456

Larger trees facilitate understory herbaceous biomass but not diversity in a South African savanna

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Abstract

Large single-standing trees contribute to the structural diversity of savannas as they strongly influence their immediate surroundings such as soils and understory plant communities. The influence of woody vegetation at a stand level on the understory vegetation has been extensively studied; however, the understanding of the role of single large trees is limited. The objectives of the study were to 1) evaluate the impact of large trees on understory plant species diversity and composition, herbaceous cover and grass standing biomass, and 2) to establish if plant size and functional qualities such as N-fixing ability modulate understory vegetation responses to overstory trees over two growing seasons (January 2022 and 2023). *Vachellia tortilis* (a leguminous tree) and non-leguminous woody species (*Searsia l*ancea and *Ziziphus mucronata*) were studied. We systematically selected 30 trees for each woody species and divided them into two size classes (i.e. small and large trees). Understory plant vegetation was assessed using quadrats under and outside the tree canopies. Plant species diversity and abundance were highest under small tree canopies and outside tree canopies compared to under large trees. Panicum maximum was the dominant grass species under large trees regardless of N-fixing ability. Nonetheless, grass cover was enhanced under large *V. tortilis* and *Z. mucronata*. Standing grass biomass was higher under the canopies of large trees compared to small trees and outside canopies, with N-fixing ability having no significant effect ($p > 0.05$). The current findings imply that in agrosilvopastoral systems and game farming, where ecological conservation is a priority for farmers, it is essential to have an overstorey composed of both small and large trees to sustain understory diversity and biomass.

Introduction

Our understanding of the role of trees of varying sizes and functional qualities is limited (Pillay and Ward, 2012). There is a considerable variance on the impact of large trees on the understory vegetation. For instance, studies conducted in a semi-arid savanna of Ethiopia have found that large trees enhance herbaceous understory richness and biomass, with significant increases recorded under N-fixing leguminous trees (Tessema and Belay, 2017). Other studies conducted in South African savannas have found non-significant effects, particularly on standing herbaceous biomass, regardless of N-fixing ability (Treydte et al., 2007).

Nonetheless, certain nitrophilous grasses, particularly *Panicum maximum* (Jacq) have been documented to colonise and flourish under trees (Smit, 2005). *P. maximum* is a shade-tolerant and highly competitive grass species (Smith et al., 2013). Consequently, *P. maximum* may threaten species richness and diversity under tree canopies. Nevertheless, effects of woody plants to understory may vary by encroaching species, and understory herbaceous species (Kahi et al., 2009), thus, site-specific assessment of herbaceous plant responses to overstory trees is crucial.

Methods and Study Site

The study was conducted at Roodeplaat experimental farm (25°56′S, 28°35′E) of the Agricultural Research Council (ARC) in Gauteng Province of South Africa. Three dominant woody species representing one leguminous (*Vachellia tortilis*) and two non-leguminous tree species (*Searsia lancea* and *Ziziphus mucronata*), found in isolation, were selected for this study. These woody species are representative of the dominant trees in the study area. We systematically selected 30 trees for each woody species and divided them into two size classes (i.e. small and large trees). Small trees had a similar canopy area (≈ 10 m^2) and height (≈ 3 m). Large trees also had a similar canopy area (≈ 40 m^2) and tree height (≈ 6 m) (Ludwig et al., 2004). In total 90 trees (three species × 30 trees) were selected for this study in a permanently fenced area where grazing was excluded.

We recorded the species composition of understory vegetation including herbaceous species as well as seedlings of woody species under and outside individual tree canopies over two growing seasons (January 2022 and 2023). Four quadrats (0.5 m × 0.5 m) in four directions (north, south, east and west) were used for herbaceous assessments under the inside and outside canopy (i.e. the area surrounding the canopy within a 2 m range) of each individual tree. Outside canopy sampling points functioned as a control for possible changes in microclimate or plant cover in the understory. To ascertain the relative contributions of each functional group, the species were further divided into grasses, forbs and woody species. All individual plant species were counted and identified to species level in each 0.5 m × 0.5 m quadrat. Herbaceous cover (grass and forb) was visually assessed within the quadrat by two individuals, and their estimates were subsequently averaged to produce a single representative measurement. Standing grass biomass regardless of species was harvested in each 0.5 m × 0.5 m quadrat. The grass samples were oven dried at 70ºC for 72 h and weighed to determine dry-matter yield.

