

RESEARCH ARTICLE

Large herbivore impact on plant biomass along multiple resource gradients in the Serengeti

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Abstract

1. Herbivores form an important link in the transfer of energy within a food web and are strongly influenced by bottom-up trophic cascades. Current hypotheses suggest that herbivore consumption and impact on plants should scale positively with plant resource availability. However, depending on the effect of resources on plant quantity and quality, herbivore impact may vary with different types of resources.
2. We test four alternative hypotheses for the relationship between plant biomass, herbivore impact on plant biomass and plant resource gradients, each based on how resources might affect plant abundance and quality to herbivores. We measured plant biomass for four non-consecutive years in a long-term grazing enclosure experiment in the Serengeti National Park that includes seven sites that vary substantially in rainfall and soil and plant nitrogen (N) and phosphorus (P).
3. Our data supported the hypothesis that herbivore impact is controlled by plant quality, in this case driven by plant P, as herbivore effects on biomass decreased with higher rainfall but increased with greater plant P, but not N content. To our knowledge, this is the first experimental study to indicate that wild mammalian herbivory is associated with P availability rather than N.
4. *Synthesis.* Our results suggest that P, in addition to water and N, may play a more important role in driving trophic interactions in terrestrial systems than previously realized. Given the uncertainties in rainfall due to climate change and increasing anthropogenic manipulations of global N and P cycles, our findings emphasize the need to consider multiple resources for understanding how trophic interactions might be influenced by environmental variables.

KEYWORDS

grazing, multiple resources, phosphorus, plant quality, response ratio

1 | INTRODUCTION

Growing uncertainties in global climate patterns (IPCC, 2014) and increasing inputs of nitrogen and phosphorus due to human activities (Peñuelas et al., 2013) emphasize the importance of understanding

how trophic interactions might be influenced by changes in resources governing primary production. Bottom-up trophic cascades may strongly influence herbivore abundance, consumption and distribution. Much of the variation in terrestrial plant consumption by insect and mammalian herbivores, estimated to be 5%–90% of

annual above-ground production (Crawley, 1989; Cyr & Face, 1993; McNaughton, 1985), has been attributed to plant resource availability and climate gradients (Hawkins & Porter, 2003; Moreira et al., 2015; Zhang et al., 2016). These attributions largely assume that plant and herbivore growth are limited by the same resource(s), and predict that herbivore populations and impacts on plant biomass should increase together with resource availability (Ben-Shahar & Coe, 1992; Cebrian & Lartigue, 2004; Griffin et al., 1998). However, a growing body of research demonstrates that plant biomass and production are simultaneously limited by multiple resources, namely water, nitrogen (N) and phosphorus (P) (Cleland & Harpole, 2010; Elser et al., 2007; Eskelinen & Harrison, 2015; Fay, 2015; Harpole et al., 2007; Harpole et al., 2011) while herbivores during plant growing seasons are generally considered to be limited by plant N. In addition, plant quality to herbivores, as plant tissue resource: carbon (Stern & Elser, 2002), is likely to increase with N and/or P supply in the soil but decrease with any resource that promotes only C assimilation (e.g. light, water, CO₂) (Jarell & Beverly, 1981; McLauchlan et al., 2010). There is a need to disentangle the separate influence of these different resources rather than consider them in aggregate as 'nutrients' (Borer et al., 2014; Borer et al., 2020; Olff et al., 2002), but few studies have done so.

We explore four non-mutually exclusive, alternative hypotheses for variation in fenced and unfenced plant biomass, and the impact of repeated herbivore consumption on steady-state plant biomass along separate gradients of rainfall, N and P availabilities. In fenced plots without herbivores, steady-state plant biomass, approximated as an average over time, is likely to increase with elevated supplies of each resource. In contrast, plant biomass response to resource supply in unfenced plots may be more complex as it depends on how herbivore abundance and consumption change with a given resource, and how plants are able to respond to herbivory. For instance, increasing resource supply may allow faster plant growth in unfenced plots leading to compensation for herbivory by plants, essentially reducing herbivore impact on biomass at higher resource supply (hereafter called *plant compensation hypothesis*) (Figure 1a) (Frank et al., 2002; McNaughton, 1983; Ritchie, 2014; Ritchie & Penner, 2020; Strauss & Agrawal, 1999). Alternatively, elevated resource supply may increase plant biomass or plant growth, which may allow more frequent consumption by herbivores, thus supporting higher herbivore densities at high resource supplies (Fritz & Duncan, 1994; Gruner, 2004; Hunter et al., 1997; Siemann, 1998). Consequently, plant biomass in unfenced plots may increase more slowly with resource supply, leading to higher herbivore impacts at elevated resource supplies (hereafter *plant quantity hypothesis*) (Figure 1b).

