32	1.52		
Periodic productivity (Dominant and subordinate sp.)		0.11	0.13					
	Intercept			219	1.35	0.48		
	Land-use			3	-0.02	0.62	0.01	NS
	Periodic daily rainfall			219	14.24	4.66	17.72	<.001
	Periodic daily rainfall ²			219	-17.01	4.70		
	Land-use × Periodic daily rainfall			219	-1.07	6.41	9.13	<.01
	Land-use × Periodic daily rainfall ²			219	18.80	6.41		
Periodic consumption		0.31	0.31					
	Intercept			84	0.26	0.12		
	Productivity			84	0.32	0.05	38.67	<.001
Periodic consumption (Dominant and subordinate sp.)		0.11	0.11					
	Intercept			215	0.28	0.07		
	Periodic daily rainfall			215	3.86	1.00	7.60	<.05
	Periodic daily rainfall ²			215	1.35	0.96		
	Productivity			215	0.03	0.01	3.42	NS
	Pool**			215	-0.22	0.10	4.84	<.05
	Pool × Periodic daily rainfall			215	-4.27	1.49	9.90	<.01
Pool × Periodic daily rainfall ²			215	-1.69	1.44			

* Four high productivity observations from one of the sites of the last harvest in May 2018, Handajega, were omitted from the model, because occurrence of burning prior to the harvest was considered to drive the response.

** Pool signifies a factor of dominant species versus subordinate species.

SEASONAL HERBIVORE CONSUMPTION

Seasonal herbivore consumption did not vary across livestock dominated and wildlife protected land-uses, although there were marginal differences with averages of $0.79 (\pm 1.04) \text{ g m}^{-2} \text{ day}^{-1}$ and $0.56 (\pm 1.20) \text{ g m}^{-2} \text{ day}^{-1}$, respectively. Specifically, consumption was slightly more variable in wildlife areas, and occasionally exceeded livestock consumption rates (see marginal histogram, Figure 5). Furthermore, higher rates of consumption did not depend on rainfall, but were significantly dependent on there being higher rates of plant productivity (Figure 4; Table 1). Observations in the driest harvest periods with average rainfall levels below 2 mm day^{-1} were $0.64 (\pm 0.36) \text{ g m}^{-2} \text{ day}^{-1}$ and $0.20 (\pm 0.52) \text{ g m}^{-2} \text{ day}^{-1}$ in pasture and wild respectively, which correspond to consumption levels in pastures being more than three times higher than in the wildlife protected areas (Figure 2). Further, periodic maximum mean consumption was found in livestock pasture area and occurred during the first harvest period in February 2017, with a daily consumption of $1.59 (\pm 1.37) \text{ g m}^{-2} \text{ day}^{-1}$. In comparison, maximum mean consumption in wildlife protected areas was $1.13 (\pm 1.30) \text{ g m}^{-2} \text{ day}^{-1}$ and occurred in the subsequent harvest period in March (Figure 2).

