AN ECOLOGICAL STUDY OF *TARCHONANTHUS CAMPHORATUS* L. IN THE NORTHERN CAPE PROVINCE OF SOUTH AFRICA

By

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ABSTRACT

An ecological study of *Tarchonanthus camphoratus* L. in the Northern Cape Province of South Africa

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Key terms: allometric, bush-thickening, coppicing ability, fire, phenology, seed production, seedling establishment, shoot growth, soil nutrients, soil seed bank, *Tarchonanthus camphoratus*

Bush-thickening resulting in decreased agricultural productivity, inaccessible thickets and increased occurrence of pseudo-droughts is a common phenomenon in the semi-arid southern African savanna. Until recently, land owners paid little attention to *T. camphoratus*, but there is a growing awareness of the potential threat that this species presents, largely because it (1) increased significantly in numbers during the past few decades, (2) reduces the productivity of the herbaceous layer, (3) is semi-deciduous to evergreen, thus requiring water all year round in a water-limited environment, (4) is a less palatable woody plant species, (5) reproduces sexually and asexually and (5) is fire tolerant.

The main objective of this study was to gain a better understanding of the ecological functioning of *T. camphoratus* to establish objective guidelines for the effective and ecologically responsible management of the species. The research was conducted in the Kimberley Thornveld on Rooipoort Nature Reserve in the Northern Cape Province on deep sandy soil and on shallow rocky soil. The influence of *T. camphoratus* on the soil nutrient status, its leaf and reproductive phenology, as well as shoot growth in relation to different climate variables, including temperature, day length and rainfall and its coppicing ability as influenced by season of disturbance, were studied. The existence of a soil seed bank and allelopathic effects in the soil, the effect of soil originating from different subhabitats on seedling growth and the response of *T. camphoratus* and co-dominant *Senegalia mellifera* to fire were also investigated. In addition, seed production was quantified and regression equations relating spatial canopy volume to leaf and wood biomass were developed from harvested undamaged and coppicing plants.

It was established that, although some nutrients, including potassium, total nitrogen and organic carbon, differed significantly between the two soil types, the soil under the canopies of *T. camphoratus* had a higher soil nutrient status compared to soil in the open grassland. Climate, especially temperature and rainfall, were strongly correlated with the leaf carriage and shoot growth of *T. camphoratus. T. camphoratus* retained more leaves during the dry period compared to other woody species in the area. All *T. camphoratus* shrubs coppiced after cutting. However, shrubs cut during the active growth season (summer) coppiced less vigorously compared to those cut during winter.

The seed production of female *T. camphoratus* shrubs was relatively high (40 469 ± 4504 seeds ETTE^{-1}), but seeds did not persist in the soil seed bank for longer than one year. High seed densities of other plants, especially grasses, in the soil under the canopies of *T. camphoratus* suggested a high restoration potential in terms of herbaceous plant establishment, where *T. camphoratus* was removed in bush-thinning operations. No allelopathic effects limiting seed germination and seedling growth were evident. The seeds of *T. camphoratus* underwent a three- to four-month dormancy period before they germinated. Seedlings grew more vigorous in the nutrient-rich soil originating from the canopied subhabitat compared to the nutrient-poor soil originating from the open grassland. This has implications for tree-thinning operations, as areas where mature trees are removed may subsequently present ideal areas for the establishment and growth of *T. camphoratus* seedlings. Furthermore, it was found that *T. camphoratus* recovered more rapidly than *S. mellifera* after a hot fire and that, in areas where these two species are co-occurring, frequent fires may eventually result in the replacement of *S. mellifera* by *T. camphoratus.*

Highly significant ($p < 0.001$) regression models with very high coefficients of determination ($r > 0.8$) relating spatial canopy volume to dry mass fractions of leaves and stems in three diameter classes (< 5 mm, 5 – 20 mm and > 20 mm) were developed for undamaged and coppicing *T. camphoratus* shrubs. This will enable the accurate assessment of the phytomass for research purposes, wildlife management and biofuel production estimates.

The positive attributes of *T. camphoratus* that include soil enrichment under their canopies, the provision of valuable browse during dry periods when deciduous woody species are leafless and a high density and species-rich seed bank in the soil under their canopies that ensure a high restoration potential after bush-thinning, may not be overlooked. Depending on the management objective, restoration of bush-thickened areas must take cognisance of the soil type, reproductive phenology (fruit maturation) and seasonal response of *T. camphoratus* to mechanical damage, as these may play an important role in the success of thinning operations and recruitment period influencing duration between follow-up treatments.

DECLARATION

I, Imke Jutta Stehn, declare that the dissertation hereby submitted by me for the partial fulfilment of the requirement for the degree of Master of Science in Agriculture (Grassland Science) at the University of the Free State is my own independent work, and that it has not been submitted by me to any other university/faculty.

Signed: Stehn...........................

Date: 20-11-2020...............................

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CHAPTER 1

Introduction

The increase in woody plant density involving indigenous species in their natural environment — also known as bush-thickening — is a global phenomenon especially common in the southern African savanna and is of great concern to landowners and ecologists. According to the Department of Environmental Affairs (DEA) report (2019), it has been extremely difficult to determine the exact extent of bush-thickening in South Africa, due to the absence of a defined starting point or 'natural' condition per bioregion from which bush encroachment can be measured. However, the latest estimates state that approximately 7.3 million ha (Turpie *et al.* 2019) of the 39.96 million hectares of savanna biome in South Africa are affected (Rutherford *et al.* 2006). Water is a key limiting factor in the savanna ecosystem (Smit 2004). Thus bush-thickening and the increased competition for water, results in a significant decrease of the grass sward, an increasing occurrence of forage shortages during normal rainfall years (pseudo-drought) and formation of inaccessible thickets, hence decreasing agricultural productivity (Haussmann *et al.* 2016), with severe economic consequences. An increase in woody plant density has been found across all rainfall gradients in all land uses, including commercial and communal farming systems, as well as conservation areas with and without mega herbivores (Stevens *et al.* 2016).