Increases in the supply of plant resources might also produce changes in herbivore impacts via changes in plant quality (resource: carbon stoichiometry, nutrient concentration and the proportion of available biomass suitable for consumption) in different ways (hereafter *plant quality hypothesis*) (Figure 1c,d). The predominant hypothesis is that herbivores prefer plants with higher nutrient content as

consumers have higher tissue nutrient content compared to that of producers (Stern & Elser, 2002). Increasing water supply may increase plant biomass without increasing plant nutrient content (Cleland & Harpole, 2010; Harpole et al., 2007) and thereby may dilute plant tissue nutrients (Luo et al., 2017; Wang et al., 2017; Welti et al., 2020) along with declines in the efficiency of herbivore growth per unit plant biomass, the proportion of palatable plant biomass and therefore, herbivore impact on plant biomass (Figure 1c). In contrast, under greater supply of limiting nutrient(s), a greater proportion of plant biomass may be suitable for herbivore consumption (Griffin et al., 1998; Mattson, 1980; Schmitz, 1994; Welti et al., 2020), thereby causing a stronger reduction in plant biomass in unfenced plots (Figure 1d) in response to increases in that nutrient but not necessarily all other resources.

Resources may also differ in their influence such that resources that limit herbivore growth may not limit plant growth or vice versa. For example, sodium (Na) purportedly limits lactation and population growth in cattle and wildebeest (Hempson et al., 2015; Kaspari, 2020; McNaughton, 1988) but has no known positive effects on plant growth (Maathuis, 2014; Pardo & Quintero, 2002), while P might limit plant growth (Elser et al., 2007; Fay, 2015) but not necessarily herbivore growth (but see Schade et al., 2003; Bishop et al., 2010 for insect examples). In the case where a resource limits herbivore growth, but not that of plants (Figure 1e), fenced plant biomass does not change with increasing resource supply, but unfenced biomass decreases with increasing resource supply because plant nutrient content and consequently herbivore consumption increases with greater resource supply. Conversely, in the case where plant growth is limited by a resource, but herbivore growth is not (Figure 1f), both fenced and unfenced biomass should increase at the same rate with increasing resource supply, resulting in no relationship between herbivore impact and resource supply (hereafter *mismatched resource hypothesis*). Studies thus far have unequivocally identified N as a key nutrient for plant-herbivore interaction (Griffin et al., 1998; Mattson, 1980; Schmitz, 1994) but the influence of other nutrients such as P or Na on wild herbivores and their impact on plant biomass needs further exploration (Staver et al., 2021).

In this paper, we tested these alternative hypotheses simultaneously, and, to our knowledge, for the first time in terrestrial ecosystems. Even though enclosure studies are popular in grazing ecosystems, data from sites that span multiple resource gradients that also have a comparable herbivore species assemblage are very rare. We used data from the long-term grazer enclosure (LTGE) experiment in the Serengeti National Park, Tanzania (Anderson et al., 2007; Ritchie, 2014; Veldhuis et al., 2019a, 2019b) which is unique as it spans natural gradients of rainfall, total soil N and P content and plant N and P content while also being grazed by similar species of wild mammalian herbivores. Therefore, we measured within-year steady-state plant biomass and herbivore impacts on plant biomass, defined as the ratio of plant biomass in fenced to unfenced plots, at the LTGE experiment and analysed data from 4 years to assess the effects of mammalian herbivores on plant biomass across multiple resource gradients.

