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Effect of soil and subhabitat differentiation on the growth of *Tarchonanthus camphoratus* seedlings from a semi-arid savanna of South Africa

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Abstract

Large areas in the savanna of the Northern Cape Province of South Africa suffer from bush thickening, especially by species such as *Tarchonanthus camphoratus*. Effective management of these areas requires an understanding of the factors such as allelopathy that can affect the establishment, survival and growth of *T. camphoratus* seedlings. The objectives of this study were to investigate whether soil originating from different subhabitats would differ in soil nutrient status and whether *T. camphoratus* exhibit allelopathic effects by affecting the survival and growth of seedlings grown in soil originating from these different subhabitats. Soil and ripe seeds were collected in the Northern Cape Province of South Africa on two sites of different soil types (deep sandy and shallow rocky) and within three subhabitats (close to the stems of mature *T. camphoratus* plants; in the middle of the canopy; and away from tree canopies in the uncanopied zone). The trial was conducted under controlled conditions in a greenhouse over a period of 18 months and consisted of six treatments with ten replications. Soil analyses, including Na, Mg, K, Ca, P and N were performed on the soil from the different subhabitats. Seeds germinated abundantly in all the soil samples, confirming that there are no allelopathic effects preventing their germination. Significantly higher ($P < 0.05$) plant heights, leaf numbers and growth rates were measured in seedlings grown in the soil originating from the canopied zone compared to those grown in soil from the uncanopied zone, while no significant differences ($P > 0.05$) existed between the seedlings grown in soil from the same subhabitat but different soil types. The better growth of *T. camphoratus* seedlings in soil from the canopied subhabitats can be attributed to the higher soil nutrient status in these subhabitats. This has important implications for tree thinning operations as areas where mature trees are removed, will present ideal areas for seedling establishment, survival and growth.

Introduction

Southern African savannas are water-limited ecosystems and bush thickening is considered a major factor contributing towards the low occurrence or even total absence of herbaceous plants, due to severe competition from the woody plants for available soil water (Smit et al. 1999). Large areas in the savanna of the Northern Cape Province of South Africa suffer from bush thickening, especially by

species such as *Tarchonathus camphoratus*. Many studies have shown a positive response of the herbaceous layer to the partial or complete removal of woody plants (Smit 2005; Harmse et al. 2016) and the success of bush-clearing or thinning operations is often measured on the basis of the recovery, productivity and stability of the herbaceous layer. However, the re-establishment of woody plants after thinning or clearing - either by resprouting or by seedling establishment from seeds - remains a serious threat and this phenomenon has been widely reported in southern African savannas (Smit 2004; Harmse et al. 2016). It is known that some plants release allelochemicals into the soil and these metabolic secretions, including long chain fatty acids, phenolic acids, terpenoids, organic cyanides and others are known to affect seed germination and seedling emergence, mortality and growth (Ghebrehiwot et al. 2014). The objectives of this study were to investigate whether soil originating from different *T. camphoratus* subhabitats (under- and between tree canopies) would differ in soil nutrient status and whether *T. camphoratus* exhibits allelopathic effects by affecting the survival and growth of seedlings grown in soil originating from these different subhabitats.

Methods

Soil and ripe seeds of *T. camphoratus* shrubs were collected from the Rooipoort Nature Reserve approximately 60 km west of the town of Kimberley in the Northern Cape Province of South Africa. The reserve is located within the savanna biome of southern Africa and Mucina and Rutherford (2006) described the area as the Eastern Kalahari Bushveld Bioregion. Twenty free-standing *T. camphoratus* shrubs of similar size (1.5 - 2.0 m height) were randomly selected on two sites of different soil potential (deep sandy soils and shallow rocky soils). Topsoil (0 - 20 cm) was excavated from three identified subhabitats (Smit & Swart 1994), namely: (1) close to the stem ; (2) in the middle of the canopy between the stem and the canopy edge; and (3) in the open uncanopied zone between the shrubs. The bulked samples were thoroughly mixed and a subsample was taken for laboratory analyses.

Large pots (18 700 cm³) were filled with an equal volume of soil and placed in a greenhouse located at the facilities of the University of the Free State, Bloemfontein, South Africa. This amounted to 3 subhabitats x 2 sites x 10 replications = 60 pots. *T. camphoratus* seeds were planted in the pots during September 2018. Plots were regularly watered and germination of seeds recorded. Seedling height was measured weekly. Eighteen weeks later all plants were harvested. The number of leaves per seedling, number of daughter shoots, stem diameter at the base and seedling height was recorded. The stems, leaves and roots were separated and the soil washed from the roots with medium pressure water. Thereafter all biomass fractions were oven-dried at 70°C to constant mass and then weighed. The Shapiro-Wilk test ($p > 0.05$) was used to test all variables for normal data distribution. Analysis of variance using the randomized complete block design (RCBD) was used to test the influence of subhabitat and soil on the different plant growth parameters.

