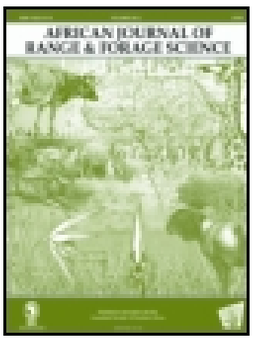

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Does defoliation frequency and severity influence plant productivity? The role of grazing management and soil nutrients

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Rangeland management approaches, including rotational grazing, rely on assumptions about plant growth responses to the intensity, or severity (sward height) plus frequency, of defoliation. We tested these assumptions at the farm, patch and plant scale using data from a grazing management trial in an Eastern Cape mesic grassland of South Africa along with field plot and glasshouse pot experiments. The grazing trial tested season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG) at equivalent stocking rates over three years. We found that grass growth responses in both potted plants and field plots were reduced under more frequent and severe defoliation but that this was mitigated under elevated soil nutrients, in line with the Compensatory Continuum Hypothesis which predicts that compensatory growth will increase across an increasing fertility gradient. In the farm trial, SLG, which theoretically causes high frequency, low severity defoliation, reduced bare ground cover and increased vegetation greenness with increasing defoliation intensity on nutrient-rich soils. This effect was not present under FCG or HPG and disappeared under very high defoliation intensities and on relatively water- and nutrient-poor soils. Managers are advised to only increase grazing frequency on relatively high nutrient soils, while maximizing recovery on poorer nutrient soils.

Keywords: high density grazing, behaviour, Selectivity, heterogeneity, holistic planned grazing

Supplementary material: available at https://doi.org/10.2989/10220119.2020.1766565

Introduction

The sustained defoliation of vegetation beyond its capacity to regrow degrades productivity and ecosystem functioning in heavily stocked rangelands across the globe (Fernández 2002; FAO 2010). Indeed, stocking rate, defined as the number of large stock units (LSUs) per hectare of available rangeland, is the most important management variable in determining vegetation and animal production (Van Poollen and Lacey 1979; Briske et al. 2008). The role of grazing management strategy, whereby grazing densities are controlled across a management unit using fencing or herding, is less influential on farm productivity (Sampson 1951; Heady 1961; O'Reagain and Turner 1992; Venter et al. 2019b). Despite the consensus of experimental evidence, the debate over the efficacy of rotational grazing relative to continuous or season-long grazing persists (Briske et al. 2011). This is possibly because rotational grazing should be able to maximise sward growth by some combination of defoliation duration, frequency and timing (McNaughton 1983). Nevertheless, plant basal cover and plant biomass are unaffected by forms of high density rotational grazing such as holistic planned grazing (Hawkins 2017; Venter et al. 2019b). To help resolve these inconsistencies between theory and praxis, We investigated plant growth responses to defoliation intensity, defined as a combination of frequency and severity, through controlled manipulative studies and compared these to responses observed in a farm-scale grazing management trial. For the purposes of this study, grazing is defined as, and includes the activities of defoliation, trampling and dung deposition.

Expansion of photosynthetic tissues is primarily a response to plant level resource sinks characterised by organs with increased demand for carbon (Wardlaw 1990; Paul and Foyer 2001; White et al. 2016). This sink regulation of photosynthetic rate determines foliar growth, and is the primary mechanism explaining grass responses to defoliation (McNaughton 1979). Removing foliar material from grasses triggers changes in both intrinsic (physiology and development) and extrinsic (resource availability) factors (McNaughton 1983), which often result in greater relative growth rates (Hilbert et al. 1981). Some of the internal plant mechanisms explaining this include an increase in light-saturated photosynthetic rates and associated carboxylating enzymes (Hodgkinson 1974; Detling et al. 1979; Lee et al. 2011), a surge of plant growth promoting hormones from roots to shoots (Avery and Lacey 1968; Iqbal et al. 2012), and reallocation of assimilate from storage organs to meristems (Gifford and Marshall 1973; Ryle and Powell 1975; Dawson et al. 2004; Machado et al. 2013). This is associated with a root pruning and a reduction in root growth (Crider 1955; Oswalt

et al. 1959; Wilson 1988) to re-establish a root to shoot balance, however as foliar material is recovered the weight allocation is shifted back toward shoots (Dunn and Engel 1971; McNaughton 1983). In older, less photosynthetically active leaves, partial defoliation particularly reduces stomatal and mesophyll resistance and thereby increases the intake of carbon dioxide and water vapor, essential for photosynthesis (Thorne and Koller 1974; McCormick et al. 2006). Extrinsic resources may also be more accessible in the post defoliation environment. Defoliation reduces shading and may increase water use efficiencies due to a reduction in leaf transpiration surface area (Baker and Hunt 1961; McNaughton 1979; White et al. 2016).

Plant growth responses to defoliation range from under-compensation, or partial replacement of lost foliar tissue, to over-compensation whereby plants regrow more foliar material than is lost during defoliation (McNaughton 1983; Belsky 1986). Reviews of the literature on compensatory growth have found under- or equal-compensation to be the norm because defoliation removes valuable photosynthetic material and thus reduces the capacity to produce carbohydrates (Belsky 1986; Georgiadis et al. 1989; Hawkes and Sullivan 2001; Wise and Abrahamson 2007). The exceptions to this norm are found when extrinsic (e.g. soil nutrients or moisture) or intrinsic factors (e.g. plant physiology and development) that limit plant growth are reduced or inhibited through defoliation (McNaughton 1983; Wise and Abrahamson 2007). For example, grasses in the Serengeti exhibit over-compensation of lost foliage (McNaughton 1979) and unchanged root biomass (McNaughton et al. 1998) partly because the grass species are a product of strong evolutionary selection for grazing tolerance and partly because nutrients and water are seldom limiting in this environment. It was this tropical savanna ecosystem that inspired McNaughton (1979) to develop the Grazing Optimisation Hypothesis which posits that above ground productivity of grazed plants is increased at low to moderate grazing intensities until productivity is maximised at an optimal grazing intensity, beyond which it begins to fall. Although some have argued that this hypothesis is true in an evolutionary sense (Hilbert et al. 1981), others have found no evidence to support it in rangeland management settings especially where resources are lacking (Belsky 1986).

In nutrient- and water-limited rangelands, grasses may fail to compensate for defoliation and thus the Grazing Optimisation Hypothesis breaks down. Simulated defoliation and nutrient limitation experiments have shown soil N (Hamilton et al. 1998) and P (Chapin and McNaughton 1989) to limit Serengeti grass growth responses to defoliation. Under-compensation in nutrient limited soils is exacerbated by the negative effects of defoliation on grass roots, which are vital for nutrient and water acquisition. In a quantitative review of experimental literature, Ferraro and Oesterheld (2002) found that defoliation of grasses reduced root biomass by 32% across all plant sizes. This may lead to eventual plant mortality and the formation of bare ground patches (Thurow 1991; Fuls 1992), or where herbivores select for palatable species, the invasion of less palatable species (Ellison 1960) with a concomitant decline in primary productivity, forage quality and animal production. The decline in vegetation greenness and increase in bare ground induced by overgrazing in arid rangelands has been observed using satellite imagery in Africa (Munyati and Makgale 2009), South America (Blanco et al. 2008) and Asia (Hilker et al. 2014). In these examples, defoliation intensity exceeds the capacity vegetation has for compensatory growth often reducing vegetation basal cover and enhancing erosion and bare ground formation.

The extent to which resource availability mediates plant compensatory growth responses to herbivory has been encapsulated in the Compensatory Continuum Hypothesis (Maschinski and Whitham 1989). Here tolerance to defoliation is predicted to be greater in high resource, low competition or otherwise benign environments. For example, fertile, moist soils facilitate fast regrowth after grazing (Hawkes and Sullivan 2001). This, combined with enhanced foliar nutrient concentrations (Bryant et al. 1983; Jones and Hartley 1999) and consequent palatability, attracts more herbivory, which promotes faster nutrient cycling via the animal gut and urine and dung deposition compared to slower microbial or physical decomposition and oxidation of plant material (Hobbs 1996; Frank and Groffman 1998; Bardgett and Wardle 2003). This process reinforces a positive feedback loop sustaining high soil and plant nutrient levels and has been suggested as one of the mechanisms behind the formation of grazing lawns in African savannas, characterised by productive, highly palatable and grazing tolerant grass species (McNaughton 1979; Hempson et al. 2015). Indeed, grazing lawns have been experimentally induced with nutrient addition, thereby corroborating the Compensatory Continuum Hypothesis (Cromsigt and Olff 2008).