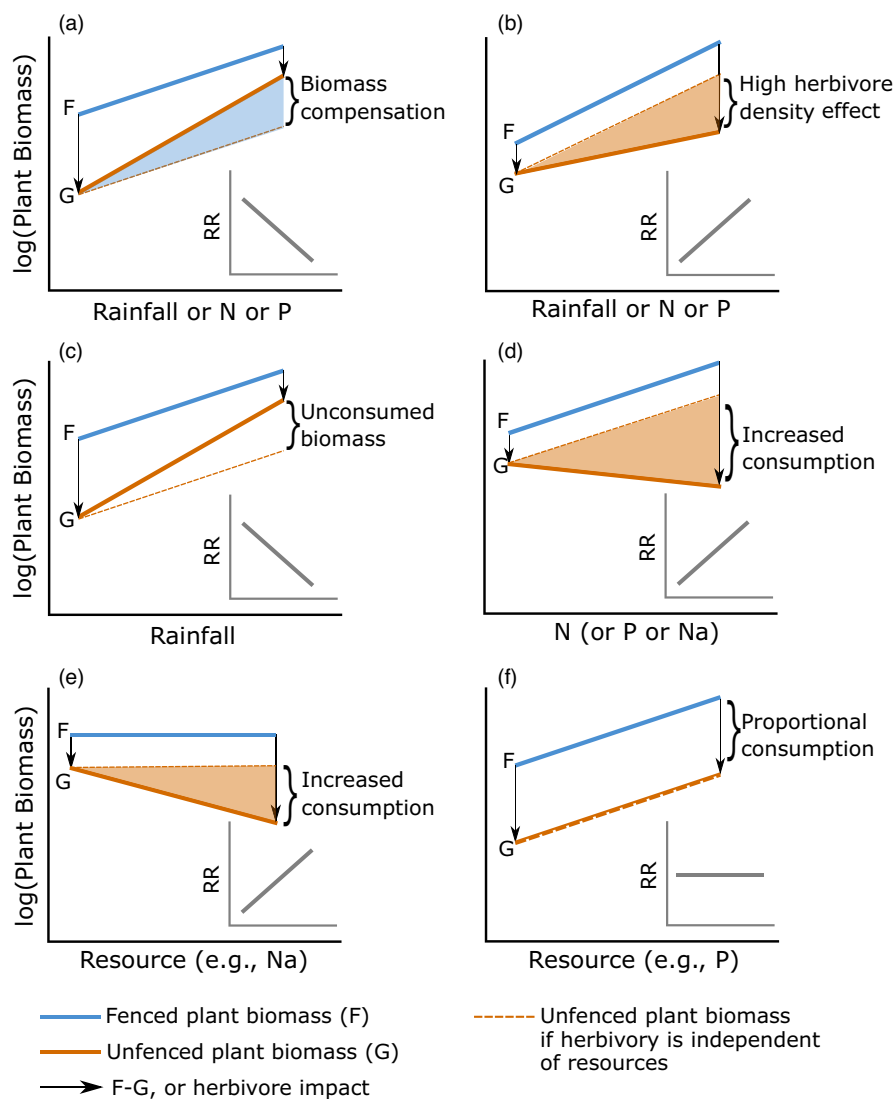


FIGURE 1 Non-mutually exclusive, alternate hypotheses for variation in fenced (F) and unfenced (G) plant biomass (log-transformed), and impact of herbivores on plant biomass (response ratio, RR) along gradients of rainfall and nutrients. (a) *Plant compensation hypothesis* [increased plant regrowth reduces RR at high resource supply for all resources]; (b) *plant quantity hypothesis* [increased herbivore densities in response to resources elevates RR at high supply of all resources]; (c, d) *plant quality hypothesis* [herbivores consume a lower proportion of plant biomass at high rainfall (i.e. low RR) but higher proportion at elevated N or P or Na (i.e. high RR)]; (e) *mismatched resource hypothesis* for resources limiting only herbivore growth [plant biomass in fenced plot does not change but herbivores consume higher proportion of plant biomass at high supply of Na (i.e. high RR)]; and (f) *mismatched resource hypothesis* for resources limiting only plant growth [plant biomass in fenced plots increases with resource and herbivores consume a constant proportion of plant biomass (i.e. no change in RR)]. The difference between the solid and dashed orange lines may be due to consumption replaced by plant regrowth (shaded blue), disproportionately higher consumption at high resource supply (shaded orange) or unconsumed biomass (unshaded)

2 | STUDY SITE AND METHODS

2.1 | Study area

The Serengeti National Park (SNP) in northern Tanzania is one of the last remaining intact grazing systems in the world, featuring more than 30 species of mammalian herbivores (McNaughton, 1985; Sinclair & Norton-Griffiths, 1979). However, year-round resident herbivores are clustered in hotspots (Anderson et al., 2010) and migration routes of

wildebeest *Connochaetes taurinus* and plains zebra *Equus quagga* vary annually, yielding substantial variation in forage consumption across the landscape, which also features substantial gradients in rainfall and soil N and P (Anderson et al., 2007; McNaughton, 1985; Ruess & Seagle, 1994). Mean annual rainfall ranges from 498 to 891 mm, total soil N varies from 0.13% to 0.33% and total soil P spans an order of magnitude from 0.007% to 0.08% (Anderson et al., 2007)(Table S1). All sampling in the national park was carried out with permits from TAWIRI, TANAPA and COSTECH, Tanzania.