In the Northern Cape province of South Africa, the main species involved in bush-thickening are *Senegalia mellifera* (black thorn)*, Tarchonanthus camphoratus* (camphor bush) and *Rhigozum trichotomum* (three thorn) (O'Connor *et al.* 2014). A sharp increase in the population density of *T. camphoratus* has been reported around Magersfontein, situated in the Kimberley Thorn Bushveld, over the last three decades (Ward *et al.* 2014). While numerous studies have been conducted on the dynamics and ecology of *S. mellifera* in southern Africa (Meyer *et al.* 2005; Sekhwela & Yates 2007; Joubert *et al.* 2008; Ward & Esler 2011; Joubert *et al.* 2013; O'Donnell *et al.* 2015; Groengroeft *et al*. 2018) very limited research has been done to understand *T. camphoratus* as a species involved in bush-thickening.

Tarchonanthus camphoratus L. (family Asteraceae) — a semi-deciduous to evergreen shrub also known as vaalbos or camphor bush (Van Wyk *et al.* 2011) — is widely distributed in the Northern Cape, North West, Gauteng and Free State provinces of South Africa, as well as in Botswana, Namibia, North Africa and Arabia. It occurs in semi-arid habitats, such as the bushveld, woodland, savanna, grassland on mountainous slopes, rocky hills, riverbanks or flats, and grows on a variety of soils, ranging from sand, loam, gravel, calcrete, and quartzite to dolomitic soils (Herman 2002).

Until recently, landowners tended to pay little attention to this shrub; however, there is a growing awareness and concern regarding this species, mainly because it:

- increased significantly in numbers during the past decades,
- is semi-deciduous to evergreen, thus requires water all year round in a water-limited environment,
- reduces the productivity and grazing capacity of the herbaceous layer,
- is not always readily browsed by domestic livestock or game,
- reproduces sexually (seeds) and asexually (root suckers), and
- is fire tolerant.

In order to ensure a more efficient and ecologically responsible management strategy for *T. camphoratus* in rangeland, this study's main objectives were to gain a better understanding of the ecological functioning and significance of the species in terms of its:

1) effect on the soil (soil enrichment),
2) phenology,
3) vegetative growth characteristics and response to mechanical cutting,
4) reproductive ecology,
5) seed germination and growth associated with different subhabitats and soil types,
6) browse production and phytomass, and
7) response to fire.

These objectives were investigated by testing the following hypotheses:

a) Increased soil-nutrient concentrations are expected under the shrub canopies compared to the uncanopied subhabitat (soil enrichment by *T. camphoratus* will occur).
b) Soil originating from shallow rocky soil will have a higher soil-nutrient status compared to soil originating from deep sandy soil (the two soil types on which *T. camphoratus* grows in the study area).
c) Leaf carriage of *T. camphoratus* will vary little throughout the year, while leaf carriage of *Grewia flava, Ziziphus mucronata* and *Senegalia mellifera* will show large seasonal variation, having no or only dry leaves during some periods of the year (winter deciduous species).
d) Leaf carriage and phenophase of all the woody species will differ between plants growing on shallow rocky and deep sandy soil.

e) Shrubs on deep sandy soil will have higher shoot growth rates and coppice more vigorously than shrubs on shallow rocky soil.
f) *T. camphoratus* shrubs subjected to mechanical cutting during winter (dormant season) will coppice less vigorously compared to shrubs cut during summer (active growing season).
g) Seed production will increase relative to shrub size.
h) *T. camphoratus* seedlings established in soil closest to the stem will grow more vigorous than seedlings growing in soil from the uncanopied subhabitat due to a higher soil-nutrient status and the absence of any allelopathic effects.
i) Where *T. camphoratus* and *S. mellifera* are co-occurring species, fire will eventually result in the replacement of *S. mellifera* by *T. camphoratus*.

In addition,

a) the seed production as well as the existence and longevity of the *T. camphoratus* soil seed-bank were determined.
b) Regression equations relating spatial canopy volume and above-ground biomass (leaves and woody) were developed from harvested *T. camphoratus* plants (both coppice growth and undamaged plants), in order to expand the BECVOL-3 model (Smit 2014).

CHAPTER 2

Study area and trial layout

2.1 Study area

2.1.1 Geographical location

This study was conducted in the Rooipoort Nature Reserve approximately 60 km west of Kimberley and 17 km east of Schmidtsdrif in the Northern Cape province of South Africa. The 42 647 ha reserve extends from latitude 28° 30’ to 28° 40’ south and longitude 24° 02’ to 24° 25’ east and lies at an altitude of 1050 - 1187 m above sea level (Figure 2.1).