Plant responses to a range of defoliation frequencies are seldom studied (Tiffin 2000) and the interaction between defoliation severity, frequency and soil nutrient levels even less so. We investigated these interactions experimentally at three different scales including a commercial farm grazing management trial, and *in situ* field plot, and *ex situ* potted plant defoliation experiments with bunch grasses from a mesic grassland of South Africa. We hypothesised that increasing defoliation intensity (frequency × severity) will reduce grass growth responses and that this would be mitigated under elevated soil nutrients, thereby supporting the Compensatory Continuum Hypothesis. Specifically, we predicted grazing intensity would reduce relative growth rates, below-ground productivity, shoot: root ratios, foliar greenness, and basal vegetation cover (the inverse of bare ground cover).

Materials and methods

Farm grazing trial

Merino Walk experimental trial was located approximately 5 km north of Cedarville, Eastern Cape, South Africa (30°21′8″ S, 29°3′29″ E) at an altitude of 1 440 m above sea level. Half of the trial was located on north-facing slopes covered by East Griqualand Grassland and the other half was located on low-lying flats covered by Mabela Sandy Grassveld and Eastern Temperate Freshwater Wetlands (Mucina and Rutherford 2006). Dominant grasses included *Themeda triandra* and *Eragrostis plana*, respectively. The area is underlain by mudstones and sandstones of the Elliot

and Molteno Formations (Mucina and Rutherford 2006), classified as Dystric Regosols (slopes) and Eutric Fluvisols (flats) according to the World Reference Base (IUSS Working Group 2015), also classified as poorly-drained and nutrient-rich haplic lixisols with high clay contents (flats) and relatively well-drained and nutrient-poor haplic acrisols (slopes) (Hengl et al. 2017). Long-term (1960–2000) mean annual rainfall and temperature is 760 mm and 15 °C (Hijmans et al. 2005), with most rainfall occurring during austral summer months.

To compare the initial soil nutrient status on the two areas of the farm, we took 14 and 19 evenly spaced soil samples on the slopes and flats respectively before the grazing trial was initiated. Using a 7 cm diameter soil auger, we collected four cores to a depth of 20 cm per sampling location. Given limited resources, a single soil depth was chosen versus stratified soil depths because 20 cm is commonly recognized as representing the A-horizon or topsoil (FAO 2006) and upon inspection, the soil pH, cation exchange capacity, soil organic carbon and total nitrogen fractions in the area did not differ between 0 and 30 cm (SoilsGrid, Hengl et al. 2017). Samples were bulked, air-dried and sieved to 2 mm. A subsample of each was sent to Bemlab (Somerset West, South Africa) for analysis of total N by the combustion method using a Leco-FP528 N analyser (Leco, St. Joseph, MI). For the determination of total P, K, Ca, and Mg, a subsample was analysed using a Spectro Xepos X-ray fluorescence (XRF) analyser (Spectro, Amatek materials analysis division, Kleve, Germany) after grinding soil to a powder. Measurements were conducted in a helium atmosphere using a silicon drift detector and were calibrated using a standard certified by the National Research Center for Certified Reference Materials, Beijing, China.

Three grazing management treatments, occupying 219 ha of land on the Merino Walk farm, were initiated as an experimental trial in December 2015. Prior to this, the land had been managed under conservative stocking rates as a commercial cattle and sheep farm. Baseline vegetation and soil measurements were taken to account for variation in legacy management effects across the treatments. Treatments included season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG) and were assigned to existing farm camps non-randomly due to management limitations (Figure 1). All treatments were stocked with year-old Bonsmara-Boran steers at a moderate stocking rate of 0.53 LSU ha^{-1} yr^{-1}, which is similar to the government recommended rate of 0.55 LSU ha^{-1} yr^{-1} (Avenant 2016). Although stocking rate was kept constant, treatments differed primarily in the number of camp divisions, and consequently the relative grazing densities, defined as the number of LSUs per subunit of area at any point in time on the rangeland. Equivalent stocking rates, but varying grazing densities, theoretically result in a range of defoliation frequencies (the inverse of recovery period from grazing) and severities (the quantity of foliage removed in one defoliation event). Rotational grazing approaches are suggested to enforce short bursts of intense and severe defoliation followed by extended periods of rest (Briske et al. 2011; Bork et al. 2017). Assuming cattle consumed equal annual forage biomass, the treatments lie on a continuum from high frequency, low severity (SLG) to low frequency, high severity (HPG), with FCG producing moderate frequencies and severities (Figure 2). These levels of defoliation severity and frequency are comparable to those applied in both plot and plot clipping experiments (see below).

In SLG grazing, one camp is grazed for an entire growing season and then cattle are moved to a second camp for the non-growing season. In FCG, cattle are rotated among three camps at varying levels of intensity, while one camp is left to rest for an entire year. In subsequent years the camp allocated to annual rest is the first camp to be grazed, and conventionally this is preceded by burning (Venter and Drewes 1969). We chose to exclude burning from this system because of difficulties in distinguishing and comparing fire and grazing behaviour effects across treatments. For this study, HPG refers to a high intensity grazing approach similar to short duration (Tiedeman 1986), cell grazing (McCosker 2000), and holistic planned grazing (Savory and Butterfield 2016). In the study we followed the adaptive management protocol of Holistic Management (HM) in which a flexible grazing plan is constructed outlining animal movements between multiple small camps with the aim of increasing animal densities and thereby increasing even utilisation and reducing overgrazing (Savory and Butterfield 2016). Portable electric fencing was employed to construct grazing strips of between one and two hectares in size. The farm manager and research team undertook an intensive three-day training course by an accredited HM trainer familiar with the South African context. This was done in order to adhere to HM principles and follow the correct HM planning procedure.

To quantify the spatial distribution of defoliation intensities, we deployed GPS collars on randomly selected cattle for 60 d on two summer (January2017 and 2018) and two winter (June 2016 and 2017) sampling occasions. GPS devices (Perthold Engineering LCC, Richardson, Texas, USA) were set to log a position every 5 min and attached to nylon belts fastened around the animals' necks. We deployed enough collars to obtain an average replication of three collars per treatment per sampling date. Three devices were placed at a known location and left for three weeks to test the spatial accuracy of the GPS. This revealed a median error of 5.4 m with 95% of the data points occurring within 22.5 m of the actual location. GPS devices remained active for an average of 29 ± 2.4 days per sampling occasion. We analysed the data from each GPS collar as a spatial point pattern using the 'spatstat' package in R (Baddeley et al. 2015). For each sampling occasion we included GPS points from all treatments over the period in which the HPG cattle were moved through one complete management unit (see camps in Figure 1). The GPS points were clipped to the boundaries of the camps occupied during the sampling period after applying a negative buffer of 10 m to each camp to account for the effects of fences on the cattle behaviour. We then defined GPS locations relevant to grazing pressure as consecutive points (5 min apart) greater than 22.5 m from one another which, according to our accuracy assessment reflects 95% certainty that the animal was not resting (i.e. grazing or walking). To estimate the spatial distribution of grazing pressure we then calculated the kernel (gaussian) smoothed density of the remaining locations, after