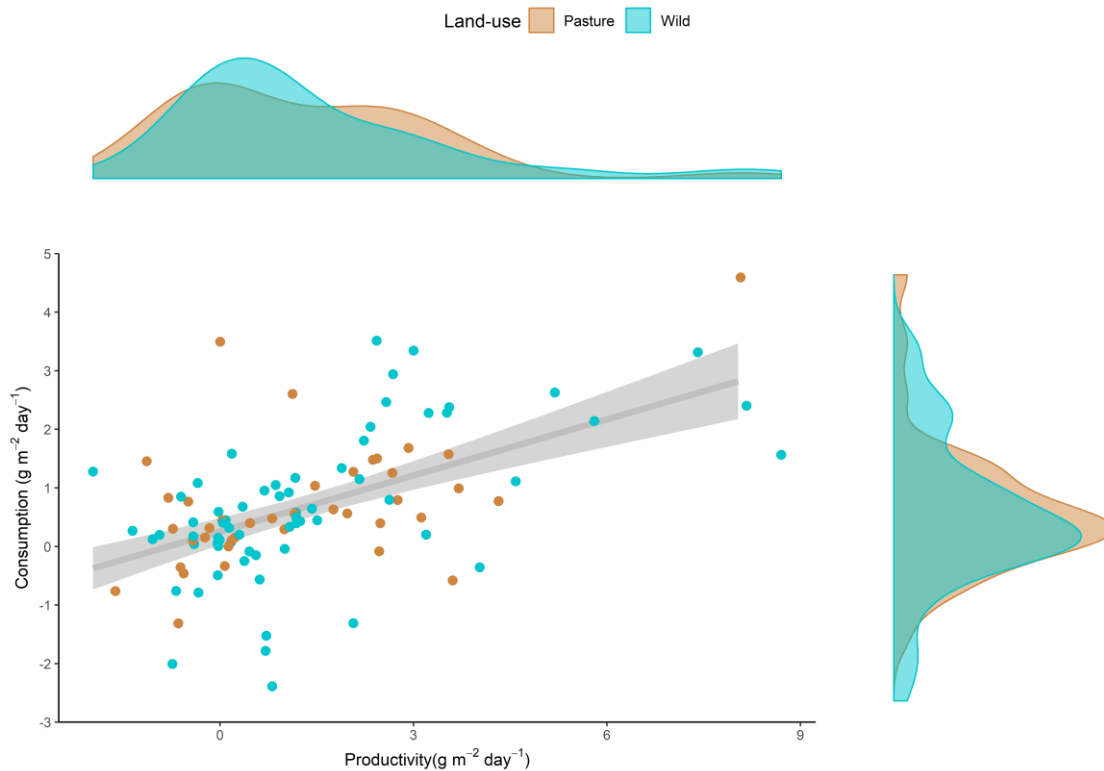


Figure 5. Daily herbivore consumption ($\text{g m}^{-2} \text{ day}^{-1}$) in relation to daily productivity ($\text{g m}^{-2} \text{ day}^{-1}$). Observations of livestock pastures and wildlife protected areas in brown and turquoise, respectively. Predicted line of best fit using a linear mixed model is shown in grey. Error margin \pm SE. Marginal histograms (top and right) show the distribution of productivity and consumption for livestock pasture (brown) and wildlife protected area (turquoise).

DOMINANT SPECIES

The seasonal consumption of the dominant species was positively related to daily rainfall, although marginal, and varied significantly from the subordinate plant community (Table 3).

Further, the consumption of dominant species was overall lower ($0.08 \pm 0.28 \text{ g m}^{-2} \text{ day}^{-1}$) compared to the subordinate species ($0.33 \pm 0.96 \text{ g m}^{-2} \text{ day}^{-1}$) and did not vary between land-uses (Figure 5). It should be noted that the consumption of dominant species and subordinate species were investigated as weighted by percentage ground coverage, and is therefore not directly related to the total community results which were not weighted by species cover (Figure 2).

ACCUMULATED PRODUCTIVITY AND CONSUMPTION

TOTAL COMMUNITY PRODUCTIVITY

Overall, accumulated productivity did not differ between the land-uses but was positively related to accumulated rainfall, although this was only marginally statistically significant ($p < 0.05$) (Table 4; Figure 6). Specifically, accumulated productivity in pastures was $470 (\pm 129.22) \text{ g m}^{-2}$ compared to $515 (\pm 228.04) \text{ g m}^{-2}$ in wildlife protected areas. The positive response to rainfall was higher in wildlife protected areas compared to in livestock pastures (Table 4; Figure 6); the least productive site was in the wildlife protected area in the dry region with $316.43 (\pm 117.85) \text{ g m}^{-2}$ compared to the most productive site reaching $725.02 (\pm 169.75) \text{ g m}^{-2}$ in the wildlife protected area in the wet region. However, when all observations from the last harvest in May 2018 were excluded (Table 4), productivity did not longer depend on neither land-use nor accumulated rainfall.

In addition, in one of the blocks within the livestock pasture in the driest region the productivity reached 631.75 g m^{-2} (Figure 6), which is surprisingly high compared to the other observations in the pasture, and nearly two times higher than the average productivity in the wildlife protected area of the same region. This might in turn partially explain the lack of response to accumulated rainfall in livestock pastures compared to the wildlife protected areas.

