Will the grass be greener on the other side of climate change?

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Increasing atmospheric [CO_2] is stimulating photosynthesis and plant production, increasing the demand for nitrogen relative to soil supply with declining global foliar nitrogen concentrations as a consequence. The effects of such oligotrophication on the forage quality of sweetveld, mixed veld, and sourveld grasslands in South Africa, which support livestock production and native ungulates, are unknown. Soil characteristics and the herbage quality of an abundant grass are described from baseline historical (mid-1980s) data collected across a sweet-mixed-sour grassland gradient in KwaZulu-Natal. Sourveld occurred on the most acidic, dystrophic soils and exhibited a pronounced decline in leaf nitrogen, digestibility, and other macronutrients during winter, in sharp contrast to sweetveld, on nutrient-rich soils, where forage quality varied little seasonally. In a carbon-enriched, warmer, and most likely drier future climate, we predict that forage quality will not be substantially altered in sweetveld where soil nutrients and temperature are not limiting but that sourveld could become 'sourer' because soil nutrients will be inadequate to match higher plant production promoted by elevated [CO_2] and warmer and longer growing seasons. Reassessing historical data and seasonal and spatial monitoring of forage quality will enable assessment of past and future impacts of climate change on grassland forage quality.

Significance:

- Grassland forage quality will likely decline with elevated [CO_2] and warming, particularly in sourveld.
- Climate change could deepen and widen the sourveld winter forage bottleneck, necessitating greater supplementary feeding of livestock.

Introduction

Grasslands, including the C_4-dominated grasslands of South Africa, face an uncertain future in a rapidly changing climate. The ongoing rise in the atmospheric concentration of anthropogenically derived carbon dioxide (CO_2) could increase carbon sequestration, biomass production, and the water use efficiency of grasses[1,2], while also favouring woody species and alien invasive plants[3]. Reduced rainfall coupled with more frequent and severe droughts will further limit the production of herbage for livestock and the indigenous herbivores that grasslands support.[4,5] Another – largely unrecognised – threat to grazing animals posed by elevated CO_2 concentrations [CO_2] is an insidious decline in forage quality globally because of an increasing limitation of soil nitrogen (N) supply to grasses growing faster over an extended growing season in a warmer, carbon-enriched atmosphere: foliar [N] has declined by 9% globally over the last four decades.[6] Diminishing foliar [N] could cascade through ecosystems, slowing protein flow from plants to insect and mammalian herbivores.[7] Even small decreases in the protein content and digestibility of forage would adversely affect animal health, reproduction, and weight gains.[7,8]

The potential impacts of elevated [CO_2] (eCO_2) and other climate change drivers on forage quality will occur across a well-recognised and agronomically important spatiotemporal gradient in South Africa, from sweetveld through mixed veld to sourveld. Livestock on sourveld require supplementary feeds and licks for up to 6 months[9] because of the marked reduction in forage quality in autumn. This drop in quality of sourveld is caused by the translocation of foliar nutrients to roots at the end of the growing season.[10] In contrast, foliar nutrients remain sufficiently high to maintain livestock production throughout the year in sweetveld areas whereas mixed veld displays intermediary seasonal quality changes.[11] Generally, with notable exceptions[11], 'sour' grassland occurs on dystrophic soils in cool areas where high rainfall favours high primary production, but nutrient supply is limited, whereas sweetveld predominates on base-rich soils in hotter, usually lower-lying, areas, where low and erratic rainfall rather than nutrient availability restricts grass productivity[11,12]. Anthropogenic climate change could substantially alter the sweet-sour forage quality gradient because temperature, soil moisture and [CO_2] interact to determine the balance between carbon assimilation and soil nutrient availability (particularly size of the mineralisable soil N pool) that determines spatial and seasonal differences in forage productivity and quality.[12,13]

To assess whether sourveld is becoming more 'sour' and sweetveld less 'sweet' owing to eCO_2 and other climate change drivers, we present historical plant quality data (collected in 1985–1986) to (1) describe soil physicochemical and plant foliar nutrient gradients across sweet-mixed-sourveld sites, and (2) provide a baseline for detecting any oligotrophication that may have already occurred over the last third of a century. Atmospheric [CO_2] has risen by more than 20% (346 to 418 ppm) since the mid-1980s (https://gml.noaa.gov/ccgg/trends/), during which spatially variable temperature increases in mean annual temperature[14] of 0.01 °C/year to 0.03 °C/year and mean annual precipitation changes[15] ranging from minus 12 mm to positive 14 mm have been recorded over South Africa. These trends are likely to accelerate because the southern African region is a global hotspot of climate change.[16] We also consider uncertainties in the future likely trajectories of forage quality shifts in South African grasslands.