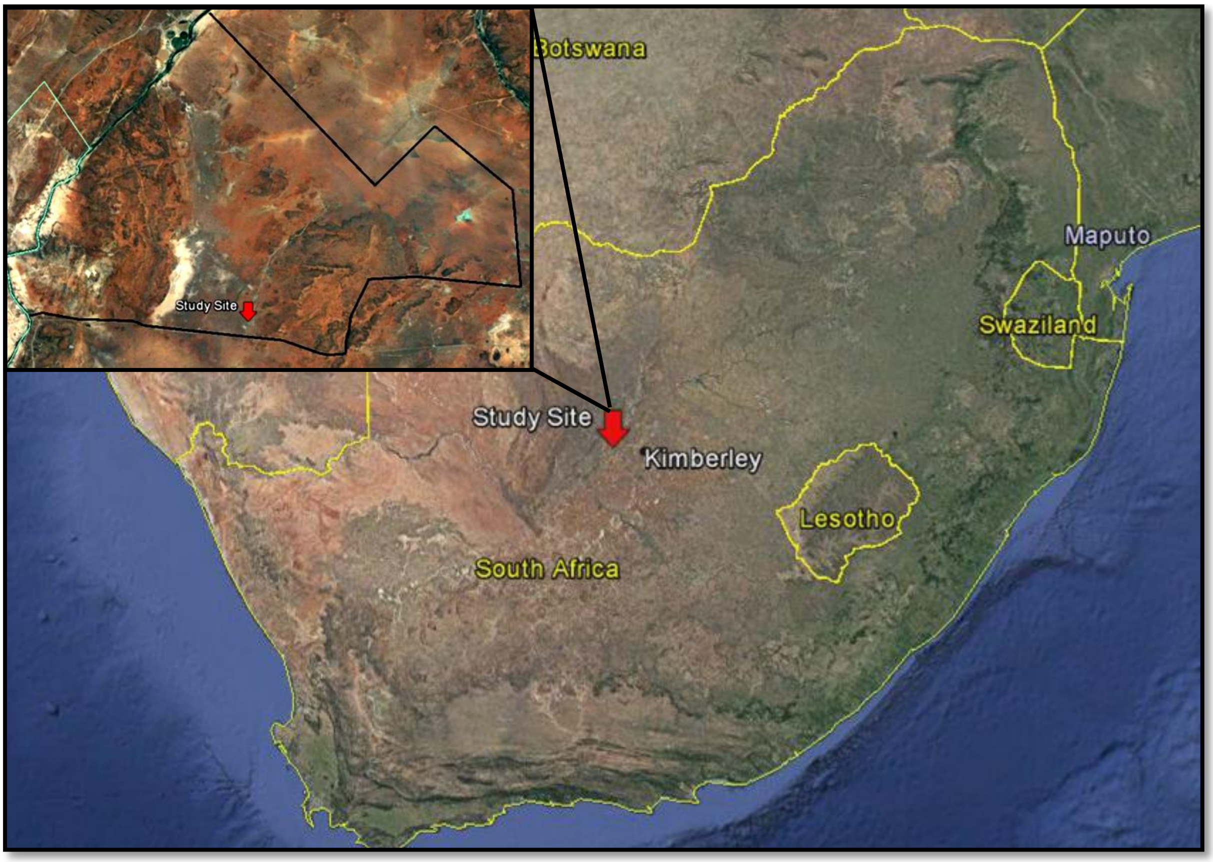

Figure 2.1: Location and boundaries of the Rooipoort Nature Reserve in the Northern Cape province of South Africa (Google earth image)

2.1.2 History of Rooipoort Nature Reserve

The Rooipoort Nature Reserve, which is one of South Africa’s oldest conservation areas, was established in 1893, when several properties were consolidated. Until 1930, Rooipoort was mainly utilised for private hunting, but was then leased for 17 years to domestic stock farmers (Berry & Crowe 1985). Horses, cattle and goats were mainly farmed on the property but poor rangeland management has resulted in heavy overgrazing with a significant impact on the vegetation including heavily bush-thickened areas and numerous bare areas (Bezuidenhout 2009). From 1947, Rooipoort was then used for private hunting again and since the early 1950s it has been developed into a private nature reserve (Berry & Crowe 1985). In 1985, the Rooipoort Nature Reserve was declared South Africa's fourth Natural Heritage Site, with its approximately 4600 Bushman rock engravings.

2.1.3 Climate

The rainfall at Rooipoort Nature Reserve is very unreliable and mostly occurs during summer (December to April). The mean annual (July to June) rainfall from 1995 to 2020, measured at nine locations within the reserve and since 2004/2005 at ten locations, is 359.5 mm, ranging between 195.7 mm (1997/98) and 580.6 mm (2016/17) (CV = 30.5%), and is presented in Figure 2.2. September to December is often associated with 'dry' thunderstorms, characterised by cloudy skies, intense lightning and very little or no rain resulting in a high risk for veld fires. Hail events are very seldom (one to two times per year) and mainly occur between January and March. The monthly rainfall obtained from a weather station at Rooipoort Nature Reserve homestead (28° 38' 13" S, 24° 16' 52" E) during the study period (October 2017 to June 2020) is presented in Figure 2.3.