TOTAL COMMUNITY CONSUMPTION

Throughout the entire study period, there was significantly greater plant biomass consumption in livestock pastures compared to in wildlife protected areas, with a total of $337 (\pm 144.45) \text{ g m}^{-2}$ consumed in pastures and $224 (\pm 154.34) \text{ g m}^{-2}$ consumed in wildlife protected areas (Table 4; Figure 6). This corresponds to $69.5 (\pm 13.84) \%$ and $40.42 (\pm 24.70) \%$ of the production consumed in livestock pastures and wildlife protected areas, respectively (A3). Furthermore, consumption was not related to accumulated rainfall alone, although there was a marginal negative effect of rainfall in wildlife protected areas ($p = 0.06$), indicating less consumption with higher rainfall levels. Specifically consumption in wildlife protected areas ranged from $162 (\pm 119.06) \text{ g m}^{-2}$ in the dry region to $289 (\pm 98.60) \text{ g m}^{-2}$ in the wet region. Consumption in livestock pastures, however, was more or less equal between the regions; with $309 (\pm 186.87)$ and $366 (\pm 108.01) \text{ g m}^{-2}$ consumed in the dry and the wet region, respectively.

Table 4. Linear mixed model results for the accumulated productivity and consumption, showing all response variables and the fixed factors that are included in the final models. Conditional R^2 (Con R^2) and marginal R^2 (Mar R^2) are given for all models, and represents the explained proportion of variance by both fixed and random effects and fixed effects only, respectively. The corresponding degrees of freedom (df), parameter estimates of each fixed factor (Estimates), standard errors (SE), F-statistics (F) and the corresponding p-values (P) from likelihood ratio test are given.

Response variable	Explanatory variables	Con R^2	Mar R^2	df	Estimate	SE	F	P-value
Accumulated productivity		0.44	0.44					
	Intercept			13	270.93	223.40		
	Land-use			3	-634.99	328.79	0.43	NS (0.51)
	Acc. rainfall			13	0.13	0.14	5.07	<.05
	Land-use: Acc. rainfall			13	0.44	0.21	4.95	<.05
Accumulated productivity*	Intercept				151.87			
	Land-use							NS
	Acc. rainfall							NS
	Land-use: Acc. rainfall							NS
Accumulated consumption		0.67	0.67					
	Intercept			12	15.05	145.31		
	Land-use			3	234.76	227.27	7.54	<.01
	Acc. rainfall			12	-0.04	0.09	2.18	NS (0.14)
	Acc. productivity			12	0.82	0.16	17.76	<.001
	Land-use: Acc. rainfall			12	-0.25	0.15	3.55	NS (0.06)
Accumulated percentage consumed		0.57	0.45					
	Intercept			13	75.91	30.55		
	Land-use			3	-32.77	12.49	7.99	<.01
	Acc. rainfall			13	-0.03	0.02	2.44	NS (0.12)
	Acc. productivity			13	0.08	0.03	5.36	<.05

Explanatory variables included in the final models, Conditional R^2 (Con R^2), marginal R^2 (Mar R^2), degrees of freedom (df), parameter estimates of each fixed factor (Estimates), F-statistics and the connected p-values (from LRT).

*The accumulated productivity without all observations of the last harvest in 2018