Methods

Plant quality and soil characteristics were assessed at 31 sites across a sweet-sour grassland gradient in KwaZulu-Natal (Supplementary table 1).[17] From 1985 to 1986, each site was visited at about 73-day intervals to harvest foliar material of a consistent age – the top two leaves and a bud of vegetative tillers – from 20 plants of *Themeda triandra* (red grass), an abundant grass at all sites. We also refer to a wider study of winter (July) grass quality in the grassland biome in other provinces that used the same methods.[18] Expert knowledge and literature were used to classify sites as 'sweet', 'sour' and 'mixed' types.

Plant quality analyses[17,18] included analysis for cellulase dry matter digestibility (%) and leaf nitrogen concentration (%), as well as chemical elemental analysis (N, P, K, Ca, Mg, Na, Zn, and S) (Supplementary table 2).

Topsoil was sampled (to 200 mm depth) from 20 combined auger points and assessed for particle size (texture), organic matter, field moisture capacity, pH, exchangeable acidity, acid saturation, effective cation exchange capacity, and P, K, Ca, Mg, Na (Supplementary table 3).[17,18]

Forage quality (all seasons) and soil physicochemical gradients in KwaZulu-Natal were examined using principal component analysis of cross-correlation matrices. Seasonal differences in N% between grassland types were assessed with permutation analyses of variance (9999 permutations).

Results

There was a strong forage quality gradient along which sourveld sites were most distinct for their low leaf digestibility, N%, and cation concentrations (Figure 1). Digestibility doubled and N% ranged five-fold across this gradient (Figure 1b,c).

Sweetveld soils were less acidic, had lower organic matter and capacity to hold water, but had substantially more exchangeable cations available than soils from sourveld; mixed veld sites were intermediate (Figure 2).

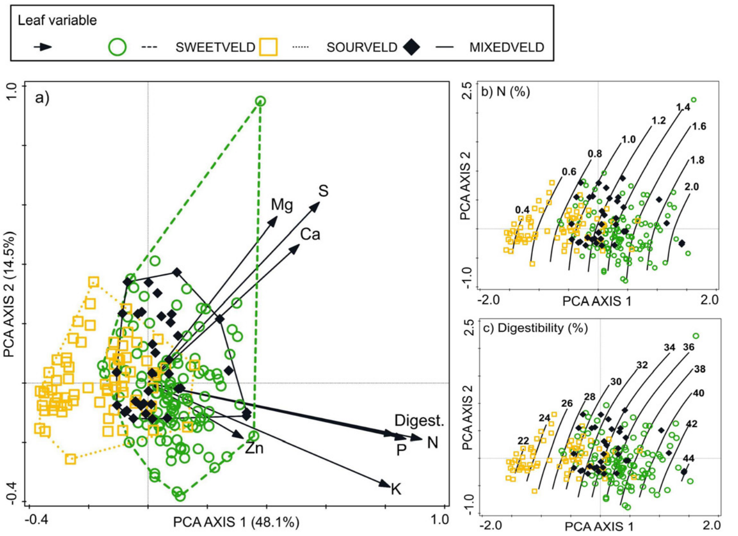
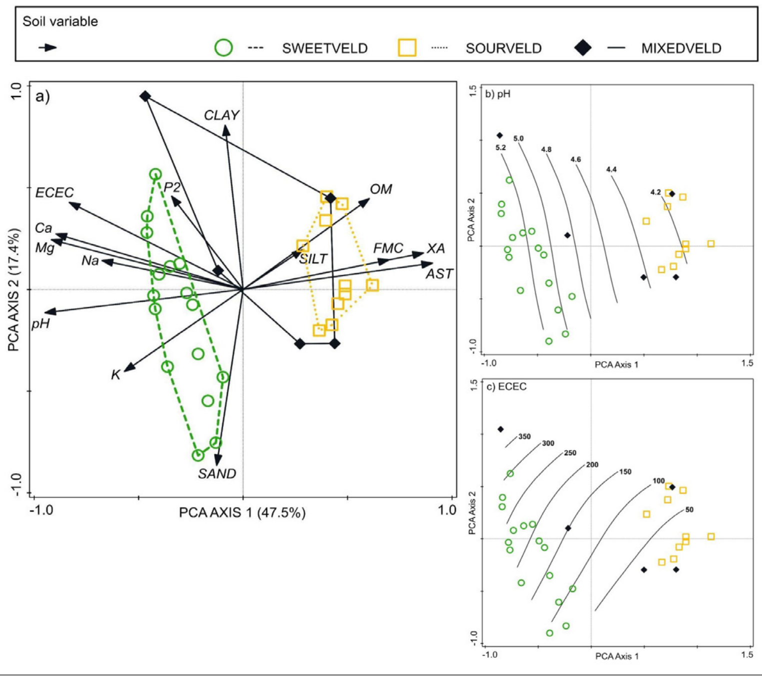


