Lowveld Savanna Bush Cutting Alters Tree-Grass Interactions

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Lowveld savanna bush cutting alters tree-grass interactions

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Abstract
Savannas are characterized by the coexistence of trees and grasses, and their interactions are modified by water availability and herbivore activity. Many savannas are experiencing bush encroachment, resulting in reduced herbaceous productivity and shifts in savanna structure. This study aims to understand the effects of tree density and tree cutting on herbaceous productivity, water use, and herbivore abundance in a mopane-dominated lowveld savanna. We present data from a 4-year mopane-cutting experiment in the Mthimkhulu Game Reserve bordering Kruger National Park (South Africa). We established three 60x60 m plots for experimental manipulation where mopane stems and re-sprouting shoots were cut 2-3 times per year (2015-2019). We established transects within the plots to measure grass productivity and herbivore activity (counts of tracks and dung). Additionally, we measured root non-structural carbohydrates within cut and uncut mopane to assess the impact of cutting on energy storage. We used stable isotopes of xylem and soil water at multiple depths to infer changes in functional water use of coexisting mopane and grass species. Cutting had limited effects on mopane survival during this 5-year period, but re-sprouting stems had reduced height and starch concentrations than uncut trees. Cutting mopane resulted in shallower-soil water use in 2017 and tended to increase variability in root water uptake across multiple soil depths. The cut treatment tended to have higher grass cover and productivity than the control treatment by the 3rd growing season. Visitation of grazers increased in the cut plots relative to uncut plots by 2017, suggesting increased grass cover promotes grazer visitation. These results emphasize the importance of top-down drivers on savanna tree cover and the impacts of bush encroachment on grass biomass and herbivore presence. We suggest repeated cutting or browsing pressure is needed to suppress woody cover and increase grass production in lowveld savannas.

Introduction
Savannas are characterized by the coexistence of trees and grasses. The distribution and abundance of these functional types are determined by the interactions of top-down and bottom-up drivers. These drivers include water and nutrient limitation (bottom-up) and disturbances such as fire and herbivory (top-down). The interaction and alteration of these drivers determine tree:grass ratios through the competitive and demographic limitations of tree establishment amongst a dense and highly competitive grass layer. For example, at high densities, grazers decrease grass cover and reduce subsequent fire intensity, resulting in increased tree establishment, growth, and survival (Holdo et al. 2009). In contrast, a high abundance of browsers decreases woody cover and opens the canopy for grass growth (Sankaran et al. 2013; Daskin et al. 2016). These top-down drivers determine the presence of tree demographic bottlenecks and are often associated with wetter systems. In drier systems, tree cover is also limited by water availability. Once established, woody plants are hypothesized to avoid water competition with grasses through hydrological niche separation, where trees use deeper water sources than grasses when shallow soil water availability is low. Changes in climate and land use at the global, regional, and local level have altered these top-down and bottom-up drivers that limit tree cover and have led to the increased cover of woody plants in savannas, a process referred to as bush encroachment.

Historically, woody plants in savannas have had important roles for human and ecosystem well-being including provisioning firewood and timber and an important food source for herbivores. However, an increased abundance of woody plants has led to negative economic and ecological shifts. For example, increased woody plant density can decrease grass biomass used for domestic livestock production (Archer and Predick 2014) and may also deplete soil moisture by rainfall interception and increased transpiration (Honda and Durigan 2016). Additionally, in areas promoting ecotourism, dense tree cover can make it difficult to see large, charismatic animals that attract tourists, resulting in lost tourism revenue for local communities. Bush cutting has been used as a way to mitigate the negative effects of woody encroachment; however, manual clearing is a labour intensive and expensive management technique. Research efforts are needed to understand the effects of bush cutting on encroaching woody species and create effective management practices to increase herbaceous cover. In addition, many encroaching woody species resprout after disturbance and there is no clear understanding on the amount of repeated cutting needed for long-term reduction in tree cover.

In this study, we assessed the consequences of repeated bush cutting in a *Colophospermum mopane* (hereafter referred to as mopane) dominated semi-arid savanna at Mthimkhulu Game Reserve in South Africa. Mopane trees were cut once to twice per year from 2015-2019. We assessed the effects of bush cutting on the sources of water used by active roots and root carbon storage of mopane trees. We also examined the effects of mopane cutting on grass productivity and monitored herbivore presence via track and dung counts. We predicted repeated cutting would (1) shift mopane root water uptake to deeper soils to avoid competition with grasses, (2) deplete nonstructural carbohydrate (NSC) storage belowground, reducing energy available for resprouting after disturbance and (3) increase grass productivity and subsequently grazer presence.