2.2 | Grazing enclosure experiment

Long-term grazing enclosures (LTGEs) were established in 1999 at seven different sites separated by 20–100 km (Figure S1), along rainfall and nutrient gradients (Anderson et al., 2007) (Table S1). Sites were chosen to be close to grazing hotspots of high densities of multiple resident herbivore species (Anderson et al., 2010), so LTGE sites are regularly grazed irrespective of annual wildebeest and zebra migration routes (Anderson et al., 2007; Veldhuis et al., 2019b). As these hotspots are also associated with reduced risk of predation (Anderson et al., 2010), top-down control of herbivores is likely to be limited and therefore, unlikely to influence our results on herbivore impact on plant biomass. Each site features six 4 × 4 m plots arranged 30 m apart along a 180 m transect, three of which were randomly assigned to be fenced plots. These enclosures are fenced with chain link (mesh size ~10 × 10 cm) at ~2 m height and then reinforced with additional chain link (mesh size ~5 × 5 mm) at ~30 cm from the ground to exclude herbivores larger than 50 g and smaller than giraffes or elephants. Although the fences are not large enough to prevent giraffes and elephants, these mega-herbivores are likely to browse on woody plants which were absent in the study sites (Anderson et al., 2007) and dung from these species is rarely found within 200 m of the enclosure sites, suggesting that their effects on plant biomass are likely to be minor. The relatively small size of the plots is also unlikely to support significant populations of small mammals, further corroborated by little evidence of small mammal activity inside enclosures (Anderson et al., 2007). Nearest neighbour fenced and unfenced plots at each site were then paired to compare biomass for each of the three plot pairs at each site.

2.3 | Plant biomass

In each plot, we measured within-season steady-state plant biomass as the biomass at the end of the growing season (late May or June), as this best measures the season-long cumulative effects of consumption and plant regrowth. We clipped all plant material at the base in four randomly chosen 25 × 25 cm² quadrants in each plot. Clipped material was sorted into live, brown litter (assumed to have been produced during the wet season) and grey litter (produced the previous wet season). Green and brown material were then dried at 45°C for 7 days to obtain biomass measurements. Biomass was sampled before any potential prescribed burns in four non-consecutive years (2001, 2006, 2009 and 2016), at all the sites except for Balanites site in 2016. Although the end of the season or peak biomass is a frequently used sampling protocol for enclosure studies (Borer et al., 2014, 2020; Veldhuis et al., 2019b; Wigley et al., 2020), there may be uncertainties associated with single time point measurements that occurred an unknown number of days since the plot was last visited by herbivores. This uncertainty was addressed partially by including data from multiple years for the same plots.

2.4 | Site characteristics

We estimated the annual rainfall as the precipitation accumulated from the start of the dry season (July) of the previous year to the end of the wet season (June) of the year in which sampling occurred, based on the monthly averages from the CHIRPS database (Funk et al., 2015). Plant foliar N and P were measured from clipped above-ground green biomass (including flowers/seeds if present), using the Kjeldahl method and persulfate digestion method, respectively, at the Sokoine University of Agriculture (SUA), in 2001 and 2016. Since we lack data on nutrient content for all the years, we used the measured values of plant N and P for 2001 and 2016 and values averaged over 2001 and 2016 years for 2006 and 2009. Soil N and P were measured for each plot during 2008 and 2016 using the same analysis methods. In statistical analyses, we used the values of soil nutrients averaged over both 2008 and 2016 for 2001 and 2006, and values from 2008 for biomass from 2009. In contrast to N and P contents which have been estimated at multiple time points, soil and plant Na were only estimated in 2016 using flame emission spectroscopy at SUA laboratory.

Geological formations across the Serengeti, varying from ash deposits in the southeast to highly leached granite-derived sands in the north, may explain some of the variation in soil nutrients across the sites (Anderson & Talbot, 1965; Sinclair et al., 2008). Although plant N increased with soil N (Figure S2a), plant P showed considerable variation that was unexplained by soil P, especially at low soil P (Figure S2b). While soil nutrients reflect underlying environmental resource availability typically driven by climate and soil properties, plant nutrients reflect the availability of resources for herbivores as bioassays of the ability of plants to acquire nutrients, due to possible feedbacks of herbivores on nutrient cycling, plant species composition (Anderson et al., 2018; Ceulemans et al., 2014) and plant-microbe mutualistic resource exchanges (Antoninka et al., 2015; Ritchie & Raina, 2016; Soka & Ritchie, 2016). Therefore, we included both plant and soil N and P in our analyses and used 'Site' as a random effect in statistical models to account for inherent differences across sites.

2.5 | Statistical analyses

We define the impact of herbivores for each paired plot as a response ratio (RR) of plant biomass in the fenced to the unfenced plot (similar to Borer et al., 2020; Staver et al., 2021). All continuous variables, fenced and unfenced plant biomass, RR and the predictors, were log-transformed for the analyses to meet the normality and heteroscedasticity assumptions of the linear models. We also checked all our models for multi-collinearity using variance inflation factors (VIFs) and simplified the models to reduce multi-collinearity if VIF > 10.