Results and Discussion

Soil nutrient status

Marked differences in soil nutrient status between the uncanopied subhabitat and the two canopied subhabitats were found (Table 1). However, the extent to which each soil nutrient was affected, differed. Subhabitat differentiation significantly ($p < 0.05$) influenced soil potassium and calcium concentrations as well as total nitrogen and organic carbon percentages on both soil types and followed a clear spatial gradient with increasing distance from the stem to the open grassland subhabitat. Magnesium concentrations differed between subhabitats on the rocky soil only, while plant available phosphorus only differed between subhabitats on sandy soil. Soil pH, calcium concentration, nitrogen and organic carbon percentage were significantly ($p < 0.05$) influenced by soil potential.

Table 1 Mean \pm 1 SE of all tested soil variables for two soil potentials (sandy and rocky) in three subhabitats

Site Subhabitat	Rocky			Sandy		
	stem	canopy middle	open	stem	canopy middle	open
pH(H ₂ O)	7.32 \pm 0.06	7.59 \pm 0.06	7.41 \pm 0.06	7.04 \pm 0.07	7.35 \pm 0.08	6.88 \pm 0.08
K ⁺ (mg kg ⁻¹)	244.37 \pm 15.19	208.82 \pm 9.98	143.47 \pm 8.99	239.42 \pm 17.61	237.97 \pm 16.50	132.96 \pm 12.424
Ca ²⁺ (mg kg ⁻¹)	475.22 \pm 27.01	436.17 \pm 44.25	306.80 \pm 18.07	339.51 \pm 20.84	279.36 \pm 12.11	233.98 \pm 17.048
Mg ²⁺ (mg kg ⁻¹)	95.17 \pm 2.88	90.31 \pm 2.49	71.22 \pm 2.57	83.52 \pm 3.37	91.47 \pm 3.69	81.28 \pm 4.609
Na ⁺ (mg kg ⁻¹)	5.10 \pm 0.18	4.91 \pm 0.33	4.80 \pm 0.22	4.58 \pm 0.10	4.72 \pm 0.10	4.30 \pm 0.078
P (mg kg ⁻¹)	6.30 \pm 1.25	7.53 \pm 1.11	4.52 \pm 0.79	7.86 \pm 1.20	4.17 \pm 0.67	3.77 \pm 0.699
N (%)	0.08 \pm 0.01	0.05 \pm 0.00	0.03 \pm 0.01	0.05 \pm 0.00	0.03 \pm 0.00	0.02 \pm 0.001
OC (%)	1.29 \pm 0.27	0.829 \pm 0.02	0.47 \pm 0.03	0.81 \pm 0.03	0.548 \pm 0.00	0.35 \pm 0.012
C:N	17.0:1 \pm 0.60	18.4 :1 \pm 0.98	20.8:1 \pm 2.70	17.2:1 \pm 0.49	22.0:1 \pm 2.21	19.9 \pm 1.127

Seed germination and growth of seedlings

Germination of the seeds commenced very slowly and only by 15 January 2019 had the majority of seeds germinated, indicating that fresh *T. camphoratus* seeds undergo some form of seed dormancy (seed rest period) for approximately three to four months. Seedlings grown in the soil originating from the sandy site differed significantly ($p < 0.05$) in height between subhabitats. Seedlings grown in the soil from the two canopied subhabitats grew significantly ($p < 0.05$) higher than the seedlings grown in the soil from the uncanopied subhabitat. In the case of the soil originating from the rocky site, only seedlings grown in the soil from the stem subhabitat grew significantly higher ($p < 0.05$) than those grown in soil from the uncanopied subhabitat (Table 2).

Seedlings grown in the soil from the two canopied subhabitats of both the sandy and the rocky site grew significantly ($P < 0.05$) thicker (stem base diameter) compared to those grown in soil from the uncanopied subhabitat. However, the stem diameters of plants grown in soil of the canopied subhabitats of both soil types did not differ significantly ($p > 0.05$) (Table 2).

The number of leaves per seedling was 138% and 88% higher for plants grown in the soil originating from the stem and canopy middle subhabitats respectively, compared to plants grown in soil from the uncanopied subhabitat of the sandy site. Similarly, plants grown in the soil from the stem and canopy middle subhabitat, had 114% and 106% more leaves respectively, than plants grown in soil from the uncanopied subhabitat of the rocky site (Table 2).

The dry mass of the seedling leaves and shoots as well as total dry mass (leaves, shoots and roots combined) yielded very similar results. Significantly ($p < 0.01$) heavier leaf dry mass, shoot dry mass and total dry mass were recorded in plants grown in the soil from the canopied subhabitats compared to plants grown in

the soil from the uncanopied subhabitat. The plants grown in the soil of the two canopied subhabitats were statistically non-significant ($p > 0.05$) in leaf, shoot and total dry mass in both soils.