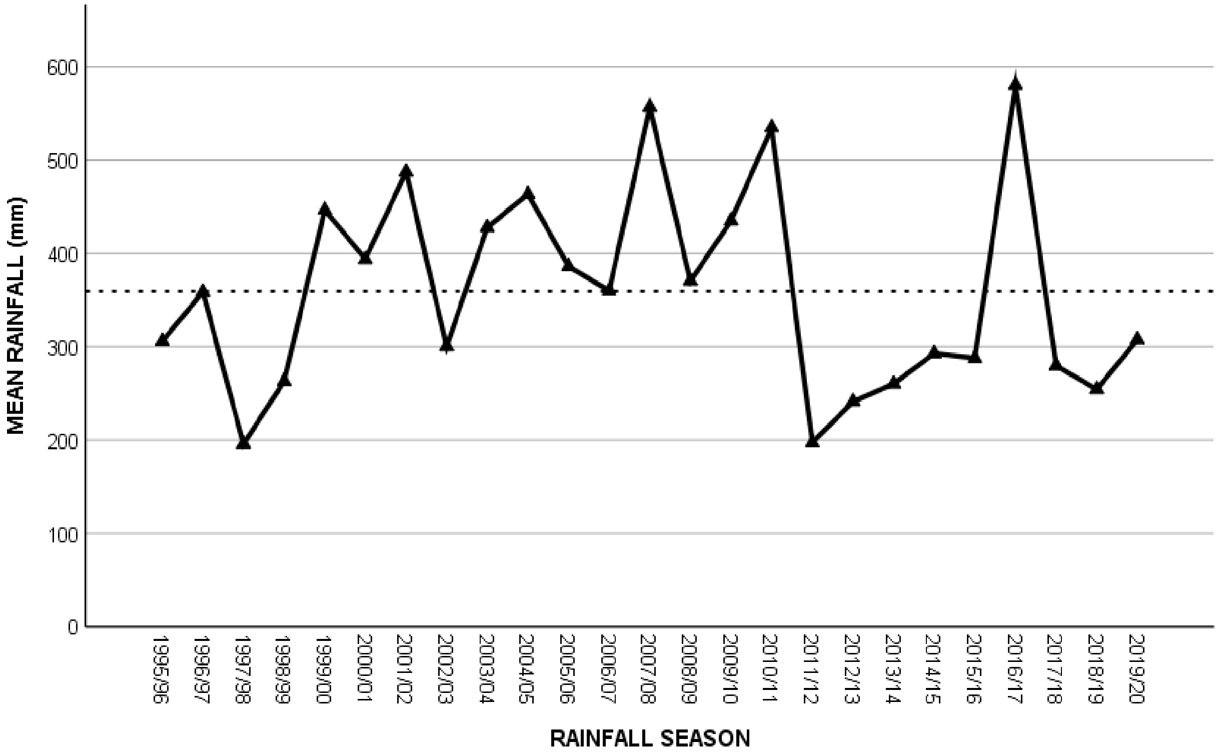

Figure 2.2: Long-term mean annual (July – June) rainfall for Rooipoort Nature Reserve. (Dashed line represents long-term average)

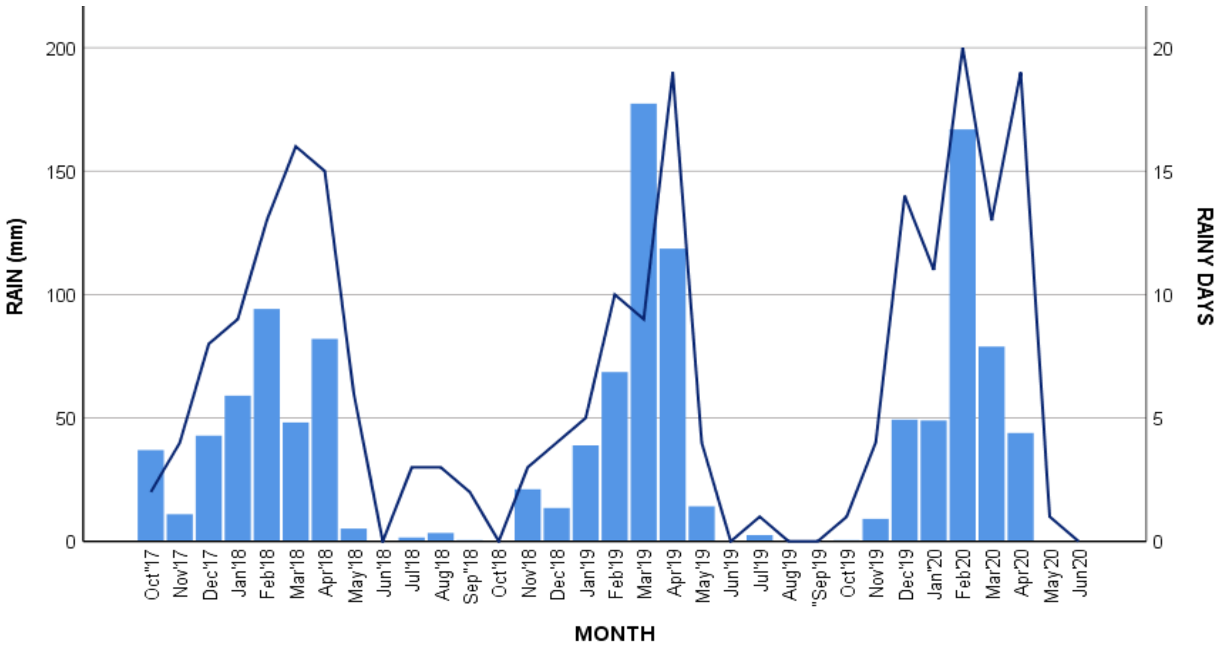

Figure 2.3: Monthly rainfall (bars) and rain days (line) during the study period (October 2017 to June 2020)

Very hot day-temperatures, above 40°C during summer months, especially December and January, and cold winter temperature below 0°C from June to August are characteristic of Rooipoort Nature Reserve. Frost during winter is not uncommon. According to Bezuidenhout (2009), frost can be experienced on as many as 107 days during winter, with the earliest frost ever recorded on Rooipoort Nature Reserve on 27 April, while latest frost occurred on 23 September. Monthly maximum, minimum and average temperatures as recorded at the weather station on Rooipoort during the study period are presented in Figure 2.4.