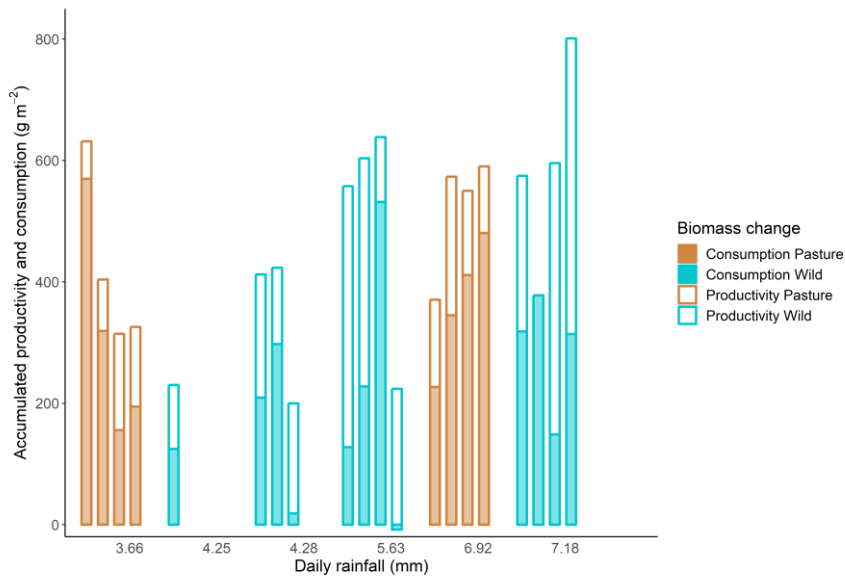


Figure 6. Total accumulated productivity (unfilled) and consumption (filled) for livestock pasture (brown) and wildlife protected areas (turquoise) inside and outside the Serengeti National Park averaged per block. Productivity and herbivore consumption has been summed over a 15 month period (February 2017 to May 2018).

DISCUSSION

Our findings highlight that in the Serengeti-Mara Ecosystem, net aboveground primary productivity is mainly driven by rainfall and maintained at relatively high levels in both livestock dominated pastures and wildlife protected areas. The capacity of both land-uses to produce similar amount of biomass is apparent on a seasonal and an annual basis alike. At the same time, there is an evident pattern of higher rates of consumption in livestock dominated pastures compared to wildlife protected areas, especially when rainfall is scarce. We suggest that there is an ongoing shift from bottom-up edaphic constraints to a more pronounced top-down control by herbivores, regulating productivity dynamics in the Serengeti-Mara Ecosystem. These findings are supported by remote satellite images that shows declining productivity at the borders of protected areas (Veldhuis et al., 2019).

SEASONAL AND ACCUMULATED PRODUCTIVITY

We found that diverse plant communities across the different land-uses of the Serengeti-Mara Ecosystem have the same capacity to produce biomass, despite the differences in grazing pressure from wildlife and livestock herbivores. The lack of productivity differences between land-uses could be associated with a positive direct effect of disturbance (i.e. dung), or plant response to disturbance (i.e. shift in growth form) in the livestock dominated pastures. Specifically, studies have found positive effects of disturbance in livestock dominated grasslands resulting from increased fertilization from dung (Augustine and McNaughton, 2006). Furthermore, we found the most dominant species in the livestock pasture in the dry region, *Chloris pycnophylla*, to keep a generally high productivity rate and reach a higher maximum productivity compared to the other dominant species (Table 2). This indicates that indeed some species, with specific growth forms, do manage exceptionally well under high livestock grazing pressure. Studies highlight that that high grazing pressure can induce a shift from perennials to annuals (Diaz et al., 2007). Annuals have more prostrate growth forms that tolerate higher grazing intensities, and can maintain high levels of productivity under high grazing pressure (Diaz et al., 2007). Otherwise, we found that the dominant and subordinate species did not vary in productivity across land-uses, although *Themeda triandra* in the wildlife herbivore wet region were overall marginally the most productive. Further, characteristics of dominant species may govern plant community responses to changes in disturbance (Koerner et al., 2014).

The maintained productivity rates across land-uses in wet seasons and overall through a 15 months study period suggests that exact compensation occurs even at high grazing intensities, consistent with previous findings (McNaughton, 1985, Milchunas and Lauenroth, 1993, Ritchie, 2014). The observation of complete removal of biomass during dry seasons is suggestive of the capacity of the system to regrow, potentially even higher in livestock pastures. For instance, in a semi-arid grassland in Kenya, productivity estimates did not decline with livestock grazing when conditions were favorable, they were rather enhanced (Charles et al., 2017). Yet, we observed that productivity differences in pastures were more extreme; high productivity in wet periods and oppositely a deficit in dry periods. This is supported by previous findings from semi-arid grasslands, where a combination of high

grazing pressure and drought reduced plant cover and production potential (Augustine and McNaughton, 2006, Porensky et al., 2013). This might be in line with the contrasting behaviour of migratory wild herbivores that follow nutrient flushes after rainfall, and livestock remaining to graze in dry periods, and thereby strengthening the deficit. However, it is difficult to pull out one specific explanation to this pattern of plant compensatory growth to grazing. Several studies point out a range of important factors that interact together with grazing intensity in explaining the role of plant compensatory growth, such as rainfall, soil texture, fire history, and plant species composition (McNaughton, 1985, Holdo et al., 2007, Ritchie, 2014). Hence, it is challenging to draw generalized conclusions regarding the response across two different land-uses with different grazing intensities, as all other factors may vary locally in space and time.