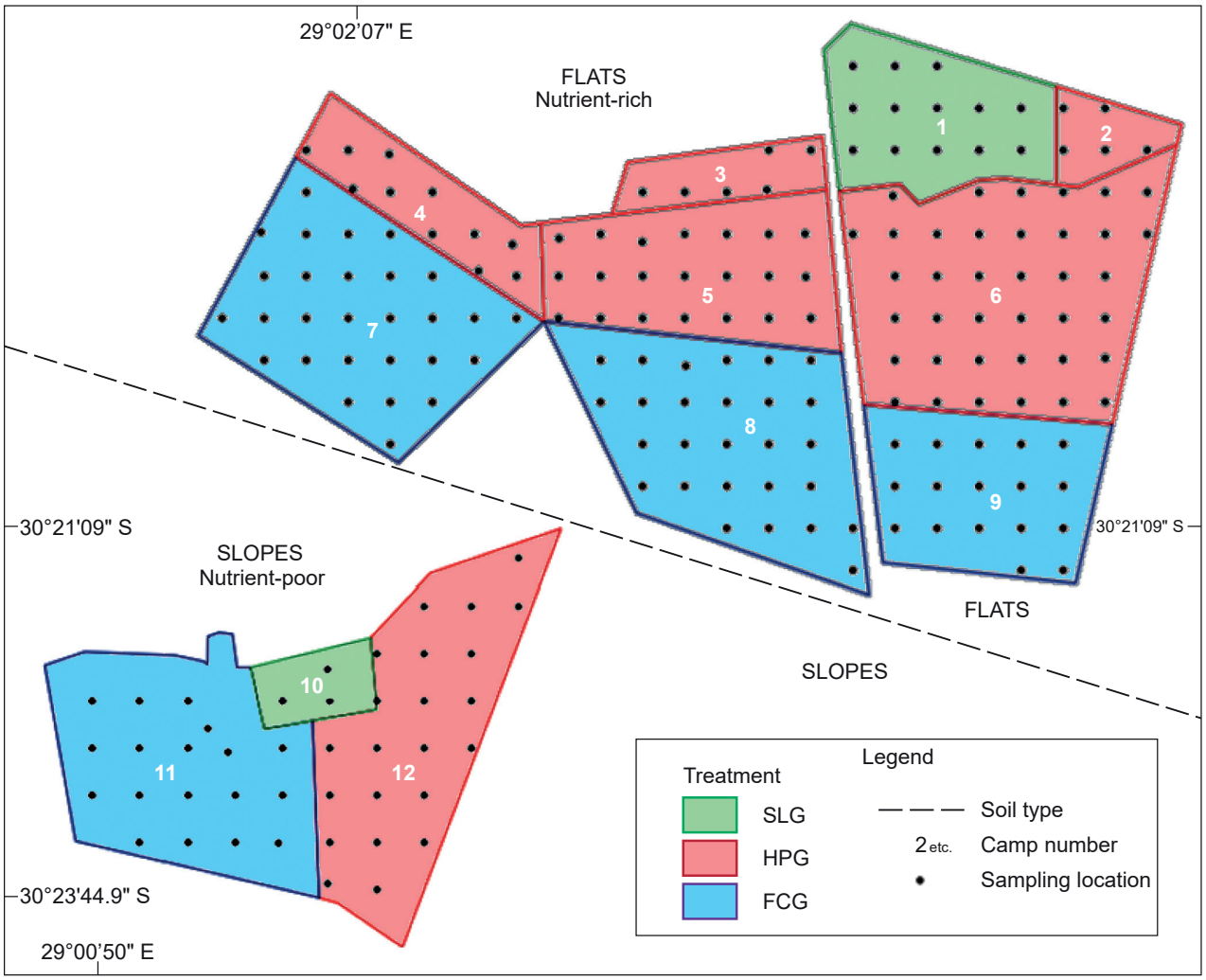

Figure 1: Merino Walk experimental trial layout for three grazing management treatments, season-long grazing (SLG), four-camp grazing (FCG), and holistic planned grazing (HPG). Vegetation biomass sampling locations are indicated with solid points. Half of the trial is covered by the East Griqualand Grassland vegetation type (Slopes), dominated by *T. triandra*. The other half is located on low-lying relatively nutrient-rich soils of the Mabela Sandy Grassveld and Eastern Temperate Freshwater Wetlands vegetation types, dominated by *E. plana*

standardising the number of points per hectare, using the 'density' function in spatstat.

A regularly-spaced sampling grid of points 90 m apart was generated over the farm producing 209 sampling locations which were revisited every austral summer and winter between 2015 and 2018 to measure standing grass biomass. We used a disc pasture meter (DPM), which relates grass biomass to the height of a disc dropped on the sward (Bransby and Tainton 1977). The DPM was calibrated by collecting and drying grass clippings directly under the disc at 60 evenly spaced points within the sampling grid. These weights were regressed on the DPM readings (R^2 = 0.78) and the linear regression coefficients were used to calculate standing biomass for all subsequent readings. We took DPM readings every metre along a 10 m line transect at each sampling point every season. To correct for baseline variations in biomass between treatments, we calculated the trend in biomass at each point as the slope of the linear regression line between 2015 and 2018.

Satellite-derived estimates of vegetation greenness and bare ground cover were obtained using the Google Earth Engine cloud computing platform (Gorelick et al. 2017). The normalised difference vegetation index (NDVI, Tucker 1979) has been widely used as an indicator of vegetation productivity, quality and vigour in rangelands (Svoray et al. 2013; Ali et al. 2016). We extracted the NDVI values over the farm from the Landsat 7 Enhanced Thematic Mapper Plus and Landsat 8 Operational Land Imager surface reflectance products at 30 m resolution after correcting for inter-sensor discrepancies using published calibration coefficients (Roy et al. 2016). Once clouds were masked using the 'pixel_qa' band, we calculated the slope of the linear trendline for each pixel by regressing NDVI on time. As with standing biomass (above), this gives a relative measure of change, accounting for any baseline differences in NDVI between treatments. To detect fractions of bare ground cover we used four high resolution (3–5 m) cloud free scenes obtained from Planet (PlanetTeam 2017) RapidEye and PlanetScope satellites

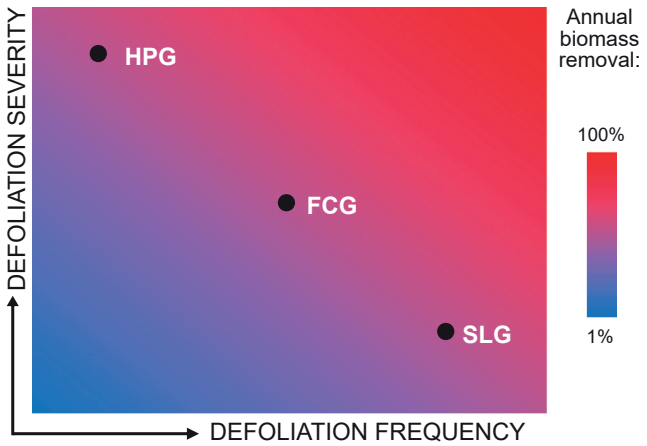

Figure 2: Theoretical defoliation severity (amount of plant removed in one grazing event) and frequency (the inverse of recovery between grazing events) experienced by a parcel of land or individual plant on the Merino Walk experimental trial at a theoretical 50% biomass removal. Season-long grazing (SLG) allows animals to range freely and thus repeatedly graze vegetation regrowth within a grazing season resulting in high defoliation frequencies. Holistic planned grazing (HPG) is at the other extreme because it restricts grazing area per day with electric fencing or herding and, in the case of our trial, enforces a minimum 60 d recovery period, resulting in low defoliation frequency. Assuming cattle remove equivalent annual biomass, defoliation severity and frequency must be inversely related. Hypothetically, SLG cattle might take one bite of a plant (low severity) and return a few days later to regraze the new regrowth, whereas the same plant might be defoliated several times within one day (high severity) due to higher cattle densities but will only be regrazed after 60 d recovery. Four-camp grazing (FCG) lies in between SLG and HPG

during Aug (winter) each year (2015–2018). The Planet data were converted to top-of-atmosphere reflectance using the calibration coefficients provided for each scene. Spectral unmixing techniques (Bateson et al. 2000) were used to derive fractional bare ground cover within each image pixel. Spectral mixing models are based on the understanding that each pixel contains a mixture of information from several spectrally distinct surface components or 'endmembers'. We created a mosaic of all Planet scenes and defined pixels characterising pure bare ground and pure vegetation cover. The mean reflectance value over these pixels for each spectral band was obtained and these values were used as endmembers in a mixing model to discriminate pixel fractions of bare ground and vegetation. After determining fractional bare ground for each winter season, and NDVI for each month, we calculated the change in both variables for each pixel over the farm as the slope of the linear trendline between 2015 and 2018.