We used mixed models in R (R Core Team, 2020) to test the effects of rainfall, N and P supplies on fenced and unfenced plant biomass, and herbivore impact on plant biomass (i.e. RR) on 4 years

(2001, 2006, 2009 and 2016) of data. For plant biomass in fenced and unfenced plots, we used the corresponding soil and plant nutrient data, and for RR we ran separate models with fenced and unfenced nutrient data. In each case, we fit linear mixed models with rainfall, total soil N and P and plant N and P as the fixed effects and Site and Year as the crossed random effects. We used the 'blmer' function from the BLME package to correct for 'boundary estimate' errors by including weakly informative priors for random effects (Chung et al., 2013). We repeated the analyses for herbivore impact by including plant or soil N as fixed effects along with other resource supplies, but only report the results in Supporting Information (Tables S6 and S7) as we do not have multi-year data for this element. We also analysed the data by considering 'Year' as a fixed effect in addition to rainfall and nutrient parameters and the results were similar to the model with 'Year' as random effect (Table S2).

We considered several models (Table S3) that differed in their main and two-way interaction effects but always had 'Site' and 'Year' as crossed random effects. We selected the model with the lowest Akaike information criteria corrected for sample size (AICc from MuMin package [Barton, 2009]) as the most parsimonious model and used a Chi-square test (likelihood ratio test) from the 'anova' function to confirm if the models were statistically different ($p < 0.05$) from each other. To assure ourselves that the trends are not an artefact arising from using soil and plant nutrient data from

multiple years, we also analysed data from 2016 for which we had the full complement of biomass and nutrient data and found that the overall patterns were consistent with the full dataset (Table S4).

We then used the estimated slope values, that is, positive or negative slopes, to test the directions of influence predicted by the hypotheses in Figure 1. For the purposes of visualizing associations of RR with different independent variables, we constructed partial residual plots (Figure 2) of variation in both dependent (RR) and independent (rainfall, total soil N, P and plant N, P) variables once the covariance between independent variables is accounted for without any random effects. These plots matched the outcomes of the most likely linear mixed model with the random effects considered.

3 | RESULTS

The end of the season plant biomass in fenced plots were not associated with any of the resource gradients (Table 1a), as evident from the random intercept model being the most likely model. In contrast, the end of the season unfenced plot biomass decreased with plant P (Slope (SE): -0.70 (0.23), Plant P model) and in some models increased with rainfall ($1.11[0.57]$, Phosphorus model), but remained unchanged with plant N, and total soil N and P when included in the model (Table 1b). In both cases, interaction terms resulted in high levels of multi-collinearity and had to be dropped from the models.