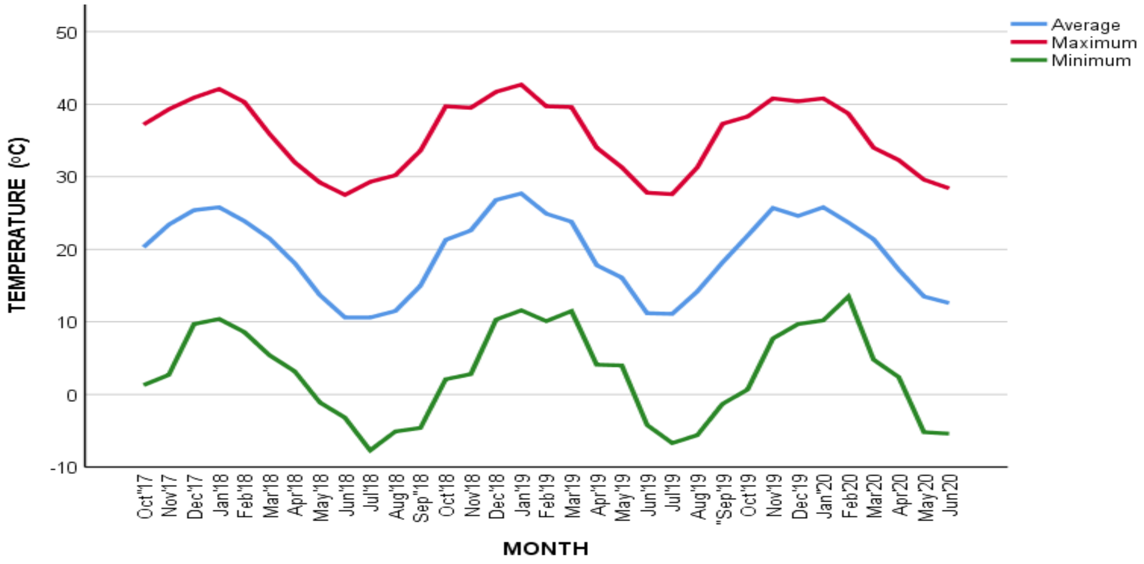

Figure 2.4: Monthly maximum, minimum and average temperatures during the study period (October 2017 to June 2020).

2.1.4 Geology and soil

The Rooipoort Nature Reserve lies at the eastern base of the Ghaap plateau. Andesitic lava outcrops and quartzite flat ridges (both Ventersdorp Supergroup), dolomite outcrops (Transvaal Sequence) and aeolian sands with surface limestone are some geological formations underlying the Reserve (Bezuidenhout 2009). The main drainage system of the area is the Vaal River, which also forms the almost 30 km long western border of the Rooipoort Nature Reserve. Rich diamond deposits were found in the 1920s in the ancient watercourse of the Vaal River in the deproclaimed Vaalbos National Park on the northern border with the Rooipoort Nature Reserve (Bezuidenhout 1994). Today, active diamond mining occurs in the northern sand dunes as well as along the Vaal River in the southwest of the reserve.

According to Bezuidenhout (2009), a wide range of soil types occur in the Rooipoort Nature Reserve. Deep Hutton and Clovelly soil forms, shallow and stony Mispah, Prieska Kimberley soil forms, moderately deep and clayey Valsrivier, Swartland, Arcadia, Rensburg and Willowbrook as well as silt clayey Oakleaf soil forms can be found.

2.1.4 Vegetation

The Rooipoort Nature Reserve is located within the savanna biome. This is South Africa's most widespread biome and covers approximately 399 600 km^2 (Mucina & Rutherford 2006). According to the original classification by Acocks (1988), the veld type is described as veld type 17 and includes the Kalahari Thornveld invaded by Karoo with a small part of False Orange River Broken Veld (veld type 40) along the Vaal River. More recently, Mucina and Rutherford (2006) described the area as the Eastern Kalahari Bushveld Bioregion, and more specifically the Kimberley Thornveld (SVK 4) and Schmidtsdrif Thornveld (SVK 6) that dominate the Rooipoort Nature Reserve, while Highveld Salt Pans (AZi 10) — forming part of the Inland Saline Vegetation Bioregion — also occur in the reserve. Bezuidenhout (2009) identified and mapped ten community types, with 15 communities on Rooipoort Nature Reserve (Figure 2.5).

The tree stratum of Rooipoort Nature Reserve is dominated by *Vachellia tortlis* and *Ziziphus mucronata* with isolated *Vachellia erioloba,* especially in the north of the reserve, while the most prominent shrubs include *T. camphoratus, Grewia flava* and *S. mellifera.* The most dominant grass species include *Schmidtia pappophoroides*, *Eragrostis lehmanniana*, *Stipagrostis uniplumis*, *Aristida congest*a and occasionally *Cymbopogon pospischilii*. Along the river bank *Vachellia karoo, Diospyros lycioides* and *Cynodon dactylon* are most dominant.