Field plot experiment

We set up an *in situ* defoliation and dung addition experiment on Merino Walk to discern interactions between defoliation severity and frequency in a more controlled environment, which allowed for more precise sampling of vegetation responses than what the farm-scale trial allowed for. One hectare of homogenous East Griqualand Grassland, which had not been grazed for the previous three years, was fenced off from livestock. After baseline vegetation sampling in 2015, we found the dominant grasses to be *T. triandra*, *Tristachya leucothrix*, and *Harpochloa falx*. We divided the area into 5 × 5 m plots. Four levels of defoliation frequency (15, 30, 60 and 90 d) were crossed with two levels of defoliation severity (defoliation to 10 or 5 cm above ground) and three randomly allocated replicate plots per treatment. The 60 d recovery by 10 cm defoliation height treatment was replicated another three times to introduce a nutrient addition treatment. We randomly assigned three undefoliated plots as controls for both experiments. Defoliation was carried out using a sit-on lawn mower, the height of which was manipulated to achieve 10 and 5 cm mowing heights. Clipped plant material was raked to the side of each plot following defoliation. Fresh cattle dung collected from the surrounding farm camps was mixed with water into a slurry and applied to the nutrient addition treatment every 60 d following a 10 cm defoliation. To determine how many dung pats to apply we lay 200 regularly spaced belt transects (1.5 × 10 m) over the farm and counted dung pats. We observed an average of 0.28 dung pats per square metre and thus applied three dung pats per application to a 3 × 3 m square within each 5 × 5 m plot. This 1 m buffer was created to prevent nutrient contamination of neighbouring plots. The addition of dung after clipping was meant to more fully simulate the effect of grazing by cattle.

We implemented the defoliation and nutrient addition treatments between February 2016 and Aug 2018 and measured bare ground cover and vegetation NDVI. To measure percentage bare ground we used a Levy Bridge (Levy and Madden 1933) to sample 10 descending points spaced 25 cm apart. The Levy Bridge was randomly dropped inside each plot three times during January of 2017 and 2018. We counted the number of point intercepts with bare ground or plant material and calculated bare ground as a percentage of the sum of all dropped points. To measure NDVI, we used the GreenSeeker Handheld Crop Sensor (Trimble, CA, USA). The device was held 100 cm above the ground and an integrated NDVI measurement was taken by walking in a spiral pattern from the edge of the plot inward with the device's trigger held down for 30 s. This measurement was repeated every two weeks for the duration of the experiment.

Glasshouse pot experiment

To study plant-level responses to defoliation intensity and soil nutrient levels, we set up a glasshouse pot experiment with a 3 × 3 factorial design, with three species and three levels of defoliation frequency (20, 40 and 60 d). We selected three perennial bunch grass species, including *T. triandra*, *E. plana*, and *Elionurus muticus*, from the same farm in which the field experiment and grazing trial took place. Empirical evidence from previous studies shows *T. triandra* decreases in abundance under heavy or selective grazing whereas *E. plana* and *E. muticus* increase (Foran et al. 1978; Tainton et al. 1980). *T. triandra* is generally considered the most important grass in sub-Saharan African rangelands due to its widespread abundance and palatability (Snyman et al. 2013). *E. muticus* and *E. plana* are both relatively unpalatable grazing-resistant grasses, which proliferate in overutilised

grassland (Brockett 1983; Barnes 1990). Because *E. plana* is the most abundant species on the farm, we chose it to apply two levels of defoliation severity (10 and 5 cm) and two nutrient addition levels (low and high).

Treatments were replicated six times. Plants of basal diameter >10 cm were randomly selected in the field, removed with 30 cm of soil, and transported to a glasshouse at the University of Cape Town (33°57′21″ S, 18°27′43″ E). Plugs containing 5–10 tillers were transplanted into plastic pots, 18 cm in diameter, filled with a mixture of course and fine grain sand (1: 1). Haifa Multicote 12 month slow-release fertiliser (Haifa Chemicals Ltd, South Africa) containing 14-7-14 N: P: K (97%) with Mg (2%), Fe, Mn, Cu, Mo, Zn, B, and Ca (1% cumulative) was mixed with soil in the top half of each pot. Nutrient additions were calculated from foliar N accumulation rates for *T. triandra* reported in Anderson et al. (2013). We applied 100% (6 g fertiliser) of the minimum nutrient requirement calculated for *T. triandra* over 360 days to each pot. For the nutrient high treatment applied to *E. plana*, *we* used 150% (9 g fertiliser) of the minimum nutrient requirement. Plants were initially clipped to 10 cm to stimulate root establishment and left to regrow under irrigation for 6 months prior to the implementation of defoliation treatments.

Plants were defoliated between October 2016 and May 2017 with secateurs and the clipped biomass was oven dried at 70 °C for one week and then weighed. The biomass removed at the first (W_1) clipping and the cumulative biomass removed at the final (W_2) clipping was used to calculate relative growth rate (RGR, Fisher 1921) for each plant, where:

$$RGR = \frac{\ln W_2 - \ln W_1}{t_1 - t_1}$$

As a relative response, RGR accounts for the potential confounding effect of baseline plant sizes. After the final harvest, roots were washed, dried and weighed and added to cumulative foliar harvest to obtain total plant biomass production.

In addition to measures of plant biomass we measured foliar NDVI every 20 days using a MAPIR Survey 2 camera, which measures reflectance in visible and near-infrared wavelengths. NDVI has been shown to correlate well to plant foliar C: N ratios, crude protein and plant vigour (Pettorelli et al. 2005; Beeri et al. 2007; Ali et al. 2016), all characteristics of forage palatability. Pots were placed within a 60 × 60 cm cardboard box covered in red paper and photos were taken from a height of 100 cm above the box using a tripod. Images were captured in RAW format and pre-processed using Image J FIJI software with the MAPIR plugin, whereby image reflectance values were corrected for solar radiance using values from a calibration target (supplied by MAPIR) measured at each sampling occasion. The purpose of the red paper background was to isolate image pixels constituting plant leaves. Using the 'raster' package in R (RCoreTeam 2016), we applied a threshold of 0.3 to mask out background pixels before calculating mean foliar NDVI.

Statistical tests of significance

We used linear mixed models (Harrison et al. 2018) to analyse the effects of treatments on response variables in pot, plot and farm trial experiments. Due to practical limitations on the farm trial the spatial distribution of camps was not randomised although we made efforts to standardise access to water and allocate equal treatment areas to the two soil and vegetation types defined by slopes and flats (Figure 1). To account for this, and the spatial autocorrelation in remotely sensed variables, we assigned camp number as a random intercept in the model, and balanced sample sizes between treatments by extracting a random subsample of pixels stratified by treatment. Management approach, soil type, and cattle density were added as fixed effects in separate models explaining biomass, bare ground, and NDVI trends.

Similarly, in field plot experiments, repeated measures of bare ground and NDVI create potential temporal autocorrelation in the data. To account for this, we assigned plot number as a random intercept in the model, with defoliation frequency, severity and dung application as fixed effects. Finally, baseline plant sizes in the glasshouse pot experiment varied between treatments, thus, after testing that it was not significant as a main effect, initial plant weight was added as a random intercept in the model to control for this. Defoliation frequency, severity, species and nutrient addition were added as fixed effects in separate models explaining each growth response variable. Model residuals were inspected for violations of linear mixed model assumptions before resorting to logit (proportional data) or log (continuous data) transformation procedures as a corrective measure. All mixed models were performed in R (RCoreTeam 2016) using the 'lme4' package (Bates et al. 2014).