Rainfall is commonly emphasized as one of the most important drivers of plant productivity. And indeed, we found that both land-uses had drastically lower productivity rates when rainfall became scarce, indicating water limitations. In a mesic grassland in South-Africa, productivity showed a threshold response to rainfall (Bonnet et al., 2010). They found that when areas became increasingly drier, grassland productivity is less reliable and less potent to support the continuous grazing activity by livestock. Our findings further show that productivity saturates with increased rainfall in livestock areas but can continue to increase in wildlife protected areas with increasing rainfall (Figure 3). This suggests a more beneficial outcome of increased rainfall in protected areas, opposed to our expectations that productivity would saturate toward higher rainfall regardless of land-use. An overall saturation effect would be in line with the hypothesis that primary productivity is first and foremost driven by rainfall and peaking at intermediate rainfall levels before leveling off at higher rainfall levels (Veldhuis et al., 2016). Our opposing findings of increased productivity with increased precipitation could be attributed to fire events (discussed in detail below). On the other hand, it could also be related to a higher water infiltration capacity in the wildlife protected areas, due to less trampling and soil compaction compared to the livestock pastures (Riginos et al., 2012).

Interestingly, and in contrast to our findings, plant biomass in the Serengeti National Park has recently been shown to depend much less on annual rainfall between 2009-2016 than between 2001-2006 (Veldhuis et al 2019). This suggests that other factors are increasingly important, such as increased grazing intensities. However, the latter period might not be directly comparable to our results, because of the occurrence of the weather phenomena El Niño, which caused dramatic increases in rainfall during 2009-2016. El Niño is a regular disturbance to the ecosystem and is often followed by another phenomena, La Niña, that oppositely causes severe droughts (Bartzke et al., 2018). Climate change is expected to lead to increased drought frequency and intensity (Knapp et al., 2008, IPCC, 2012). These climatic changes may in combination with a replacement of wild herbivores by domesticated livestock show even more evident negative effects on productivity in the future, as observations in drier periods in our study indicates. At the same time, it should be noted that this system has always been highly variable in space and time (Sinclair, 2012). Therefore, the resident biota has adapted to the environmental fluctuations with a long-term co-evolutionary history. The

Serengeti-Mara Ecosystem might therefore be more robust than other more fragmented protected natural areas.

SEASONAL AND ACCUMULATED CONSUMPTION

Seasonal consumption was driven by variation in productivity, which was not surprising considering consumption is regulated by what is actually being available. On the other hand, the lack of significance of neither rainfall nor land-use on seasonal consumption is somewhat surprising. We expected consumption to be higher in livestock pastures regardless of seasonality, and more variable in wildlife protected areas due to migratory wild herbivores. Instead, consumption in relation to productivity was quite equally spread out between the two land-uses (Figure 5), and consumption was sometimes higher in wildlife protected areas than in livestock pastures, i.e. in May and October 2017 (Figure 3). Considering the accumulated consumption, however, the magnitude of consumption in the livestock dominated pastures is much greater and less dependent on accumulated rainfall, compared to the wildlife protected areas. The greater consumption is most likely attributable to higher biomass densities of livestock than wild grazers.

Holechek (1999) characterized moderate grazing as 35-50% of the palatable production being consumed, considering a global range of different grasslands. Our observations of 70% consumption in livestock pastures are far greater than that of moderate grazing, and fall within the range of heavy grazing. Holechek defined this as 75% of palatable production consumed without permitting regrowth by foraged species. Even though the observed consumption levels in the wildlife protected areas were much lower (40%), both land-uses stands out as areas with strikingly high consumption rates in a global perspective. Yet, this coincides well with the knowledge that savannahs support highly productive vegetation through a long co-evolutionary history with grazing herbivores, and that the ecosystem has the capacity to support the current high levels of grazing.