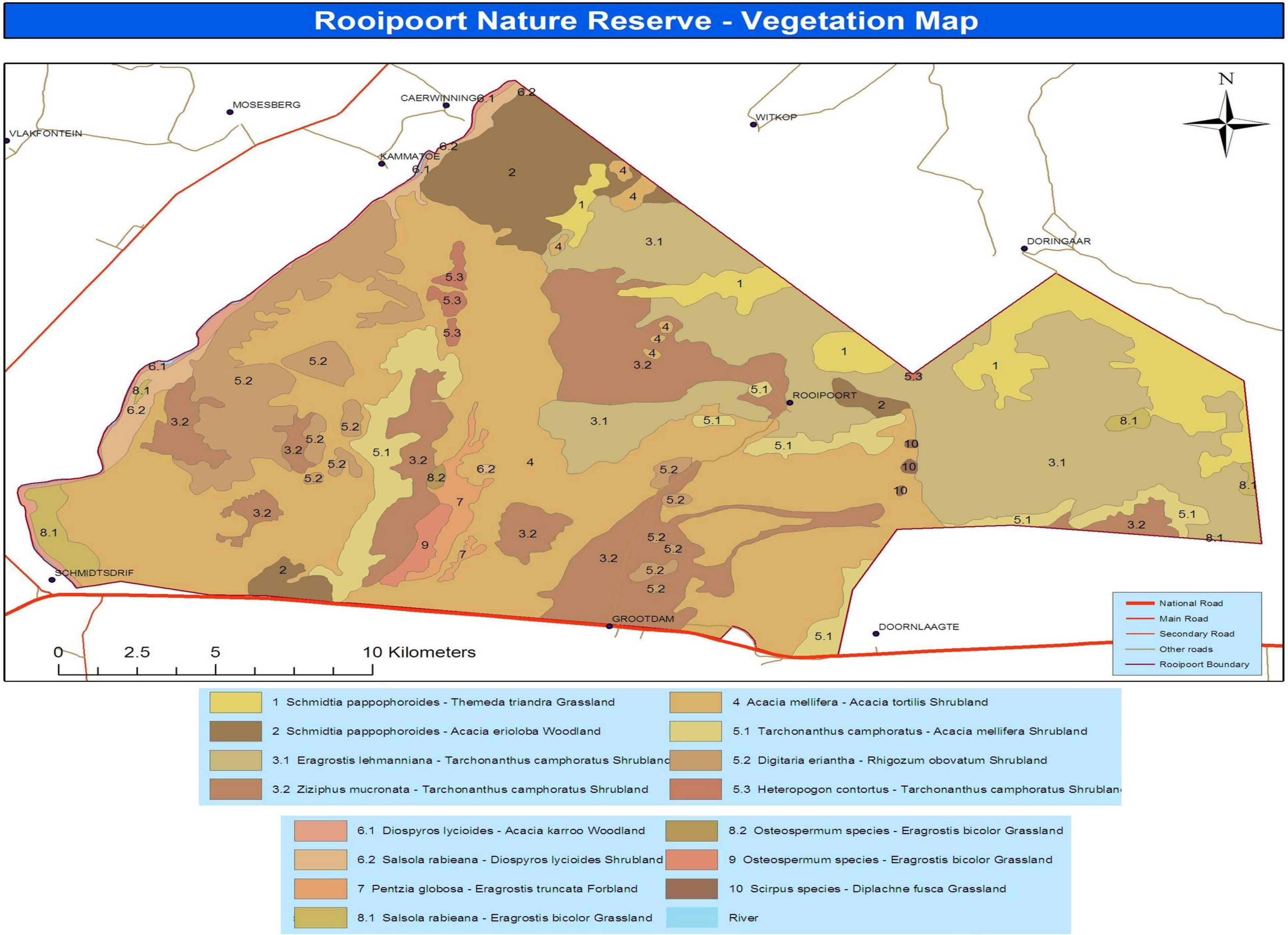

Figure 2.5: Vegetation map of Rooipoort Nature Reserve (Bezuidenhout 2009)

2.2 Trial layout

2.2.1 Experimental site selection and location

The objective for the selection of the experimental sites was to find two sites:

- with a relatively dense and homogenous stand of healthy *T. camphoratus* shrubs,
- on differing soil types – one a deep sandy soil and the other a shallow rocky soil,
- in close proximity to each other to ensure similar weather conditions, and
- which are relatively easily accessible.

The first experimental site is located at 28° 42’ 22” S, 24° 13’ 33” E and lies about 1074 m above sea level (Figure 2.7), while the second experimental site is located about two kilometres northwest of the first site, at 28° 41’ 22” S 24° 12’ 45” E, and lies a little lower, at 1063 m above sea level (Figure 2.6 and Figure 2.8).

During November 2018, a third experimental site was added as an opportunistic study, when an accidental veld fire had burnt a stand of *T. camphoratus* co-occurring with *S. mellifera.* This site is located at 28° 38’ 12” S, 24° 18’ 44” E and lies at an altitude of 1156 m.