Methods and Study Site

Mthimkhulu Game Reserve (MGR) is a 7500-hectare community-owned reserve that shares open borders with the northern portion of Kruger National Park in South Africa. The site is dominated by the C_4 grass *Urochloa mosambicensis* and has undergone encroachment by mopane, a dominant tree in the northern half of Kruger National Park. Mopane can form dense, monodominant stands that shade out herbaceous species living in the understory. In 2015, we established three 60 x 60 m plots and randomly assigned half of each plot to a repeated cutting treatment. Within the cut treatment, mopane trees standing < 4 m tall were cut at the base 1-2 times per year and measurements began in 2016. Within each plot, we established two 2 m wide x 50 m long transects. Animal tracks and scat along these transects were identified to species. Grass biomass (g m^{-2}) was clipped in four 0.5 x 0.5 m quadrats in each plot. Samples were dried at 80°C for two days and weighed.

To assess if bush clearing causes plants to shift their root water uptake, we matched the stable isotopic signature of xylem water of mopane trees and grasses to that of the soil water at various depths in the soil profile (protocol outlined in Nippert and Knapp 2007). To assess differences in water use, we analysed each year (2016-2018) separately. Since δD and δ^{18}O were collinear and varied similarly with soil depth, we collapsed δD and δ^{18}O into a single axis using PCA to analyse both water isotopes in a single analysis (see Holdo et al. 2018 and Case et al. 2020). The PCA approach is a useful alternative to isotope mixing models when plant isotopic signatures fall outside of the range of sampled soil isotopic signatures, indicating plants are using water from deeper sources than the soil sampled. To assess root NSC, mopane root samples were collected 20-30 cm below the soil surface at the same time as samples for isotopic analysis. NSC extraction followed the procedure outlined in O'Connor et al. 2020. We used R program to analyse differences between cut and uncut treatments using mixed effects ANOVAs with plot as a random effect to account for inherent variation between plots.

Results

Soil water isotopic composition tended to become depleted with depth, whereas shallow soil layers had isotopically enriched signatures. PC1 declined significantly as log-transformed depth increased in 2017 and 2018 ($P < 0.05$) and moderately in 2016 ($P = 0.068$). Mopane trees used deeper soil water than grasses ($P < 0.05$; Fig. 1). In 2017, mopane trees used shallower soil water than uncut trees ($P < 0.05$; Fig. 1) but there were no significant differences in source water use in 2016 and 2018. Variability in mopane source water use was high in all treatments but cutting tended to increase this variation. On average, the coefficient of variation of cut trees were 1.4, 2.7, and 1.2 times greater than uncut plots in 2016 - 2018, respectively.

NSC starch concentrations were significantly lower in cut than uncut mopane trees in 2016-2018 ($P < 0.05$). Differences in starch concentrations between cut and uncut mopane trees increased with repeated cutting, where average starch concentrations were 1.8, 2.6, and 7.8 times greater in the uncut than cut trees in 2016-2018, respectively.

In 2017 and 2018, grass biomass (g m^{-2}) tended to be higher in cut than uncut plots, but one plot in the uncut treatment diminished these differences in 2019 and differences were not significant. By 2017, track and dung counts tended to be higher in the cut than uncut plots indicating higher animal

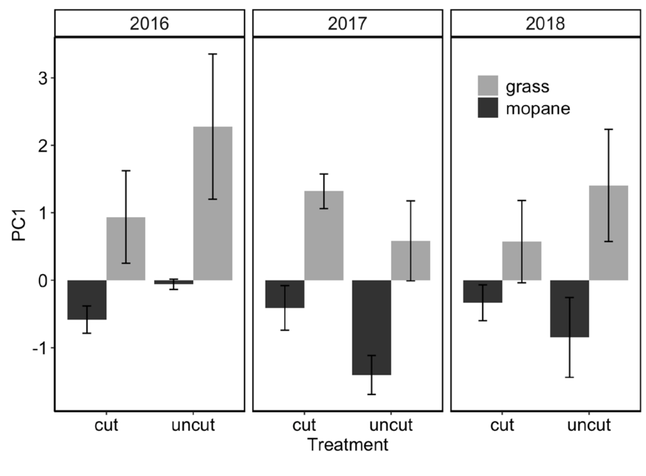

Fig. 1. Mean mopane (black) and grass (grey) PC1 isotope scores in cut in uncut plots in 2016-2018. The PC1 axis represents both δD and δ^{18}O values. Lower PC1 values correspond with deeper soil water. Shown are means ± 1SE.

presence. Grazer track and dung counts were significantly higher in cut than uncut plots in 2018 and 2019 ($P < 0.05$) for herbivores including buffalo, hippo, impala, warthog, waterbuck, wildebeest, and zebra (Fig. 2).