Results

Nutrient addition in the glasshouse pot experiments had the strongest (highest χ^2 values) positive effect on total biomass, shoot: root biomass production ratios and NDVI relative to declining defoliation frequency and severity , whereas frequency had a greater influence on RGR and root biomass (Table 1a; Figures 3a to 3d). In the field plot experiments, dung addition at 60 d defoliation frequency completely prevented the formation of bare ground and significantly enhanced NDVI relative to both clipped and unclipped treatments without dung (Table 2b; Figures 4b and 4c; Figure S1). In the pot experiment, the positive effect of nutrient addition on root and total biomass was enhanced at lower clipping frequencies but was unaffected by defoliation severity (Table 1a, Figures 3b and 3c). In contrast to this, when considering shoot biomass alone (as foliar RGR), the effect of nutrient addition was enhanced under more severe defoliation but unaffected by defoliation frequency (Table 1a; Figure 3a). Increasing defoliation frequency (60 to 20 d) and severity (10 to 5 cm) generally reduced RGRs, total biomass and root production, whereas this effect was not apparent for shoot: root biomass or NDVI. Severe defoliation enhanced shoot: root biomass independent of frequency (Table 1a; Figure 3d), whereas frequent defoliation at low severity resulted in a relatively enhanced NDVI within each nutrient level (Figure 3e). In the field plot experiments, bare ground cover and NDVI were unaffected by defoliation frequency, however, severe defoliation increased bare ground cover across all levels of

Table 1: The effects of defoliation frequency (20, 40 or 60 d), severity (10 or 5 cm sward height) and nutrient addition (high or low) on the growth response of potted *E. plana* (a), and effects of defoliation frequency on the growth responses of three species (*E. plana*, *E. muticus* and *T. triandra*) under low nutrients and low defoliation severity (b) in a glasshouse pot experiment. Results are based on linear mixed models explaining plant responses

(a) Frequency × Severity × Nutrients				(b) Frequency × Species			
	χ^2	df	*p*		χ^2	df	*p*
RGR (g d^{-1})				RGR (g d^{-1})			
Frequency	109.1	2	< 0.001*	Frequency	102.9	2	< 0.001*
Severity	22.7	1	< 0.001*	Species	52.5	2	< 0.001*
Nutrients	27.5	2	< 0.001*	Frequency × Species	8.1	4	0.087
Frequency × Severity	5.9	2	0.053	Total biomass (g)			
Frequency × Nutrients	2.2	2	0.333	Frequency	21.3	2	< 0.001*
Severity × Nutrients	8.1	1	0.004*	Species	75.3	2	< 0.001*
Total biomass (g)				Frequency × Species	14.6	4	0.005*
Frequency	103.2	2	< 0.001*	Root biomass (g)			
Severity	12.1	1	< 0.001*	Frequency	261.3	2	< 0.001*
Nutrients	285.7	1	< 0.001*	Species	31.1	2	< 0.001*
Frequency × Severity	0.8	2	0.658	Frequency × Species	12.3	4	0.016*
Frequency × Nutrient	27.1	2	< 0.001*	Shoot: root biomass ratio			
Severity × Nutrients	2.5	1	0.11	Frequency	1 120.9	2	< 0.001*
Root biomass (g)				Species	460.6	2	< 0.001*
Frequency	77.8	2	< 0.001*	Frequency × Species	60.7	4	< 0.001*
Severity	21.4	1	< 0.001*	NDVI			
Nutrients	13.1	1	< 0.001*	Frequency	1.9	2	0.393
Frequency × Severity	1.4	2	0.501	Species	813.8	2	< 0.001*
Frequency × Nutrients	8.4	2	0.015*	Frequency × Species	0.6	4	0.963
Severity × Nutrients	3.0	1	0.082				
Shoot: root biomass ratio							
Frequency	0.7	2	0.692				
Severity	6.0	1	0.014*				
Nutrient	272.3	1	< 0.001*				
Frequency × Severity	1.4	2	0.495				
Frequency × Nutrient	1.6	2	0.443				
Severity × Nutrient	2.9	1	0.087				
NDVI							
Frequency	14.3	2	< 0.001*				
Severity	0.8	1	0.371				
Nutrient	23.1	1	< 0.001*				
Frequency × Severity	8.5	2	0.014*				
Frequency × Nutrient	6.4	1	0.011*				
Severity × Nutrient	1.3	2	0.001*				

RGR stands for relative growth rate and NDVI is the normalised difference vegetation index
χ^2 is the Chi-square statistic
$p < 0.05$ indicated by *

defoliation frequency , whereas it increased NDVI at 15 d frequency alone (Table 2a; Figures 4a and 4c).

Grass species in glasshouse pot experiments differed in their response to defoliation frequencies for all response variables (Table 1b; Figures 3f to 3j). Growth responses and NDVI of *T. triandra* were unresponsive to defoliation frequency whereas RGR and total biomass production in *E. muticus* and *E. plana* were reduced under 20 d relative to 60 d defoliation frequencies (Figures 3f and 3g). *T. triandra* produced lower total biomass at 60 d recovery compared to *E. muticus* and *E. plana* (Figure 3g). Increasing defoliation frequency reduced root biomass and increased shoot: root production in *E. muticus*, whereas these responses were unaffected in *E. plana* and *T. triandra* (Figures 3h and 3i). Species foliar NDVI increased with increasing palatability (*E. muticus* < *E. plana* < *T. triandra*, Figure 3j), where palatability was inferred from previous empirical studies on grazing tolerance (Tainton et al. 1980). Foliar NDVI was unaffected by defoliation frequency (Table 1b).

At the farm scale, cattle density was unrelated to changes in standing biomass, and this did not change across management approaches or soil types (Table 3; Figures 5a to 5c). Soil analyses confirmed that the flats were significantly richer in N and P compared to slopes (Table 4), confirming *a priori* soil type classifications. Over the course of the trial, bare ground increased more on nutrient-poor compared with nutrient-rich soils, where the extent of this effect increased with increasing cattle densities in SLG and HPG (Table 3; Figures 5d to 5f). Although cattle density had no overall effect on bare ground, higher densities reduced bare ground on high nutrient soils and increased bare ground on low nutrient soils (Figure 5d) where relatively high and low nutrient soils were dominated by grass species *E. plana* and *T. triandra*