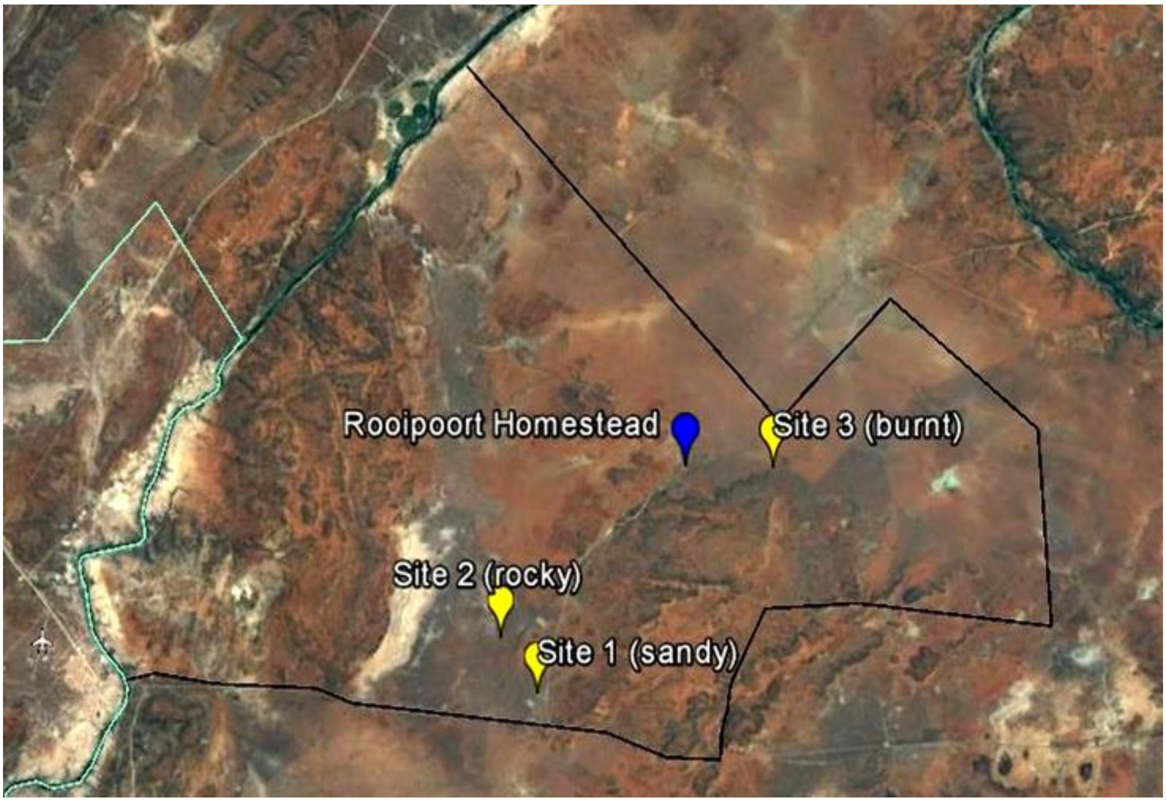

Figure 2.6: Location of site 1 (sandy soil), site 2 (rocky soil), site 3 (burnt site) and the homestead on the Rooipoort Nature Reserve (Google earth image)

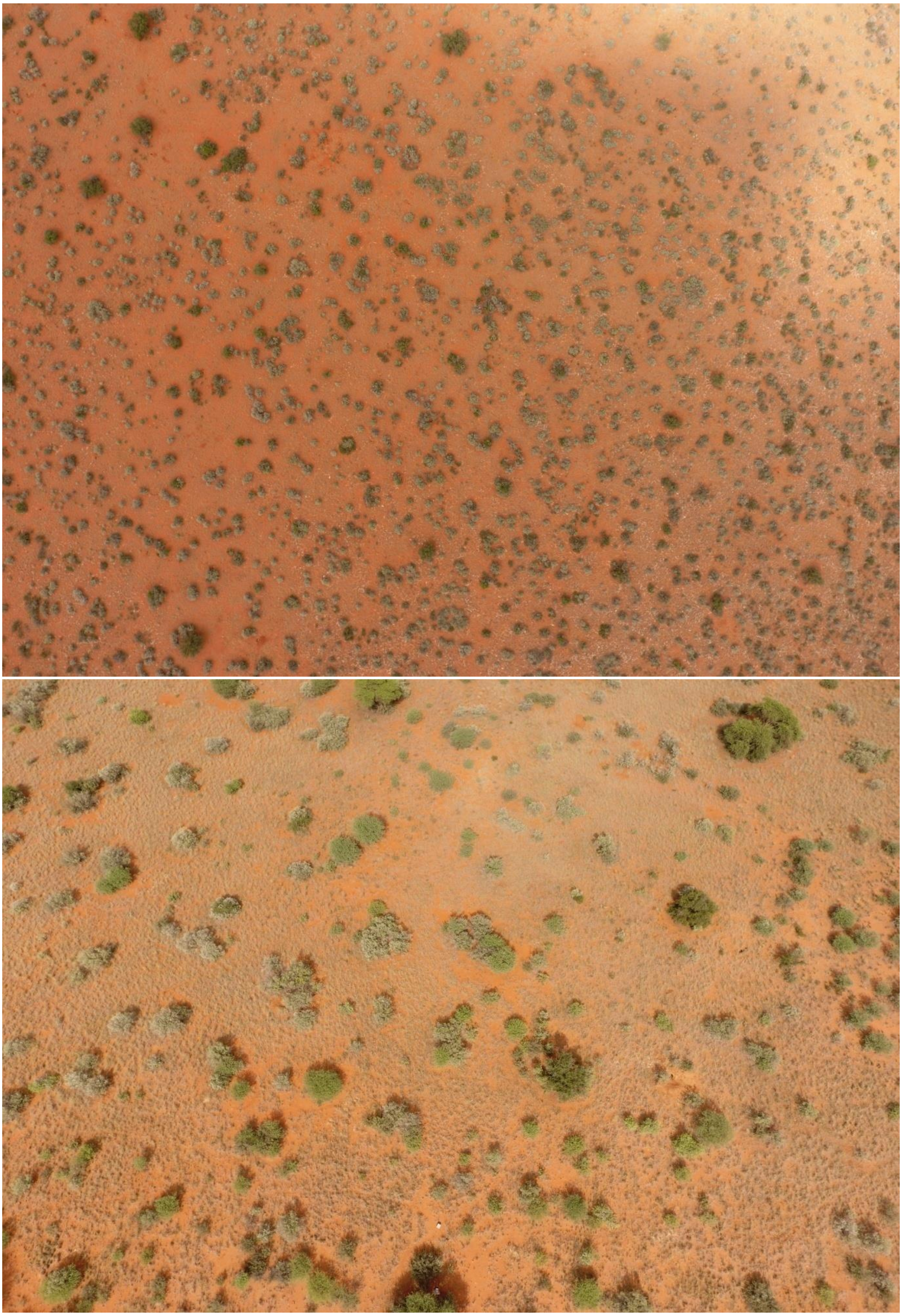

Figure 2.7: Aerial photographs of the first (sandy) experimental site 120 m (top) and 80 m (bottom) above the ground. Lens focal length – 20 mm (35 mm film format) (Photo: GN Smit)