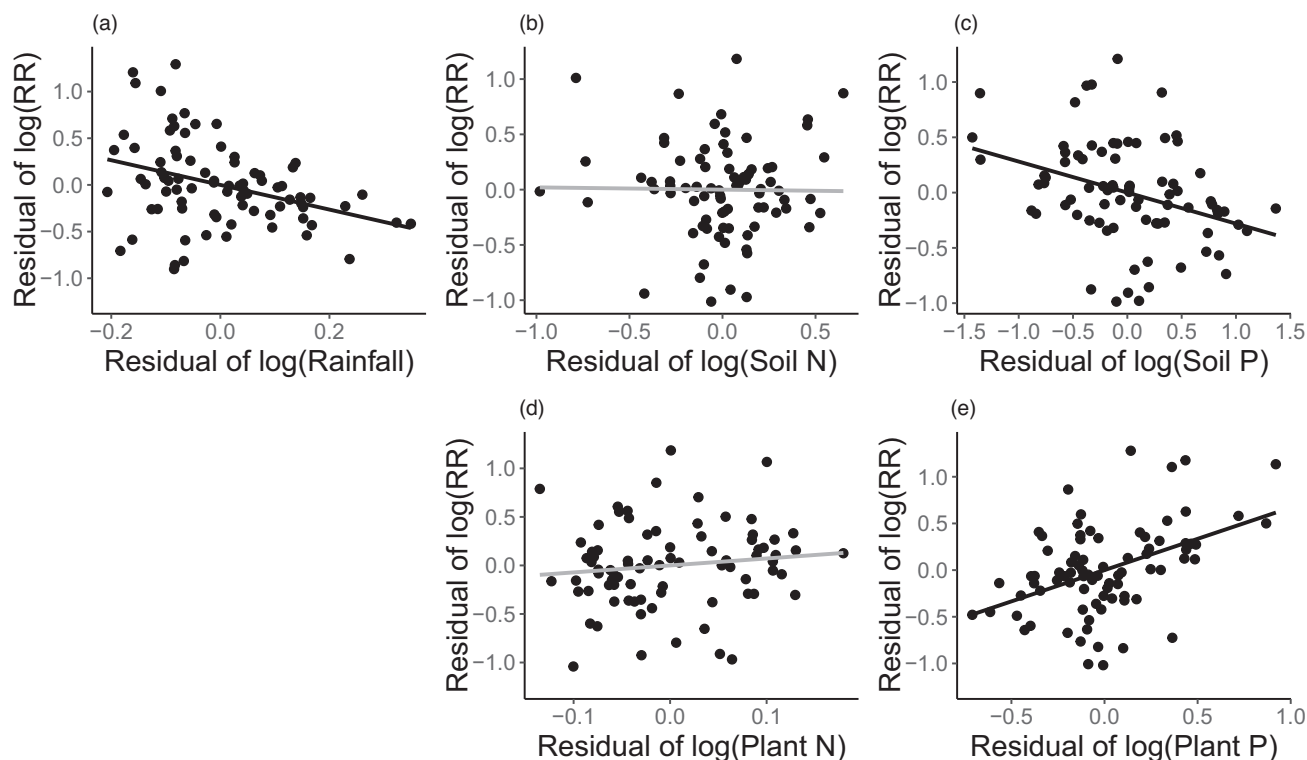


FIGURE 2 Variation in response ratio (RR) along gradients of (a) rainfall; (b) soil N; (c) soil P; (d) plant N; and (e) plant P based on the full model (no interactions). These patterns match the results from the most parsimonious model, that is, P model. Both x and y axes are partial residuals to visualize the trend after accounting for other effects. Dark regression lines correspond to significant slopes ($p < 0.05$); light-coloured lines indicate non-significant trends. See Section 2 for details on the calculation of partial residuals

TABLE 1 Estimates of AICc and slopes (SE in parentheses) associated with rainfall, soil and plant nutrients for the most likely models for (a) fenced plant biomass, (b) unfenced plant biomass and (c) response ratio or herbivore impact. Estimates from other models that were not statistically different from the most likely model are also included. Values in bold are statistically significant

	Intercept	MAP	Soil N	Soil P	Plant N	Plant P	AICc
(a) Fenced plant biomass							
Random intercept model	6.53 (0.18)						100.06
Plant P model	6.23 (0.36)					−0.20 (0.22)	101.45
Soil P model	6.25 (0.38)			−0.07 (0.09)			101.49
Plant N model	6.79 (0.38)				−0.40 (0.52)		101.54
Soil N model	6.46 (0.31)		−0.04 (0.15)				102.21
Rain model	6.40 (2.96)	0.02 (0.44)					102.33
(b) Unfenced plant biomass							
Plant P model	4.63 (0.38)					−0.70 (0.23)	144.48
Phosphorus model	−2.44 (3.76)	1.14 (0.58)		0.16 (0.14)		−0.75 (0.26)	145.51
Plant model	−1.39 (3.75)	0.98 (0.56)			−0.45 (0.72)	−0.55 (0.23)	146.49
Full model (No interactions)	−0.53 (3.83)	1.11 (0.57)	0.37 (0.21)	0.18 (0.14)	−1.36 (0.90)	−0.74 (0.26)	147.50
(c) Response ratio (RR)							
Phosphorus model	8.68 (2.81)	−1.15 (0.44)		−0.24 (0.10)		0.68 (0.17)	112.36
Full model (No interactions)	8.46 (2.83)	−1.19 (0.43)	0.003 (0.17)	−0.24 (0.09)	0.58 (0.69)	0.63 (0.17)	115.53
Plant P model	1.62 (0.25)					0.49 (0.16)	116.54

The response ratio measuring the impact of fencing on biomass varied almost by an order of magnitude from near 1 (no impact) to over 10 across sites and years. The environmental variables explained a significant amount of variation in RR and the patterns were similar irrespective of whether fenced or unfenced plot nutrient data were used (Table S5). Of the several models, the most likely model was one with rainfall, total soil P and plant P as the fixed effects, without any interaction terms (Phosphorus model, Table 1c). The second most likely model which was not statistically different from the previous model, was the one with rainfall, soil N and P and plant N and P as the fixed effects, without any interaction terms (Full model [no interactions], Table 1c). Yet again, interaction terms were insignificant and also resulted in high multi-collinearity and were dropped from the models. In both models, RR exhibited a significantly negative slope with rainfall (−1.15[0.44]) (Table 1c, Figure 2a) and soil P (−0.24[0.10]) (Table 1c, Figure 2c), and a positive slope with plant P (0.68[0.17]) (Table 1c, Figure 2e). Unexpectedly, the slope of RR was not significantly different from zero with either total soil or plant N content (Table 1c, Figure 2b,d). Sodium supply, either as soil Na or plant Na, was not associated with herbivore impact in this system (Tables S6 and S7).