Furthermore, timing of grazing might be as important as the grazing intensity in terms of enhanced or reduced regrowth. A sporadic grazing by sedentary livestock may cause increased productivity, as compensatory regrowth is hypothesized to increase with time between grazing events (Augustine and McNaughton, 1998). This might be the case during wet season when grass is abundant and herders move their cattle around in the open range to graze sporadically, and thereby leaving the grass to regrow for shorter periods. However, due to climate change it is unclear at what consumption levels the vegetation will no longer be able to support the herbivore densities and compensate for the increased defoliation. In this study we did not account for the illegal grazing activity into wildlife protected areas, which could also potentially offset even more detrimental impacts on pasturelands. Even though we did not observe it in particular, continuous grazing and frequent trampling might expose the ground surface to erosion and compaction and reduce hydrological function and nutrient cycling (Hempson et al., 2015). The soil will be less suitable for new grasses to establish, eventually leading to reduced soil organic carbon. Ritchie (2014) found that plant compensatory responses are indeed important in the influence on soil carbon stocks.

Specifically, plant compensation in presence of frequent fire at intermediate grazing intensities enables an increase in carbon stocks.

The dominant species were consumed to a much lower degree than the subordinate species (Figure 4). Even though the lack of difference in productivity between dominants and subordinate species could be an indication that all grass species are grazed equally by the herbivores, it rather seems that herbivores in both land-uses are leaving the most dominant species, and that they are performing well under the current level of grazing pressure. Further, all dominant species except for one, *Chloris pycnorrhiza*, were perennials, which are generally contributing more to biomass production than annuals in savannahs (Ash and McIvor, 1998). Even though we studied grasses in particular, and did not collect forbs to any extent, it was evident that there were more forbs and small shrubs in livestock pastures than in the wildlife protected areas (pers. obs.). This increase in unpalatable forbs and shrubs is a tendency in areas with high densities of resident wildlife or livestock (Knapp et al., 2012, Veldhuis et al., 2019).

A fundamental challenge of the moveable enclosure method in estimating productivity and consumption is to reduce heterogeneity of plots as much as possible at the onset of each harvest interval (Sala and Austin, 2000). Heterogeneity in vegetation covers between paired enclosures and open plots may increase the variability in biomass estimates for determining productivity based on dry weight biomass. The resulting negative productivity rates in our study may be caused by this occasional heterogeneity between plots, and an increased negative value if open plots initially had more biomass than enclosures and are not necessarily grazed. There are techniques to get around variability caused by other interacting factors, such as burning the plots initially and excluding the driest harvest intervals from the annual estimates due to mostly negative production rates (Veldhuis et al., 2016). Shorter, more frequent intervals may also better reflect the effect of rainfall temporality and grazing events on short term productivity.

Further, we suggest that the ecosystem is to an increasing extent subject to a top-down regulation of biomass due to the high consumption rates rather than a bottom-up regulation based on productivity rates (Holdo et al., 2007). Moreover, a recent study by Veldhuis et al. (2019) found that the increased livestock impact around the edges of the protected national park area is squeezing the migrating animals into smaller areas and making migrating animals more vulnerable to droughts. This may further increase risk of undercompensation in response to more continuous grazing by larger masses of herbivores. As pointed out by Hopcraft et al. (2010), the combination of changing human land-use and changing rainfall patterns due to global warming might further alter the system in terms of availability of key environmental resources. These changes in available resources may in turn directly regulate herbivore distributions and multiple top-down and bottom-up processes in the savannah system.

