Soil seed banks along a woody plant removal gradient in a semi-arid savanna of South Africa: implications for restoration

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Abstract. Woody plant encroachment threatens ecosystem services and functions, thereby reducing herbaceous plant population persistence and community stability. Consequently, woody plant control projects are implemented in South Africa to restore herbaceous vegetation. Because persistent seeds drive passive restoration and vegetation trajectories, management following woody plant control entails examining soil seed bank (SSB) size and composition. However, a knowledge gap exists regarding how SSB characteristics respond along a woody plant removal gradient. This study was conducted at Roodeplaat in Gauteng Province of South Africa to assess the impact of woody density reduction [hereafter woody plant removal intensity (WPRI)] on SSB density, composition, diversity and richness. Selective tree removal was applied to downscale woody density (4065 plants ha-1) of the control (0% WPRI) to 10, 20, 50, 75 and 100% WPRIs in four blocks, resulting in four replicates per WPRI. A total of 120 soil samples (n = 20 per WPRI) collected at 5-cm depth were examined using germination method. Fifty-one species, mainly forbs (n = 26) and grasses (n = 16) were recorded from 32 237 seeds. The SSB densities of grasses increased from 649 to 6000 seeds m-2 from 0 to100% WPRI whilst sedges and forbs exhibited differential declining trends along WPRI gradient. Cyperus rotundus accounted for more than one-third of the SSB densities at 0 and 10% WPRIs, whereas Panicum maximum contributed nearly half (46%) to the SSB density at 100% WPRI. Woody removal increased SSB diversity (H') and richness, but diversity peaked at 20% WPRI (H' = 1.78); thereafter it declined. Increased SSB size and species richness of grasses at 100% WPRI indicated that complete woody clearing is key for restoration of woody-encroached rangelands. However, this means that savanna will be converted completely to a grassland, leading to a loss of other important savanna ecosystem services. Thus, on account of conserving the ecosystem services of the savanna, a research is warranted to test other woody density proportions to determine a potential optimal woody density.

Introduction

The competition for light and soil resources posed by woody plants fosters early senescence of understory species, subsequently reducing seed production and soil seed bank (Bakker et al. 2014). For example, seed production of perennial grasses was relatively low in Juniper-encroached relative to cleared rangelands (Bates 2005). Soil seed bank density of perennial grasses and forbs decreased with increase in woody cover elsewhere (Koyama et al. 2015). In a long-term, depletion of the soil seed bank reduces plant population persistence and community stability. Hence, woody encroachment control using non-destructive methods to soils is crucial to restore herbaceous vegetation (Mndela et al. 2022; Monegi et al. 2022).

Soil seed bank responses to woody plant control have been studied extensively in savannas (Mndela et al. 2019; Zida et al. 2020). However, to our knowledge, an optimal woody density that may optimise the soil seed bank for successful restoration is yet to be ascertained. Most dominant are studies that monitored short-term dynamics of the soil seed bank in cleared and their adjacent uncleared treatments (Mndela et al. 2020). The shortfall of these studies is that they overlook the ecological significance of optimal woody plant density on herbaceous vegetation. To the extreme, these studies downplay the importance of resource or niche heterogeneity, as different herbaceous species have affinity for different niches in savannas (Smit 2005). Some species, mostly shade-tolerant species have high affinity for resource-rich microsites under trees, whereas others prefer inter-tree spaces (Maponga et al. 2021).

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. The following woody plant removal intensities (WPRIs) were assigned: 0% (no removal/control), 10% (very light removal), 20% (light removal), 50% (moderate removal), 75% (high removal) and 100% (total removal). The treatments were downscaled from the total woody plant density (4065 trees ha-1) of the control through selective tree removal using chainsaws. Each WPRI was assigned randomly, once in each block, resulting in four replicates per WPRI. The replicates were 30 m × 30 m in size and were separated by a 5-m wide buffer to avoid treatment-treatment spillover effects.

Soil samples were collected using auger at the end of winter in July 2021, three years after selective tree removal. Two samples were collected in each corner and at the center of each replicate plot (n = 10 samples), totaling to 240 soil samples. Soil samples were 5 cm deep and 9 cm wide, with each soil sample making an area of 63.59 cm2. The seeds are reported to be more concentrated at a depth of 5 cm (Snyman 2004). After sampling, soils were bagged and transported to the laboratory, where they were air-dried and kept under dry conditions at 4°C. Debris and stones were removed by passing soil through a 5-mm sieve. The seedling method was employed to examine viable seeds in the soil (Baskin and Baskin 2014). Two soil samples for each sampling point were bulked and spread evenly on top of 3-cm deep sterilised sand in plastic trays (20 cm × 30 cm), giving a total of 120 trays.

Two-way ANOVA was conducted using general linear models (GLMs) to examine the main effects of woody plant removal intensity and plant functional groups (PFGs) and their interactions on the SSB density and richness. However, for species diversity and the relationship between SSB and AGF, we generated one-way ANOVA. The experimental blocks were included as a random factor in the GLMs, with replicates nested within the blocks. The significant effects of treatment and functional groups were assessed using Tukey test, with significant effects affirmed at 95% confidence interval.