4 | DISCUSSION

We show that the relative impacts of large mammal grazing on plant biomass, measured as a response ratio (RR), can vary dramatically with RR decreasing with rainfall and soil P, increasing with plant P,

and remaining unchanged with soil and plant N (Table 1c). These different associations with three resources that commonly limit plant biomass indicate that herbivore consumption, to the extent it affects biomass, may be driven by the influence of multiple resources on both plant growth and quality. The patterns of RR decreasing with rainfall and increasing with plant P support the *plant quality hypothesis*, under an assumption that herbivores are limited by plant P. To our knowledge, this is the first terrestrial study that has explicitly shown that effects of terrestrial mammalian herbivores on plant biomass are associated with P supply. Additionally, we find that the steady-state plant biomass in unfenced rather than fenced plots varied significantly across resource gradients, suggesting that plant biomass (in the absence of herbivory) may be co-limited by multiple resources, and it further interacts with herbivory to drive patterns in unfenced plant biomass and RR. These findings underscore the need to consider multiple resources for understanding how trophic interactions might be influenced by environmental variables, especially those like water, N and P that are subject to ongoing climate change and anthropogenic manipulation of global N and P cycles (IPCC, 2014; Peñuelas et al., 2013).

Our data are consistent with the *plant quality hypothesis*, where plant quality is presumably driven by plant P, and not by fibre. This outcome is somewhat surprising since most previous studies suggest that mammalian herbivore growth is limited by N (Griffin et al., 1998; Mattson, 1980; Schmitz, 1994), Na (Kaspari, 2020; McNaughton, 1988) or calcium (Ca) (Grunes & Welch, 1989; Mládková et al., 2018) but not P (but see Murray, 1995; Moen & Pastor, 1998 for theoretical expectations). However, relatively few

studies have considered variation in dietary P independently of other nutrients in mammalian growth and reproductive studies (Dykes et al., 2018). In addition to being a key component of DNA and RNA, P is also important for bone development in mammals (Grasman & Hellgren, 1993). Thus, it is reasonable that P might limit herbivore growth and that herbivore impacts on plant biomass might increase with plant P. As expected from previous studies, herbivore impact on plant biomass declined with increasing rainfall, consistent with a mechanism by which plant biomass accumulation supported by high water availability 'dilutes' nutrient content (Wang et al., 2017), leading to lower plant tissue concentrations.

The association with P may also be influenced by other mechanisms. For example, high P sites may support higher herbivore densities in response to faster plant growth (quantities we did not measure) resulting in higher impact rather than a direct limitation of herbivore growth by plant P. However, the lack of association of fenced plant biomass with resources, but positive and negative association of unfenced plant biomass with rainfall and plant P, respectively, suggests that plant quality rather than quantity may drive these patterns in the Serengeti. Alternatively, the *mismatched resource hypothesis* under the assumption that only herbivore growth is limited by P can explain the negative association of P supply with unfenced plot biomass and no association with fenced plot biomass. But it is unlikely given that previous research from the Serengeti and Eastern Africa indicate potential for both P and/or N limitation of plant growth in these grasslands (Kenya, 1973; McNaughton & Chapin, 1985; Propster & Johnson, 2015; Seagle & McNaughton, 1993). The historical emphasis on N as the key resource for plant-herbivore interactions (Bryant et al., 1983; Holdo et al., 2007; Mattson, 1980; McNaughton et al., 1997; Ritchie, 2000), in addition to relatively difficult methods for P estimation may have led to P being overlooked as an important resource for plant-herbivore interactions. Nonetheless, as evidence accumulates in favour of P (Bishop et al., 2010; Joern et al., 2012; La Pierre & Smith, 2016; Schade et al., 2003) from different systems (temperate and tropical regions, mammal and insect herbivores), more work will be needed to elucidate the different mechanisms by which P might influence herbivore impact.

Support was generally lacking for the alternative hypotheses (Figure 1). The decline in RR with increasing rainfall does not support the *plant quantity hypothesis* that higher rainfall yields faster plant growth, higher herbivore abundance and greater herbivore impacts. Our data also do not support the *plant compensation hypothesis* that herbivore impacts would be reduced at higher resource availability, which would support greater plant compensation to herbivory events at high resource availabilities and therefore declining RR at higher N and/or P (Frank et al., 2002; McNaughton, 1983). Although our finding shows a negative association between RR and rainfall and soil P, which would support the plant compensation hypothesis, we found positive, not negative associations between RR and plant P. Additionally, both unfenced and fenced plant biomasses are not associated with soil P, further negating the plant compensation hypothesis. However, the weak negative response of RR to soil P may arise from potential negative association between soil

P and arbuscular mycorrhizal fungi that typically colonize grasses in the Serengeti (Soka & Ritchie, 2016), which may enhance plant P (Smith & Read, 2008) at low soil P, similar to other systems (Johnson et al., 2015; Liu et al., 2012; Miller et al., 1995; Propster & Johnson, 2015).