A two-way ANOVA was conducted using general linear models (GLMs) to determine the main effects of tree species and microsites on mean total species richness and diversity, herbaceous cover and standing grass biomass.

Results

A total of 26 plant species were recorded with perennial species being the most abundant, with grasses recording the highest contribution (n = 14). Poaceae was the most dominant family with predominantly native species, whilst forbs were mostly invasive species**.**

Plant species diversity was substantially affected by microsites ($F = 26.429$; $p < 0.001$), tree species ($F = 11.818$; $p < 0.001$) and their interactions ($F = 5.723$; $p < 0.001$). A Bonferroni post hoc test indicated that small *S. lancea*, *Z. mucronata* and *V. tortilis*, and outside of the canopies recorded a greater species diversity compared to large *S. lancea* and *Z. mucronata*. Plant species richness was significantly greater under small trees and outside canopies than under large trees ($p < 0.05$), particularly under large *S. lancea* and *Z. mucronata*.

Grass cover was substantially low under large *S. lancea* trees compared to outside canopies, and under large V. tortilis and Z. mucronate ($p < 0.05$). Large trees of *S. lancea*, *V. tortilis* and *Z. mucronata* significantly increased understory standing grass biomass ($p < 0.05$). In addition, large *S. lancea*, *V. tortilis* and *Z. mucronata* trees were associated with a higher abundance the highly nutritious *P. maximum* than other understory grass species.

Discussion

Effects of mediated microsites on plant species diversity and richness

Reduced species diversity under large trees could be attributed to the dominance of *P. maximum* under large trees, which significantly reduced understory diversity and richness. In support, Mlambo et al., (2005) demonstrated that *P. maximum* increases in abundance under large *Colophospermum* mopane trees. The findings from the current study suggest that an increase in abundance of *P. maximum* under tree canopies result in a significant reduction in understory species diversity. Nonetheless, the results from the current study indicated that the facilitative effects of smaller trees on the diversity and richness of understory vegetation out-weighed the competitive effects of trees on understory species. Thus, our result confirmed that the facilitative effects would lead to more number of species and plant abundance under canopies of smaller trees compared to large trees. However, this relationship shifts as tree size increases.

The effects of tree-meditated microsites on herbaceous cover and standing grass biomass

The substantial reduction in grass cover under large *S. lancea* trees was attributed to that herbaceous cover under woody plants with evergreen leaf phenology significantly decline (Belay and Moe, 2015). The study findings suggest that the traits of specific woody plants are more useful for predicting the effects of woody plant encroachment on grass herbaceous cover than increased tree densities. Although grass cover declined under large *S. lancea* trees, grass biomass was substantially enhanced under large trees of all the study species. we attributed the increased standing grass biomass under large trees to the enhanced soil fertility through N-fixing ability (i.e. *V. tortilis*) and greater litter biomass that returns to the soils (i.e. *S. lancea* and *Z. mucronata*). Nonetheless, our study shows that the impact of small trees on standing grass biomass may operate independently of diversity and richness because small trees had a similar number of species compared with outside canopies but distinct standing grass biomass, particularly *V. tortilis* and *Z. mucronata*.

Responses of plant species composition to mediated microsites

Large *S. lancea*, *V. tortilis* and *Z. mucronata* were associated with a high abundance of *P. maximum*, which was not surprising result because of the possible elevated micro-climate under the canopies of these species. The study findings demonstrate that the increased abundances of *P. maximum* plants under canopies of large trees is more important for grazers because of the high nutritional value of this species (Hare et al., 2021). Although *P. maximum* was the dominant plant species under large trees, the invasive Lantana camara was also associated with large trees, particularly *V. tortilis*. These results concur with McMahon and Ward (2021) who reported a higher abundance of *L. camara* under large trees, particularly of leguminous species.

Conclusions

Overall, the findings showed that understory plant vegetation, particularly of the herbaceous layer, responses regarding grass cover and biomass, diversity and composition depend on the tree sizes and microsites (i.e. under or outside the canopies). The increased standing grass biomass under large trees indicate that it may be beneficial to maintain large trees in savannas, particularly where pastoralism and game farming are the main objectives, although herbaceous diversity may decline. Additionally, the dominance by *P*. *maximum* under large trees have the greatest potential for providing forage for herbivores its high production and nutritive value (Hare et al., 2021).

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