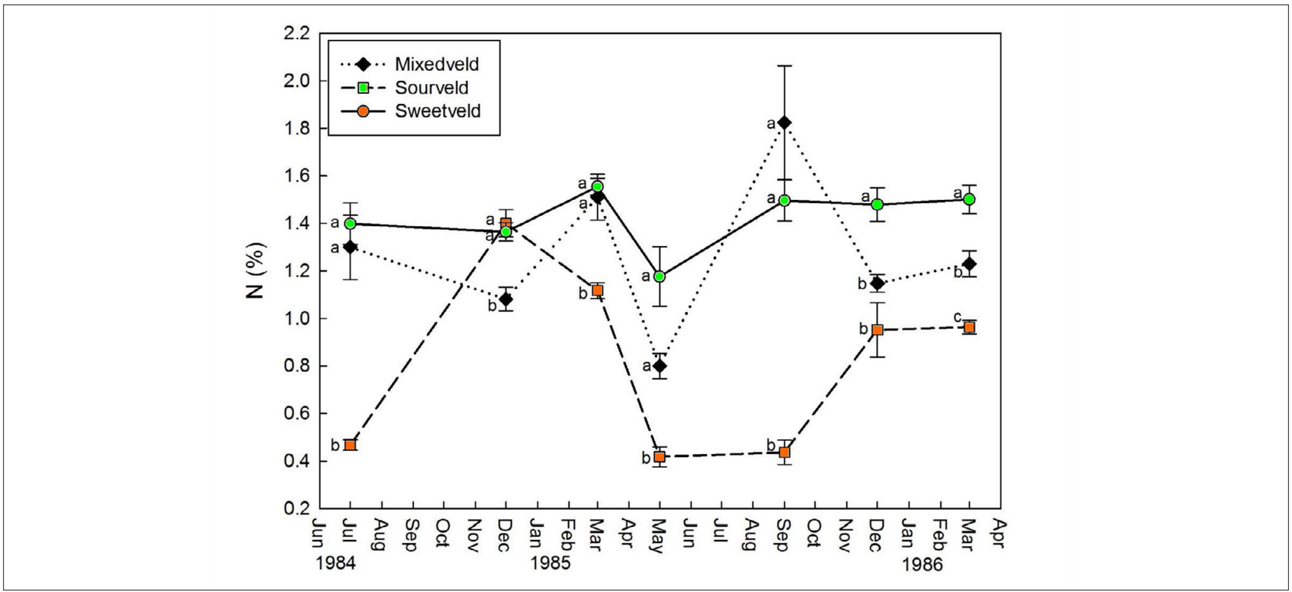
Figure 1: First two axes of a principal component analysis (PCA) of leaf variables measured at 31 locations in three grassland types in KwaZulu-Natal (a), and trend in leaf nitrogen (b) and digestibility (c) across the ordination.



AST, acid saturation; ECEC, effective cation exchange capacity, FMC, field moisture capacity; OM, organic matter; XA, exchangeable acidity

Data from Zacharias[17]

Figure 2: First two axes of a correlation-type principal component analysis (PCA) of topsoil variables measured at 31 locations in three grassland types in KwaZulu-Natal.



Data from Zacharias[17]

Figure 3: Seasonal trends in mean (±s.e.) leaf nitrogen concentration (%) measured in three grassland types in KwaZulu-Natal. Means within sampling dates with letters in common were not different ($p = 0.05$).