Unexpectedly, we found no influence of N (or Na) supply, as either soil or plant N (or Na), on plant biomass or herbivore impact, as would be expected under the *plant quality hypothesis* (or *mismatched resource hypothesis*) under presumed N (or Na) limitation of herbivore growth (Kaspari, 2020; Mattson, 1980; McNaughton, 1988). One possible explanation for lack of correlation with N is, despite widely varying soil N of 0.05%–0.36% across plots and sites, the relatively narrow range of plant N (1.75%–2.75%) encountered in our study may have weakened our ability to detect association of herbivore impacts with plant or soil N. Plant N was largely greater than a proposed threshold of 1.5% above which herbivores may select diets that balance other important nutrients (Behmer & Joern, 2008; Felton et al., 2016). Some dominant grasses in the Serengeti such as *Themeda triandra*, *Digitaria macroblephara* and *Cenchrus meianus* exhibit root-associated nitrogen fixation (Ritchie & Raina, 2016; Ritchie et al., in prep), which may allow plants to have greater N than can be expected from soil N alone. For Na too, limited variation in soil and plant Na across our seven sites may explain the lack of association with RR.

Strikingly, relationships in RR and unfenced plant biomass along resource gradients were stronger with plant concentrations of P rather than soil P. Such a pattern may reflect the frequently observed disconnect between total soil nutrients and plant-available nutrients due to immobilization of nutrients in soil minerals and organic matter and dependence of N mineralization on plant carbon sources (Binkley & Vitousek, 1989). Thus, plant tissue nutrients may be better indicators of nutrient supply to trophic interactions than soil measurements, especially total soil nutrient measures that include nutrients bound to minerals and/or organic matter.

Additionally, differences in bedrock geology at our sites likely also contributed to variation in soil nutrients across the landscape which may then support plant communities that differ in their N and/or P requirement and plant nutrient content, thus indirectly influencing herbivores (Anderson & Talbot, 1965; Sinclair et al., 2008). For instance, it is possible that high nutrient regions may have allowed for herbivore behaviour that resulted in the formation of grazing lawns due to enhanced nutrient turnover (Hempson et al., 2015). But the fact that patterns in RR were similar for both fenced and unfenced plant nutrients suggests that herbivore feedback on soil and plant nutrients did not influence associations between herbivore impact and resource supplies in this study (Tables S5 and S6, Figure S3). However, inherent differences in the geology of the seven sites may have affected other aspects of herbivore behaviour which we did not measure and therefore, only accounted for such site differences statistically using random effects.

Compensation to herbivory by plants likely affected our biomass measurements in unfenced plots, as plots could have differed in the time since the most recent grazing events, with accompanying

greater regrowth and lower RR (Mitchell & Wass, 1996). However, time since the most recent grazing event would likely be longer at sites with lower herbivore density and fewer grazing events, implying that any reduction in RR would have been at sites with the lowest herbivore consumption. Therefore, plant compensation following herbivory is unlikely to affect the direction of relationships we detected but might account for some of the variation in RR not explained by our statistical model.

Furthermore, it is possible that the fenced plots acted as a refuge from predators and large animal trampling for small mammals, thus increasing their activity in fenced plots as has been reported for other grazing exclosures in African grasslands (Keesing, 1998, 2000; Keesing & Young, 2014). If so, we may have underestimated 'fenced' plant biomass and hence RR. However, such effects are unlikely to change the broader patterns that we see in our study. If small mammal populations do not change with resource gradients, similar to the findings of Young et al., 2015, then the relationships of plant biomass and RR would remain the same. Alternatively, small mammals may be more likely to seek refuge at sites with high herbivory levels implying that we may have underestimated herbivore impact from large herbivores at high grazing intensity sites, which can only weaken the associations of RR with resources. Therefore, the associations we observed would have likely been stronger in the absence of small mammals.

5 | CONCLUSIONS

We tested several competing hypotheses about the influence of multiple resources on herbivore impact on plant biomass and conclude that herbivore impact is influenced by multiple resources. Our results were consistent with the 'plant quality hypothesis' that herbivore impacts would be higher in response to forage nutrient content, in this case P, and lower in response to higher rainfall. This pattern represents the first time, to our knowledge, that impact of large mammalian herbivory on plant biomass has been shown to be positively associated with plant P rather than plant or soil N. However, it is unclear whether this pattern implies that herbivore growth might be limited by P or whether the pattern results from indirect positive influences of P on plant growth and herbivore density. Nevertheless, our results highlight the need to consider multiple plant resources in the environment in determining the strength of trophic interactions and herbivory in particular. Given the projected variation in rainfall in response to climate change and increasing anthropogenic inputs of nitrogen and phosphorus into the ecosystems, it will be crucial to understand the interactive effects of resources on plant-herbivore interactions.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

M.E.R. collected all the data; N.M. analysed the data and wrote the first draft of the manuscript. Both authors contributed significantly to revising the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Raw data are available from Dryad Digital Repository <https://doi.org/10.5061/dryad.b303788> (Veldhuis et al., 2019a).

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SUPPORTING INFORMATION

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