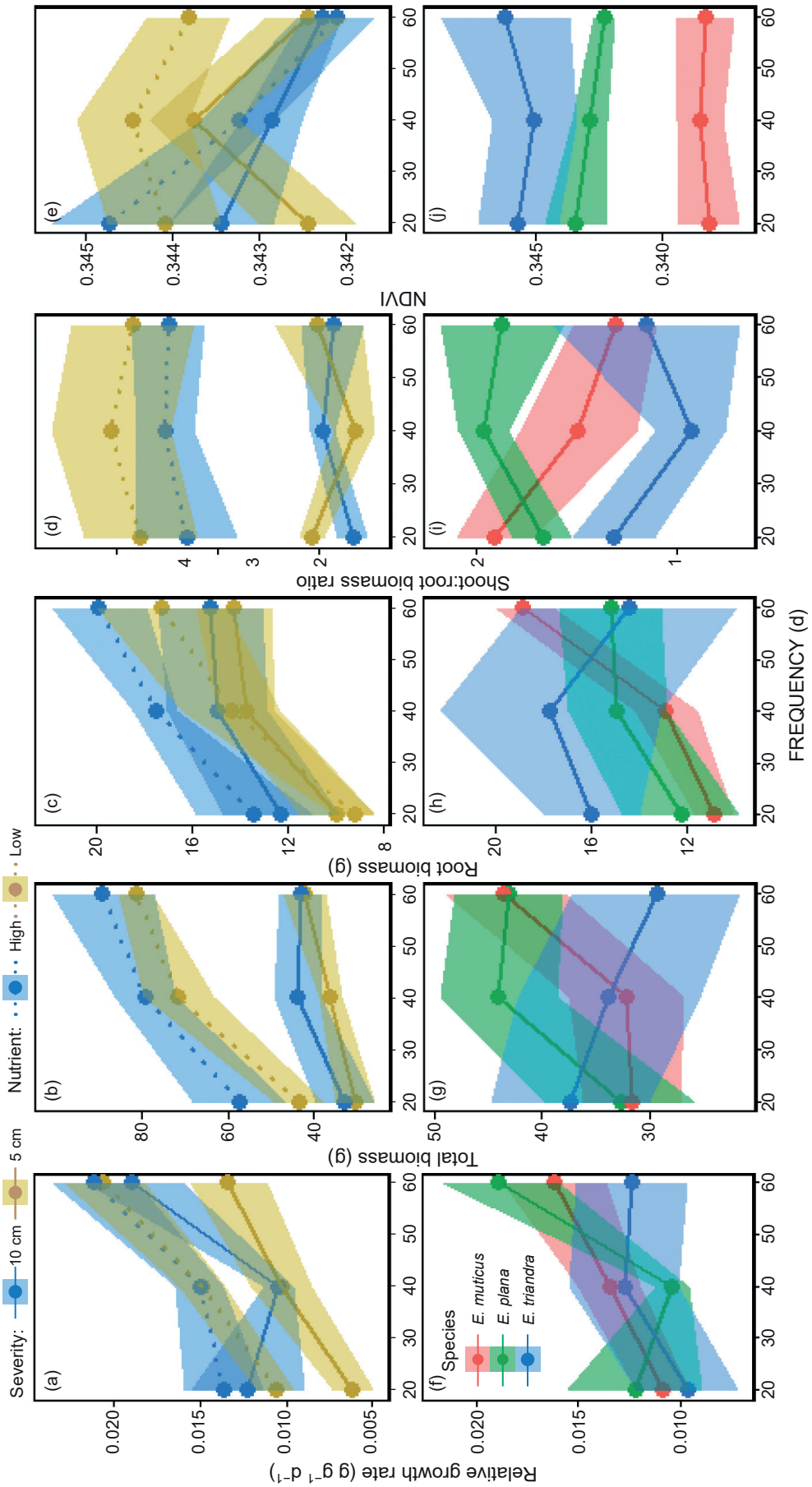

Figure 3: Plant growth responses from a glasshouse pot experiment with three bunch grasses removed from Merino Walk experimental farm. Experimentally induced defoliation frequency, severity and nutrient input was applied to *E. plana* (top row). The defoliation frequency treatment was applied to three grass species (*E. plana*, *E. muticus* and *T. triandra* at 10 cm severity and low nutrient levels to assess species-specific responses (bottom row). Growth responses included relative growth rates (a, f), total cumulative plant biomass at harvest (b, g), root biomass (c, h), shoot: root biomass ratios (d, i), and foliar greenness as measured by the normalised difference vegetation index (NDVI, e, j). Data points and colour ribbons represent treatment means ($n = 6$) and 95% confidence intervals, respectivel

Table 2: The effects of defoliation frequency (15, 30, 60 or 90 d) and severity (10 or 5 cm) on percentage bare ground cover and NDVI (a) in the field plot experiments as modelled with linear mixed models. The effects of dung application (versus no application) to plots defoliated every 60 d to 10 cm sward height were also modelled (b)

(a) Frequency × Severity				(b) Dung			
	χ^2	df	*p*		χ^2	df	*p*
Bare ground (%)				Bare ground (%)			
Frequency	8.9	4	0.062	Dung	9.0	2	0.011*
Severity	17.9	1	< 0.001*	NDVI			
Frequency × Severity	3.2	3	0.364	Dung	28.9	2	< 0.001*
NDVI							
Frequency	10.9	2	0.004*				
Severity	10.0	3	0.018*				
Frequency × Severity	8.9	3	0.031*				

NDVI is the normalised difference vegetation index
χ^2 is the Chi-square statistic
$p < 0.05$ indicated by *

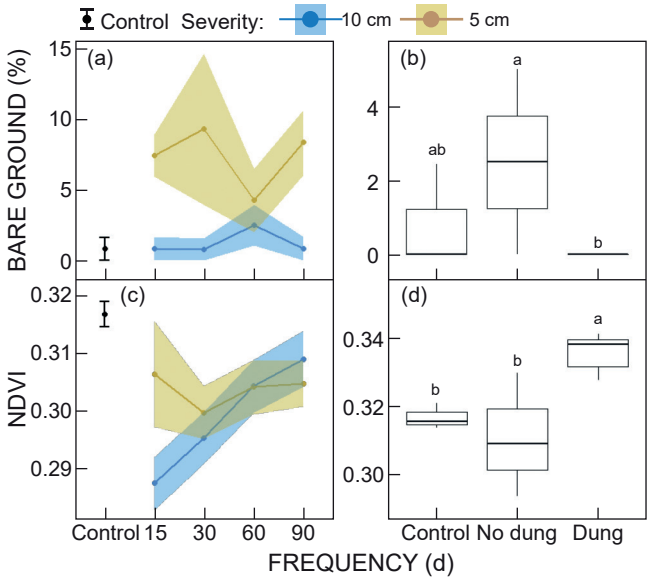

Figure 4: Percentage bare ground (a, b) and vegetation greenness (c, d), as measured by the normalised difference vegetation index (NDVI), for experimental plots located on the Merino Walk (Goedehoop section) experimental farm. Responses to defoliation frequency and severity (a, c), and dung application with 60 d defoliation at 10 cm severity (b, d) are shown in contrast to control plots that did not receive defoliation or dung. In a and c, data points and colour ribbons represent treatment means (n = 3) and 95% confidence intervals, respectively. In c and d, data medians are represented as horizontal lines within boxes which stretch to the 25th and 75th data percentiles. Whiskers extend to the largest and smallest values no farther than 1.5 times the interquartile range

Table 3: The effects of cattle density (GPS points m^{-2}), grazing management (season-long, four-camp, or holistic planned grazing), and soil type (nutrient-rich *E. plana* dominated areas on the flats, or relatively nutrient-poor *T. triandra* dominated areas on the slopes) on vegetation biomass, bare ground and NDVI trends on the Merino Walk experimental trial. Results are based on linear mixed models explaining vegetation responses. Location and respective soil chemical characteristics are given in the supplementary material (Figure S1 and Table S1).

	χ^2	df	*p*
Biomass trend (kg ha^{-1} yr^{-1})			
Cattle density	0.3	1	0.581
Grazing management	0.2	2	0.888
Soil type	0.7	1	0.389
Cattle density × Grazing management	1.0	2	0.612
Cattle density × Soil type	2.0	1	0.161
Grazing management × Soil type	1.8	2	0.401
Bare ground trend (% yr^{-1})			
Cattle density	0.01	1	0.789
Grazing management	1.3	2	0.522
Soil type	8.1	1	0.004*
Cattle density × Grazing management	39.6	2	< 0.001*
Cattle density × Soil type	19.1	1	< 0.001*
Grazing management × Soil type	0.7	2	0.712
NDVI trend (units yr^{-1})			
Cattle density	32.5	1	< 0.001*
Grazing management	0	2	0.999
Soil type	2.2	1	0.138
Cattle density × Grazing management	43.2	2	< 0.001*
Cattle density × Soil type	0.5	1	0.489
Grazing management × Soil type	0	2	0.998

NDVI is the normalised difference vegetation index
χ^2 is the Chi-square statistic
$p < 0.05$ indicated by *

respectively. The reduction in bare ground under increasing SLG cattle densities on nutrient-rich soils saturated at very high densities and was not apparent under FCG or HPG. The response in NDVI trends to cattle densities (Figures 5g to 5i) were inversely related to those of bare ground, but only under SLG (Figure 5g), where NDVI was enhanced with increasing cattle density on high nutrient soils. This effect also plateaued at very high cattle densities. NDVI was measured during both growing and non-growing seasons and displayed positive trends over the entire farm, whereas bare ground, measured during the non-growing season alone due to data limitations, increased in some areas and decreased in others. Although NDVI trends were positive over the entire farm, the magnitude of this increase was unaffected by cattle density across all treatments on low