Results

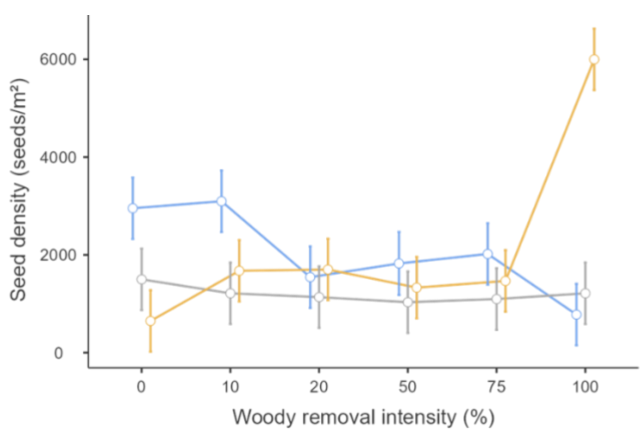

Fig. 1: Soil seed bank density of forbs ( ), sedges ( ) and grasses ( ) across a gradient of woody plant removal intensity. Woody plants were not included due to low seed bank densities.

Discussion

Effect of woody plant removal intensity on soil seed bank densities

The results showed that woody removal, more so removal of all woody plants (100% WPRI) positively increased SSB density. This result is not surprising given that reduction in competition, largely for light via woody removal allows more herbaceous recruitment and seed production (Bates 2005). However, SSB responses to woody plant removal were interspecific, driven mainly by the interaction between WPRI and PFGs, suggesting that herbaceous plants tolerance to woody encroachment varies by PFGs. This was true, considering that sedges had higher seed densities at 0 and 10% WPRIs which are characterized by high woody density whilst grasses attained higher seed densities at 100% WPRI. A dominant sedge (*Cyperus rotundus*) accounted for more SSB densities than did other species at 0-75% WPRIs, indicating that SSB size of this species was enhanced by woody plants. Thus, given that this species is adapted to moderately moist conditions (Lanza et al. 2017), its high seed densities were enhanced probably by wet conditions under trees.

On the other hand, low seed densities of *Panicum maximum* at 0 and 10% WPRIs was surprising, given that this grass species is shade tolerant. The possible explanation for this is the negative relationship between P. maximum and *C. rotundus* which likely indicates that these two species rarely coexist (Fig. S3). This result is supported by Laza et al. (2017) who found higher abundance of *C. rotundus* than *P. maximum* under high tree densities of 3 200 trees ha-1, signifying that the former was more shade-tolerant than the latter. High seed densities of *P. maximum* were also reported by Lin et al. (2022) following forest opening by fires elsewhere. In this study, the contrasting responses of *P. maximum* at 0 and 100% suggest that higher SSB density at 100% WPRI was a function of seed production of the AGF after woody plant removal. Higher seed bank densities of *P. maximum* were also reported in non-encroached than in wild sage-encroached southern African rangeland (Tedder et al. 2012).

Soil seed bank communities and their associations with woody plant removal intensity

The soil seed bank communities were separated by clustering, with the communities having different affinities for woody plant removal intensity. Community 1 characterized largely by forbs and grasses, with *P. maximum* dominating, was the largest community, with grasses being positively related to 100% WPRI and negatively related to 0 and 10% WPRI. This indicated that high woody density reduced SSB of grasses including *Heteropogon contortus*, *Aristida congesta*, *Eragrostis racemosa* and *P. maximum*. Most of these grasses are grassland species adapted to high light intensity, thus reduced light by woody canopies reduces seed production.

Effect of woody removal on soil seed bank diversity, evenness and richness

Generally, SSB species diversity was highest for 20 to 75% than 0 and 100% WPRIs, showing that dominance by single species, as observed at 0 and 100% WPRIs reduced SSB diversity. Moreover, habitat heterogeneity due to scattered trees at 20-75% WPRIs promote diversification of growing conditions (Teleki et al. 2019) and thus species coexistence (Helbach et al. 2020). As a result, some opportunistic species quickly inhabited nutrient-rich microsites previously occupied by woody plants, whereas others colonise under remaining canopies and in inter-tree spaces.

The SSB species richness recorded in this study is higher than that found by Coffey and Otfinowski (2018) in wood plant cleared woodlands, despite longer time of recovery in their study relative to this study. These differences could be due to the types of cleared woody species, as most encroachers were leguminous in this study, whereas cleared species were non-leguminous in Coffey and Otfinowski (2018). Despite comparatively high species pool at 20 and 100% WPRIs, SSB diversity was relatively low at 100% compared to 20% WPRI. This result indicates that high SSB diversity at 20% WPRI was determined not only by species richness, but also increased abundance of other species.

Conclusions

The results of this study indicated that woody removal increases soil seed bank size and richness of herbaceous plants, largely grasses. The increase in SSB densities of grasses coincided with the decline in SSB densities of forbs and sedges as woody plant removal intensity increased. The greatest increases in SSB density and richness were most noticeable at 100% WPRI. This suggests rejection of the hypothesis that there is an optimal woody density that maximizes SSB size and richness in the studied bush-encroached rangeland of southern Africa. However, our results imply that savannas have to be completely converted to grasslands in order to maximise SBB size and richness, but this would occur at the expense of other important ecosystem services and functions of the savanna. Thus, on account of conserving savanna ecosystem services, we warrant a research that will test other woody density proportions to determine a potential optimal woody density that would optimise the SBB size and richness.

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