The exceptionally high productivity observations from the wildlife protected area in the wet region of the last harvest was likely due to a recent burning in that area during the preceding months, combined with a high level of rainfall to stimulate grass productivity. We have reason to believe this, because when the last harvest was omitted from the data, accumulated

productivity was no longer driven by neither land-use difference nor accumulated rainfall (Table 4). Furthermore, fire and the additional effect of moderate grazing have been found to increase soil nitrogen and subsequently increase productivity (Holdo et al., 2007, Riginos et al., 2012). Herbivores are also shown to preferentially graze burned rather than unburned areas (Fuhlendorf and Engle, 2004), and an additive effect of both disturbances could possibly contribute to the observed high productivity. Although no fire was supposed to occur at the sites during the experiment period, the different land-uses usually experiences very different fire regimes. This incident in particular demonstrates the effectiveness of the fire management inside the protected park area and the potential for enhanced regrowth (Knapp et al., 2012) since the level of rainfall in this period would supposedly affect both land-uses similarly. However, whether the observed pattern is altered by herbivore assemblages, difference in species composition, fire management regimes or other contributing factors was not within the scope of this thesis and needs further testing.

CONCLUSION

Our findings demonstrate that productivity in this system is more driven by seasonal rainfall patterns than by land-use difference. This further indicates that both wildlife protected areas and adjacent livestock dominated pasturelands sustain a high productivity and consumption in wet periods and on an annual basis. Contrastingly, in dry periods when productivity is low, the proportional consumption is much higher in livestock pastures than in wildlife protected areas. As human livelihoods depend on high intensity grazing by livestock even in dry periods, and drought frequencies is predicted to increase in the future, productivity potential might decline. As a consequence, this may increase illegal grazing and hunting and amplify competition with nearby wildlife in protected park areas. However, the long-term effect of this land-use change remains unclear.

Extensive knowledge on grassland functional heterogeneity in space and time is specifically important, as this provides a baseline for what the system is able to sustain in terms of disturbances (Hopcraft et al., 2010, Fynn, 2016). Protectionism alone is insufficient to sustain biodiversity, and the need of a socio-ecological management is evident, yet challenging due to human-wildlife conflicts over restricted resources. The observed deficit of plant productivity in dry periods and the supporting knowledge that intense grazing in growth season over time might reduce productivity in the following seasons, should be a warning that establishment of proper management regimes are important; i.e. grazing rotation in domesticated areas, or reducing stocking numbers during dry periods (Fynn, 2016). Therefore, it is necessary with further research to determine what the optimal resource ratio in these areas are and what level of stocking densities the grasslands are able to support, with a special emphasis on the interannual seasonal variability across multiple years.

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APPENDIX

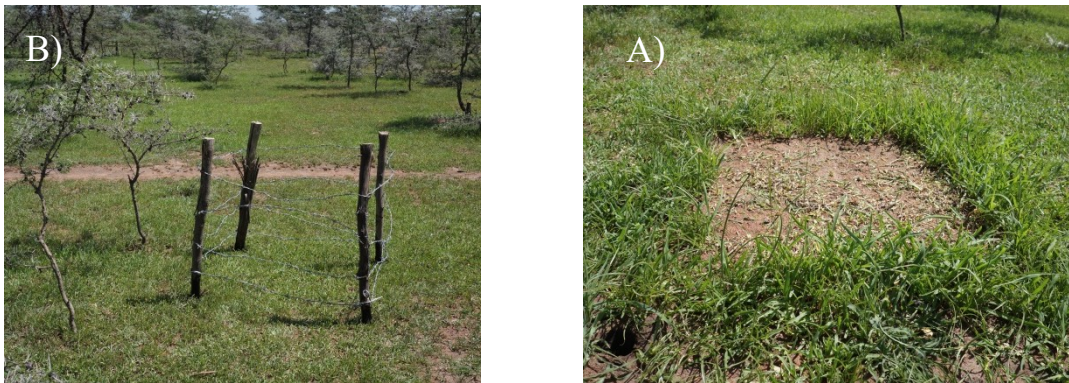


Figure A1. A) Barbed wire enclosure (0.8×0.8 m) made by wooden poles pounded into the ground and four rounds of barbed wire to keep grazers away. B) In an area of 0.6×0.6 m within the enclosure aboveground biomass was harvested.