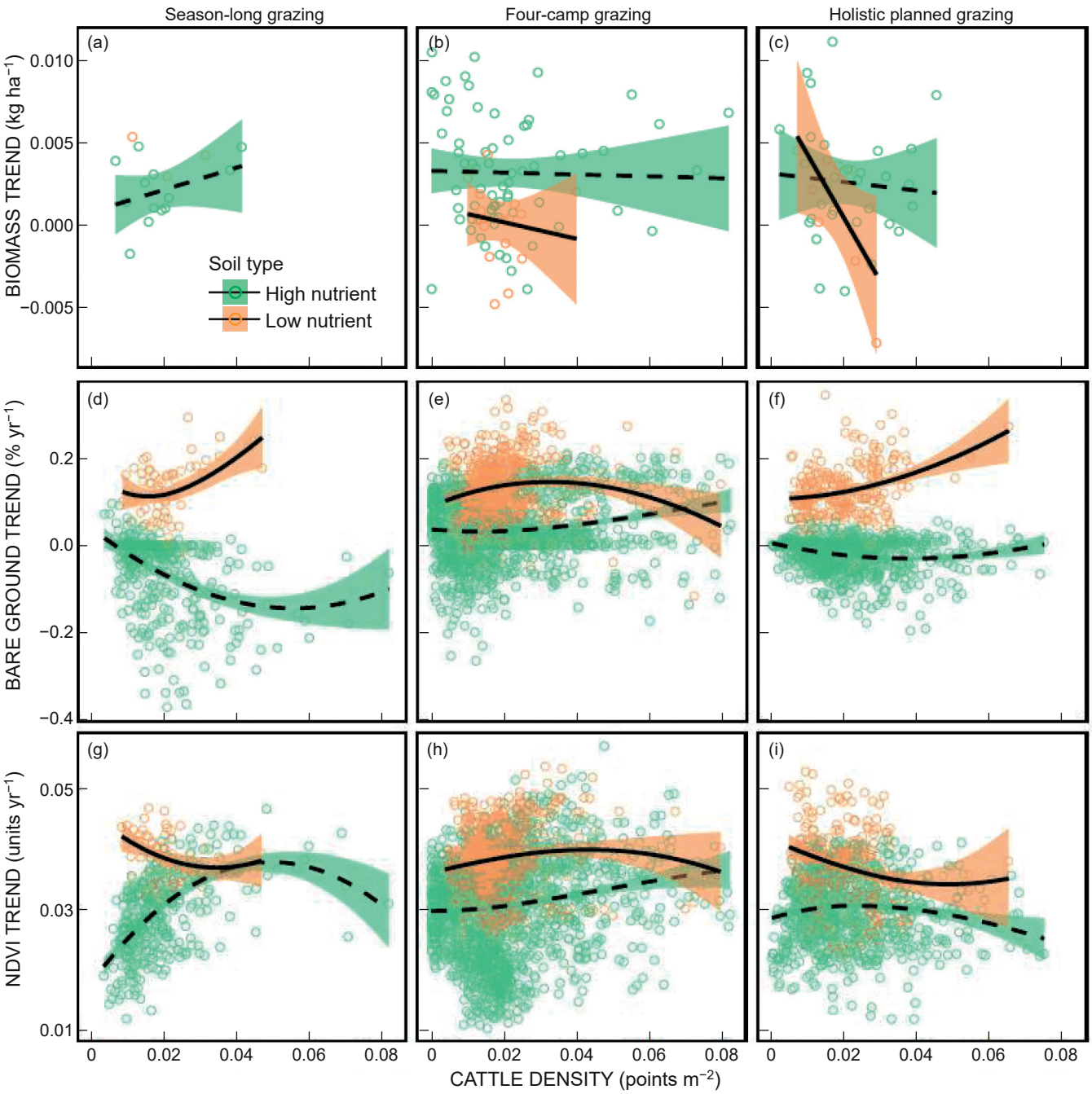

Figure 5: Vegetation cover responses (panel rows) in relation to observed cattle grazing densities on low and high nutrient soils on the Merino Walk experimental farm. Management approaches (panel columns) included season-long grazing, four-camp grazing and holistic planned grazing. Grazing densities were inferred from the density of GPS collar locations over the farm. The kernel smoothed densities of GPS points were rasterised and related to satellite derived raster images of NDVI and bare ground trends, whereby each data point represents a 30 × 30 m raster pixel over the farm. Biomass trends were derived from seasonal disc pasture meter readings at points along a defined sampling grid. Grazing density values were extracted for each biomass trend sampling location. Trend values were calculated as the slope of the linear trendline through all available time points for each vegetation response from 2015 to 2018. Lines plotted through bare ground and NDVI trend data are loess regressions. Linear regressions produced a better fit to the data for biomass trend data. The trendline was excluded for low nutrient soils in A due to deficient data. Coloured ribbons indicate 95% confidence intervals

nutrient soils. The pot experiment corroborates the finding on the farm trial in that the growth responses, including NDVI, of *T. triandra* (the dominant species on low nutrient soils) were resilient to defoliation frequency.

Discussion

Increasing defoliation intensity (frequency × severity) generally reduced grass growth responses across

Table 4: Soil nutrient concentrations on the flats and slopes of Merino Walk experimental farm. The flats are covered by Mabela Sandy Grassveld and Eastern Temperate Freshwater Wetlands (Mucina and Rutherford 2006) with poorly-drained haplic lixisols with high clay contents (Hengl et al. 2017). The slopes are covered by East Griqualand Grassland with relatively well-drained haplic acrisols. Soil nutrient concentration means ± standard errors are reported. Different letters after standard errors represent significant differences between flats and slopes. ANOVA results are also reported

Soil nutrient	Flats			Slopes			*F*	df	*p*
N (%)	0.140	±	0.006[a]	0.096	±	0.003[b]	14.970	1	< 0.001
P (%)	0.044	±	0.002[a]	0.038	±	0.002[b]	4.300	1	0.043
K (%)	1.030	±	0.019[b]	1.210	±	0.052[a]	16.130	1	< 0.001
Ca (%)	0.535	±	0.036	5.540	±	0.212	0.019	1	0.890
Mg (%)	0.148	±	0.026	0.144	±	0.079	0.005	1	0.945

glasshouse-, field- and farm-scale experiments. This supports the well-established principle that plant compensatory growth is inhibited at excessive levels of defoliation (McNaughton 1979). Few studies explore the interaction between defoliation frequency and severity even though grazing management decisions require an understanding of how plants respond to various combinations of grazing frequency and severity. The bulk of studies testing a range of defoliation frequencies have found reduced plant growth under high frequency defoliation whereas those investigating the effect of defoliation height (severity) have found no changes in growth response (Ferraro and Oesterheld 2002). A review of ryegrass responses to defoliation showed that re-grazing grasses before they have recovered two leaves per tiller retards regrowth because plants are unable to recover sufficient photosynthetic surface area (Fulkerson and Donaghy 2001). Nevertheless, grazing severity can be as significant as frequency, depending on the height of defoliation. For example, Snyman et al. (2013) found that seed production and biomass can be drastically reduced in *T. triandra* but only if defoliation is severe enough to remove the apical meristems of tillers, which are located close to the soil surface.

The most consistent finding in this study was that higher soil nutrients mitigated the negative effects of defoliation on plant growth. This supports the Compensatory Continuum Hypothesis, which predicts that compensatory growth will increase across an increasing fertility gradient (Maschinski and Whitham 1989). In contrast to this, a review of 16 defoliation experiments found that both high and low soil N levels led to a more severe reduction in growth by defoliation relative to moderate N levels (Ferraro and Oesterheld 2002). N limitations reduce the capacity for plants to replenish N stores that are removed during severe defoliation (McNaughton and Chapin 1985). Conversely, when N is abundant, plants grow at high growth rates anyway and thus defoliation would not promote compensatory growth (Georgiadis et al. 1989). The Limiting Resource Model is perhaps better at capturing these nuances than the Compensatory Continuum Hypothesis because it predicts that plant responses to grazing are dependent on whether defoliation exacerbates any one of multiple growth-limiting nutrient resources (Wise and Abrahamson 2005). For example, P deficiency reduced plant ability to replenish nutrient and biomass losses to grazers in the Serengeti (Chapin and McNaughton 1989). Furthermore, Zhao et al. (2008) concluded that the lack of growth response to N addition in their study was likely because their N application did not surpass a critical threshold of N availability. Globally, grasslands have been found to be predominantly N-limited (LeBauer and Treseder 2008). Given the ratio between N and P in the present study did not differ greatly between nutrient-rich and poor soils, it is likely that growth responses were inhibited by a co-limitation of N and P in nutrient-poor soils. Further, the inhibited growth found at elevated nutrients by Ferraro and Oesterheld (2002) is arguably an artefact of experimental manipulations applying nutrient levels in excess of that which is commonly found in natural settings.