Table 2 Soil effect on seedling height, stem diameter, number of leaves and number of daughter shoots (mean \pm SE) as per subhabitat (n=10). The same letter for each subhabitat represents statistical non-significance ($p > 0.05$).

Subhabitat	Site	Seedling height (mm)	Stem diameter (mm)	Number of leaves	Number of daughter shoots.
Stem	Sandy	683.8 \pm 71.5 ^a	8.2 \pm 0.5 ^a	243.7 \pm 31.8 ^a	28.3 \pm 4.2 ^a
	Rocky	664.6 \pm 84.3 ^a	8.7 \pm 0.5 ^a	206.3 \pm 25.6 ^a	28.2 \pm 5.3 ^a
Canopy middle	Sandy	655.9 \pm 49.8 ^a	8.6 \pm 0.4 ^a	192.0 \pm 13.8 ^a	24.4 \pm 2.8 ^a
	Rocky	570.0 \pm 68.2 ^a	8.1 \pm 0.8 ^a	198.4 \pm 27.0 ^a	21.6 \pm 3.2 ^a
Uncanopied	Sandy	405.7 \pm 46.1 ^a	5.7 \pm 0.3 ^a	102.3 \pm 11.5 ^a	8.7 \pm 2.0 ^a
	Rocky	418.9 \pm 29.8 ^a	5.8 \pm 0.2 ^a	96.4 \pm 8.6 ^a	8.0 \pm 2.1 ^a

The only significant ($p < 0.05$) difference in root dry mass was found between plants grown in the soil from the canopy middle and uncanopied subhabitat of the rocky site (Table 3).

Table 3 Soil effect on leaf dry mass, shoot dry mass, root length and root dry mass (mean \pm SE) as per subhabitat (n=10). The same letter for each subhabitat represents statistical non-significance ($p > 0.05$).

Subhabitat	Site	Leaf dry mass (g)	Shoot dry mass (g)	Root length (mm)	Root dry mass (mm)	Total dry mass (mm)
Stem	Sandy	15.6 \pm 1.8 ^a	9.9 \pm 1.9 ^a	486.8 \pm 18.3 ^a	9.6 \pm 1.4 ^a	35.1 \pm 5.04 ^a
	Rocky	13.0 \pm 1.6 ^a	7.8 \pm 1.6 ^a	454.4 \pm 32.9 ^a	8.3 \pm 1.0 ^a	29.2 \pm 3.9 ^a
Canopy middle	Sandy	14.4 \pm 1.2 ^a	7.9 \pm 0.7 ^a	480.0 \pm 26.3 ^a	8.7 \pm 0.9 ^a	31.0 \pm 2.8 ^a
	Rocky	13.9 \pm 2.0 ^a	7.5 \pm 1.4 ^a	449.6 \pm 26.9 ^a	10.3 \pm 1.7 ^a	31.7 \pm 4.9 ^a
Uncanopied	Sandy	6.8 \pm 0.6 ^a	2.9 \pm 0.5 ^a	484.0 \pm 37.1 ^a	7.2 \pm 0.6 ^a	16.9 \pm 1.5 ^a
	Rocky	6.3 \pm 0.3 ^a	2.3 \pm 0.2 ^a	417.1 \pm 25.0 ^a	5.9 \pm 0.4 ^a	14.5 \pm 0.8 ^a

Conclusions

This study demonstrated the importance of *T. camphoratus* in soil enrichment and confirms the well documented development of “nutrient hotspots” under woody plant canopies. The delayed germination of ripe seed of *T. camphoratus* confirmed the existence of a dormancy period of three to four months. This is possibly an adaptation to prevent the seeds from germinating too early in the rainy season when the risk of desiccation is high.

No allelopathic effects that limit seed germination and the survival of *T. camphoratus* were observed in the soil collected from underneath their canopies. While above-ground seedling growth was generally higher in the soil from close to the stem compared to those in soil from the middle of the canopy, the differences between the two canopied subhabitats were statistically non-significant ($p > 0.05$). In contrast to the above-ground growth parameters, no statistically significant ($p < 0.05$) difference could be established between the root dry masses of seedlings grown in the soil of all three subhabitats.

Higher nutrient availability under the shrub canopy compared to the uncanopied zone is considered to be the primary cause for the observed increased above-ground growth of the *T. camphoratus* seedlings that were grown in the soil from the two canopy subhabitats. No statistically significant ($p < 0.05$) differences in any of the measured growth parameters could be identified between soil originating from the sandy or the rocky sites, clearly demonstrating the importance of *T. camphoratus* as a biological agent that is able to create islands of enhanced soil nutrients (soil enrichment), regardless of soil type. From this, it can be concluded that subhabitat differentiation has more definite effects on seedling growth than differences related to soil type. This has important implications for tree thinning operations as areas where mature trees are removed, will present ideal areas for seedling establishment, survival and growth.

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