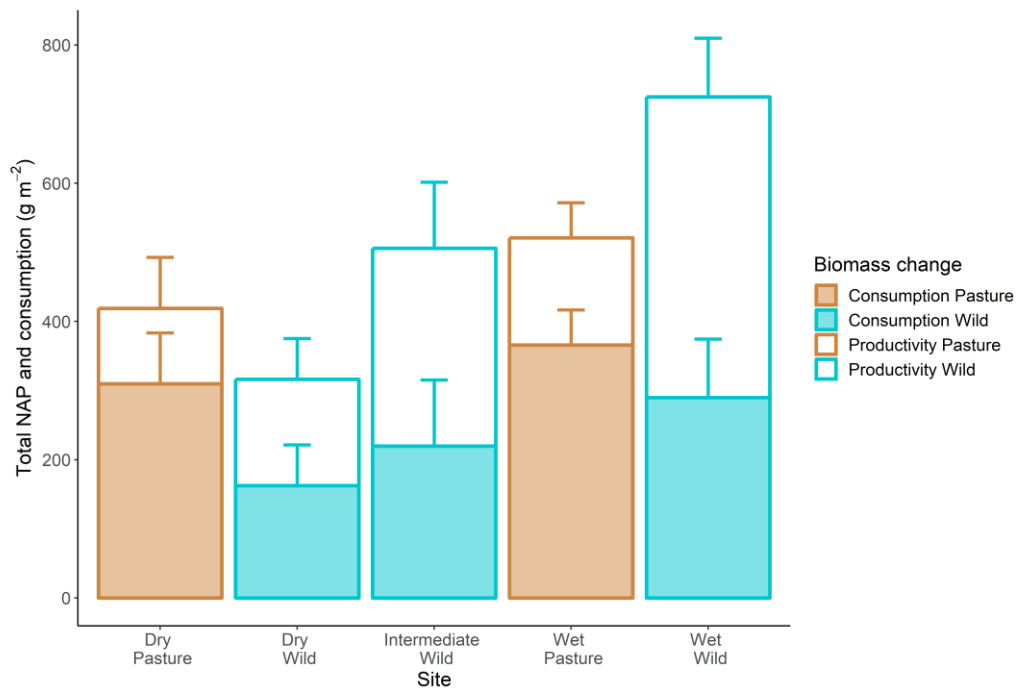


Figure A2. Accumulated productivity (unfilled) and consumption (filled) for all seven harvest periods, per site. Livestock pasture is shown in brown and wildlife protected areas in turquoise.

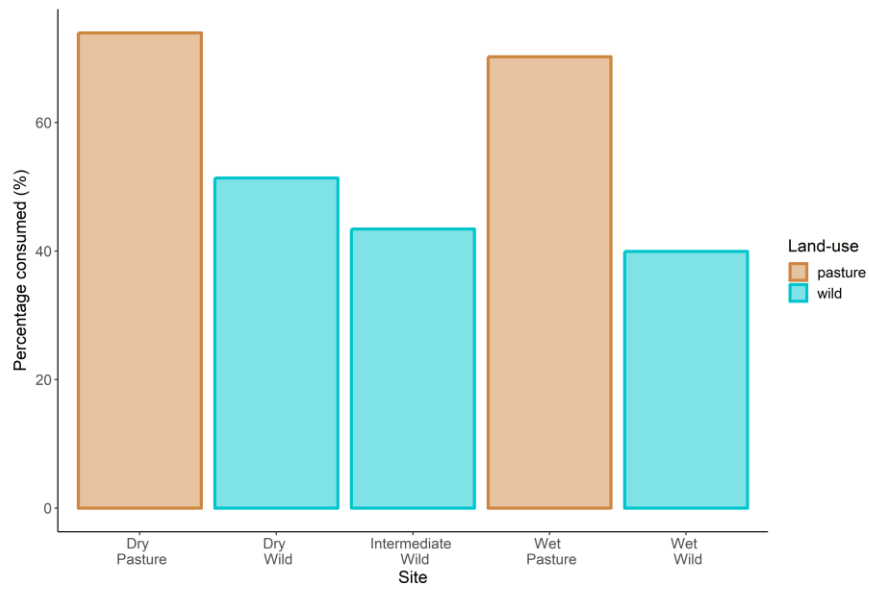


Figure A3. Percentage of accumulated production that was consumed for all sites across pasture (brown) and wild (turquoise). Productivity and herbivore consumption has been summed over a 15 month period (February 2017 to May 2018).