Sweetveld had consistently high foliar N%, declining only somewhat towards the winter of the second sampling season (Figure 3). In contrast, N concentration, similar to digestibility[17], declined to markedly low levels from late summer through to early spring in sourveld. Quality trends for mixed veld were not consistent nor pronounced. Summer and winter levels of N above 1.0% and below 0.5%, respectively for sweetveld and sourveld in KwaZulu-Natal, matched the winter extremes measured elsewhere in the grassland biome.[18] Also, in sourveld, and to a lesser extent in mixed veld, leaf concentrations of the macronutrients, P, K, Mg, and S were seasonally variable.[17]

The links between forage quality, soil characteristics and environment were weak, with increasing altitude the only consistent predictor of 'sourness' in KwaZulu-Natal.[17,18]

Discussion

Future reductions in the forage quality of sourveld and sweetveld will depend on how other major climate change drivers (temperature and precipitation) interact with the carbon fertilisation effect (CFE) to alter the balance between plant growth-driven demand for, and soil supply of, nutrients, primarily N.[6,7,12] The CFE would be most pronounced when resources and environmental conditions do not restrict plant growth.[19] However, the effects of multi-way interactions between climate drivers on plants and soils, particularly on forage quality, are poorly understood; these interactions can be complex, multiplicative[20,21], and species-specific[22]. Given these uncertainties and the current growth limitations prevailing in sour- and sweetveld[11,12], we tentatively predict the following potential shifts in plant quality (leaf [N], digestibility, and fibre content) under climate change.

Sweetveld mostly occurs in semi-arid regions, where soil moisture, not nutrients, limit plant growth.[12] Despite lower rainfall and increased evaporative demand with warming predicted for semi-arid regions[5], plant growth could increase because of more efficient water use under eCO_2 resulting from stomal closure[1,22]. Elevated temperatures combined with the CFE could stimulate grass production, lowering the N content and digestibility of herbage.[8] However, extreme and prolonged droughts and heat waves, both of which will become more frequent with climate change[5,16], will limit carbon assimilation and nutrient availability by curtailing microbial decomposition and nutrient cycling[19,20]. The consequences of climate change in semi-arid regions are still uncertain[21] but it is not likely that sweetveld will experience a consistent large directional change in productivity and forage quality in the future.

In sourveld, predominately in higher lying, cooler, moister climes, nutrient-poor soils and low temperatures act together to constrain the quality of forage during the non-growing season.[11,12] Warming, especially in spring and autumn, and eCO_2 would likely enable a longer period of growth, further limiting soil nutrient supply[6] and reducing winter forage quality. Increased N mineralisation with warming could mitigate this potential future decline in forage quality on organic mountain soils[23] but not on the dystrophic mineral soils of outlier sourveld areas at low elevations[11].

The critical winter forage bottleneck in forage quality in sourveld (Figure 3) is likely to be exacerbated in the future because eCO_2-driven reductions in protein content and digestibility in late summer and autumn occur when nutrients in senescing plants are already below critical levels for livestock.[9,24] Consequently, supplementary feeding costs will increase[8] while wild ungulates would need to forage differently to match their metabolic requirements[25]. Higher-quality C_3 grasses that remain greener for longer in autumn could obtain a competitive advantage over C_4 species in the future[26] but only at the higher and far western margins of the grassland biome, and perhaps not to any significant extent[2].

Research is required across a sweet-mixed-to-sourveld gradient to understand patterns and mechanisms of seasonal nutrient flows between plant parts – our knowledge of these is still surprisingly rudimentary.[10] Also requiring investigation are species-specific responses to interactions between multiple climate change drivers[22], the potential effects on plant growth and quality of ongoing atmospheric nitrogen deposition[20], and the extent to which CFE effects on plant quality could be modified by downregulation of photosynthesis through acclimation and progressive N limitation over time[1,7,8]. We also recommend resampling sites with historical plant data, such as those presented here (Supplementary tables 1 and 2), to establish the extent to which CFE-driven shifts in forage quality may have already occurred over the last few decades, and to regularly, widely, and seasonally monitor shifts in leaf stoichiometry (at minimum C:N ratios[7,13]) to establish the degree and extent of climate-driven oligotrophication[8].

Conclusion

Climate change has the potential to alter, in agronomically important ways, the current spatial and seasonal patterns of grass forage quality in South African grasslands. We predict the greatest 'souring' will occur in sourveld, with a minimal response in sweetveld, but there are many uncertainties as to the direction and rate of change in forage quality and the extent to which such changes will affect livestock production and wild ungulates. Further detailed research and regular monitoring are required to assess if, where, how, and why forage quality of grasslands in South Africa is responding to climate change.

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Competing interests

We have no competing interests to declare.

Authors' contributions

C.D.M. conceptualised the study. P.J.K.Z. and K.P.K. undertook the original field studies. C.D.M. analysed the data and wrote the draft manuscript with editorial input from P.J.K.Z. and K.P.K.

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