The influence of soil nutrient status on plant growth responses to defoliation in the pot experiment were corroborated by measures of vegetation basal cover and biomass production in the field plot experiment and farm trial. Bare ground formation increased with defoliation frequency, but this was completely and partially mitigated by dung addition and soil nutrient status in the field plots and farm trial, respectively. A reduction in bare ground is likely a result of increased compensatory growth to defoliation because of increased basal vegetation cover. Other studies have found similar effects when livestock are corralled into small areas, thereby concentrating dung and enhancing vegetation basal cover (Porensky and Veblen 2015) or mitigating woody plant encroachment (Veblen 2013; Venter et al. 2018). Soil moisture, a factor not tested in our pot experiments, is likely also a significant contributor to growth responses in the field plot and farm trial experiments where dung application and soil type both enhanced moisture availability in association with enhanced nutrients. Cattle dung decreases soil crusting and bulk density thereby enhancing soil infiltration and water holding capacity (Haynes and Naidu 1998). Further, the farm trial flats, where a significant reduction in bare ground occurred under SLG, have high clay contents and thus a higher water holding capacity than the slopes (Hengl et al. 2014). Given that water and nutrient availability enhance plant growth rates, it is not surprising that plants in environments with abundant resources can recover faster from defoliation than those in resource-limited environments (Hawkes and Sullivan 2001).

Despite the importance of resource availability, the grazing management debates remain focussed on the trade-offs between grazing severity and frequency induced by forms of

rotational grazing. One of the main aims of rotational grazing is to extend rest periods (reduce defoliation frequency) between grazing events, and therefore by necessity increase the grazing severity per grazing event (Derner et al. 1994; Volesky 1994). A study in Canadian mixed grass prairie reported no difference in forage yields between high frequency, low severity grazing, and low frequency, high severity grazing (Bork et al. 2017). Similarly, our results reveal no direct trade-off between grazing severity and frequency, although soil fertility on the farm trial mediated an indirect trade-off where increasing the density of grazing pressure under SLG (high frequency, low severity) reduced bare ground cover and increased vegetation NDVI on soils where nutrients and moisture were abundant. In contrast, forms of rotational grazing, FCG and HPG, showed no such effect. Likewise, in the pot experiments, increasing defoliation frequency enhanced NDVI under elevated soil nutrients. Although we did not measure foliar nutrients directly, NDVI has been shown to correlate with a range of forage quality and digestibility indices including foliar N and crude protein content (Svoray et al. 2013; Ali et al. 2016). This effect on NDVI may be similar to the formation of grazing lawns observed in African savannas (Hempson et al. 2015b). Grazing lawns establish with the frequent re-grazing of grasses which, combined with concentrated dung deposition, stimulates palatable grass regrowth, eventually changing species composition and shifting the system into an alternative stable state. *Eragrostis* (e.g. *tricophora* and *curvula*) and *Themeda* grasses, abundant on the flats and slopes of the farm trial respectively, include facultative lawn grasses because they can switch growth forms to prostrate growth or form caespitose lawns of small cushion-like plants under regular defoliation (Hempson et al. 2015b; Venter et al. 2019a). Indeed, *T. triandra* displayed stronger tolerance to frequent defoliation in the pot experiments as well the highest NDVI values (Figure 3j), supporting the idea that grazing lawns might induce a shift to grazing tolerant and more palatable species.

In the farm trial, the positive effect of SLG on vegetation NDVI trends and reducing bare ground disappeared at very high grazing pressures on high nutrient soils and was absent on low nutrient soils. Given that root biomass was significantly reduced under frequent defoliation in the pot experiment, we expect that the grazing lawn effect under SLG might not be sustainable over the long-term if root biomass becomes insufficient to sustain the nutrient and water demands of compensatory growth. Although most regrowth after defoliation results from current photosynthesis, and not root carbon reserves (Richards and Caldwell 1985), sustained defoliation may lead to the preferential allocation of photosynthates to leaf growth instead of root growth and thereby reduce root biomass assuming resources become limiting (Harper 1989; Dawson et al. 2004). For example, a number of studies on African grassland species have attributed the decline in grass cover under heavy grazing to the loss of non-structural carbohydrate reserves in root and/or crown material (Opperman et al. 1970; Danckwerts and Gordon 1990; Oosthuizen and Snyman 2003). However, the reduction in root biomass under defoliation is highly variable across studies from around the world (Ferraro and Oesterheld 2002), depending on context-specific factors such as resource availability, defoliation intensity and most importantly, plant species. A study on 35 studies from Australian rangelands including 829 species showed that 41% of these species responded inconsistently to grazing (Vesk and Westoby 2001). Thus, although persistent frequent grazing may deplete root reserves and degrade rangeland through bare patch formation and invasion of unpalatable species, additional research is required to ascertain how resilient different rangelands and their grazing lawn-like systems are to frequent grazing (Hempson et al. 2015b).

We also found variable regrowth responses to defoliation frequency between the three bunch grass species selected for our glasshouse pot experiment. Contrary to *a priori* definitions of grazing tolerance, where increaser species thrive and decreaser species decline under grazing pressure (Tainton et al. 1970; Vesk and Westoby 2001; Del-Val and Crawley 2005), we found that the decreaser species *T. triandra* was remarkably resilient to frequent defoliation compared to supposed grazing tolerant *E. muticus* and *E. plana*. Another defoliation experiment on South African grassland species (Morris 2016) also found that palatable decreasers such as *T. triandra* are no more intolerant of grazing than increaser species; however they are more likely to be persistently selected for by grazers (Snyman et al. 2013). In the case of increaser species, chemical and structural strategies for grazing avoidance (e.g. tannins, lignin, awns) are more important than grazing tolerance (Briske 1996). Although some studies do provide empirical evidence for the correspondence between grazing tolerance and the increaser-decreaser continuum (Del-Val and Crawley 2005), they highlight the importance of environmental pressures on plant fitness such as competition, moisture or nutrient limitations. For example, *T. triandra* is notoriously sensitive to high soil nutrient levels (Snyman et al. 2013) and can be out-shaded by taller grasses under fertiliser application in the absence of defoliation (Fynn and O'Connor 2005). Yet, under frequent defoliation, it loses fewer nutrient reserves than taller grasses and can thus gain the competitive advantage, especially when competing for a limiting soil nutrient (Fynn et al. 2005). In our farm trial, the biomass of *T. triandra* dominated areas (nutrient-poor slopes) was unaffected by cattle densities suggesting *T. triandra* is resilient to defoliation in the competitive *in situ* context.

Conclusion

We find evidence across multiple experimental scales that increasing both defoliation severity and frequency retards growth responses in bunch grasses of a mesic South African grassland but that this effect is mitigated at elevated soil nutrient levels under season-long grazing management that may induce frequent defoliation over selected patches of grass at moderate livestock densities. Managers who are able to manipulate grazing frequency and severity using forms of high intensity rotational grazing should aim to maximise grazing frequency on nutrient-rich soils, and grazing recovery on nutrient-poor soils. Further, it would be worth testing whether the grazing lawn effect might be induced by rangeland managers through fertilisation paired with high frequency grazing, and whether this would lead

to sustained productivity. Despite the interactive effect of grazing approach and defoliation intensity on bare ground on high nutrient soils, our farm trial revealed no direct rotational grazing effect on combined vegetation responses, supporting the thesis that grazing management approach is less important than stocking rate as a determinant of rangeland productivity. Finally, our study challenges the assumption that grazing pressure exacerbates indicators of rangeland degradation such as bare ground formation in mesic grasslands. On moist, fertile soils dominated by grasses able to switch growth form in response to herbivory, high frequency grazing at moderate cattle densities sustains basal cover and vegetation palatability.

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