Discussion [Conclusions/Implications]

The increased cover of woody species has caused numerous economic and ecological consequences in lowveld savannas. In areas where the drivers limiting woody cover have been altered, bush cutting may be a necessary management technique to increase grass cover and reverse the negative consequences of bush encroachment. Active and frequent management practices are likely to become increasingly necessary in a changing climate and fragmented landscapes where the return of disturbance to the system is insufficient to limit bush encroachment (Case et al. 2017; Collins et al. 2021). In this study, we found repeated cutting reduced mopane starch reserves and opened the canopy, promoting increased grass productivity and herbivore presence.

Although we did not find consistent significant shifts in root water uptake by mopane in response to cutting, our results support hydrological niche separation between trees and grasses (Holdo et al. 2015; Case et al. 2020). Mopane roots have been shown to be shallow with the majority of fine roots in the top 40 cm of soil and coarse roots between 40-60 cm of soil (Smit and Rethman 1998). This shallow and sprawling root system suggests shallow roots play an important functional role for the species and differences in niche partitioning between trees and grasses may occur over small spatial scales (Kulmatiski and Beard 2020). Slight increases in variation in cut mopane water use may be associated with increased plasticity. Repeated cutting may reduce belowground carbon investment and increase reliance on fine roots in the surface soils, as seen in 2017.

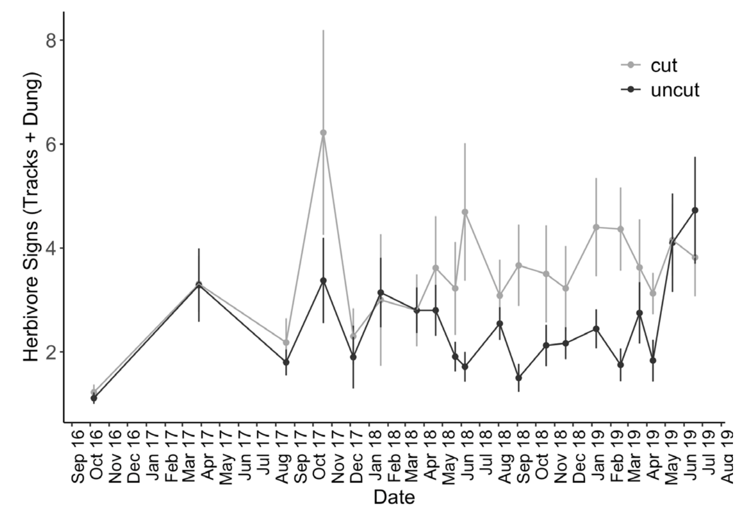

Fig. 2. Mean herbivore track and dung counts cut (grey) and uncut (black) treatments over time. Dates show the month and year. Herbivores include buffalo, hippo, impala, warthog, waterbuck, wildebeest, and zebra. Shown are means ± 1SE.

Five years of repeated cutting resulted in low tree mortality, but significantly decreased root starch concentrations. Woody plants in disturbance-prone areas tend to have high NSC storage belowground used to resprout after disturbance (Wigley et al. 2019). Repeated cutting depleted NSC reserves and starch concentrations became lower in the cut trees over time. This suggests that mopane trees are not able to restore belowground carbon stores when faced with frequent and repeated disturbance. Interactions among multiple disturbances (e.g., cutting and fire) have the potential to result in even greater reductions in NSC concentrations, with resulting increased tree mortality (as documented in O'Connor et al. 2020). Imposing multiple disturbances likely holds the most promise to drive the long-term reduction of woody cover in mopane savanna. Perhaps most importantly, in locations with cut mopane, we found increased grass biomass and signs of herbivores within only a few years. Increased grazer presence may have both ecological and applied benefits for the landscape. In summary, this study shows bush cutting requires repeated and active management but can be an effective management tool for decreasing woody cover and promoting herbaceous biomass and herbivore presence within sites.

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