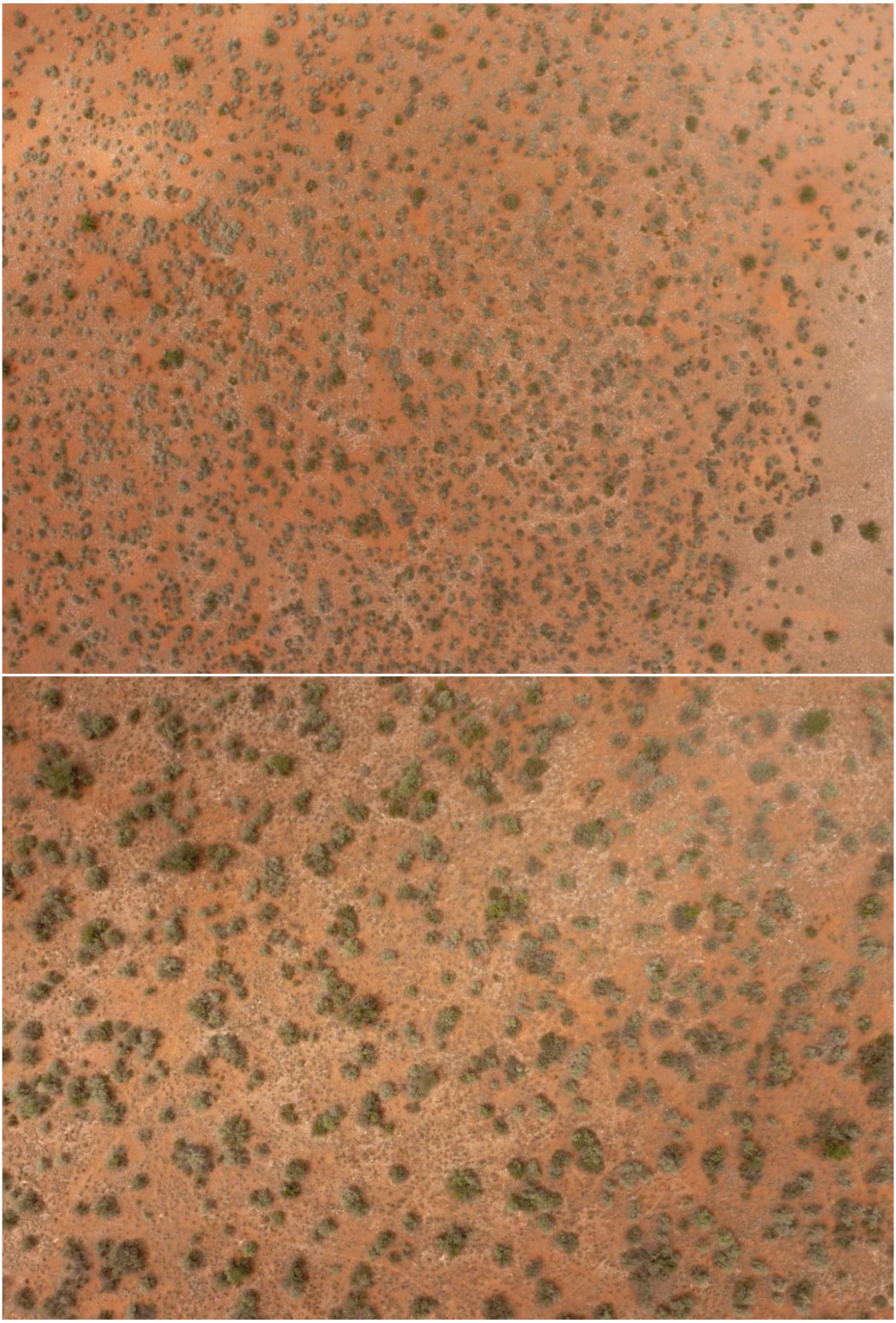

Figure 2.8: Aerial photographs of the second (rocky) experimental site 120 m (top) and 80 m (bottom) above the ground. Lens focal length – 20 mm (35 mm film format) (Photo: GN Smit)

2.2.2 *Soil at the experimental sites*

Three soil profiles were dug along the length of each of the two main experimental sites (Figure 2.9). On the first experimental site, all three soil profiles indicated very deep (> 0.8 m) well-drained red-brown sandy soil with < 2% rocks (hereafter referred to as the "sandy site"). Hutton soil form is most dominant throughout the site, while Kimberley soil form associated with a soft carbonate subsoil horizon occurs on the southern end of the site (Figure 2.10) (Le Roux *et al*. 2013; Le Roux 2015). The soil in the second experimental site is mostly very shallow (< 0.2 m) and has > 40% calcareous surface rocks (profiles 6) (Figure 2.11) mainly of the Coega soil form (Le Roux *et al*. 2013; Le Roux 2015; Van Rensburg 2018) (hereafter referred to as the "rocky site"). A few 'sand pockets' occur throughout the site, which are sandier and deeper, but have a hardpan carbonate soil subsoil horizon at a depth of 0.3 – 0.6 m and are classified as Prieska soil form (Le Roux *et al.* 2013). For a full description of soil profile 1 to 6 refer to Table 2.1 and Table 2.2.

In the third experimental site, Mispah soil form is most dominant, consisting of well-drained red-brown topsoil and a hard rock subsoil horizon (Le Roux *et al.* 2013; Le Roux 2015). Soil depth varies from shallow (< 0.3 m) to moderately deep (< 0.6 m) and 40 – 80% surface rocks can be expected.

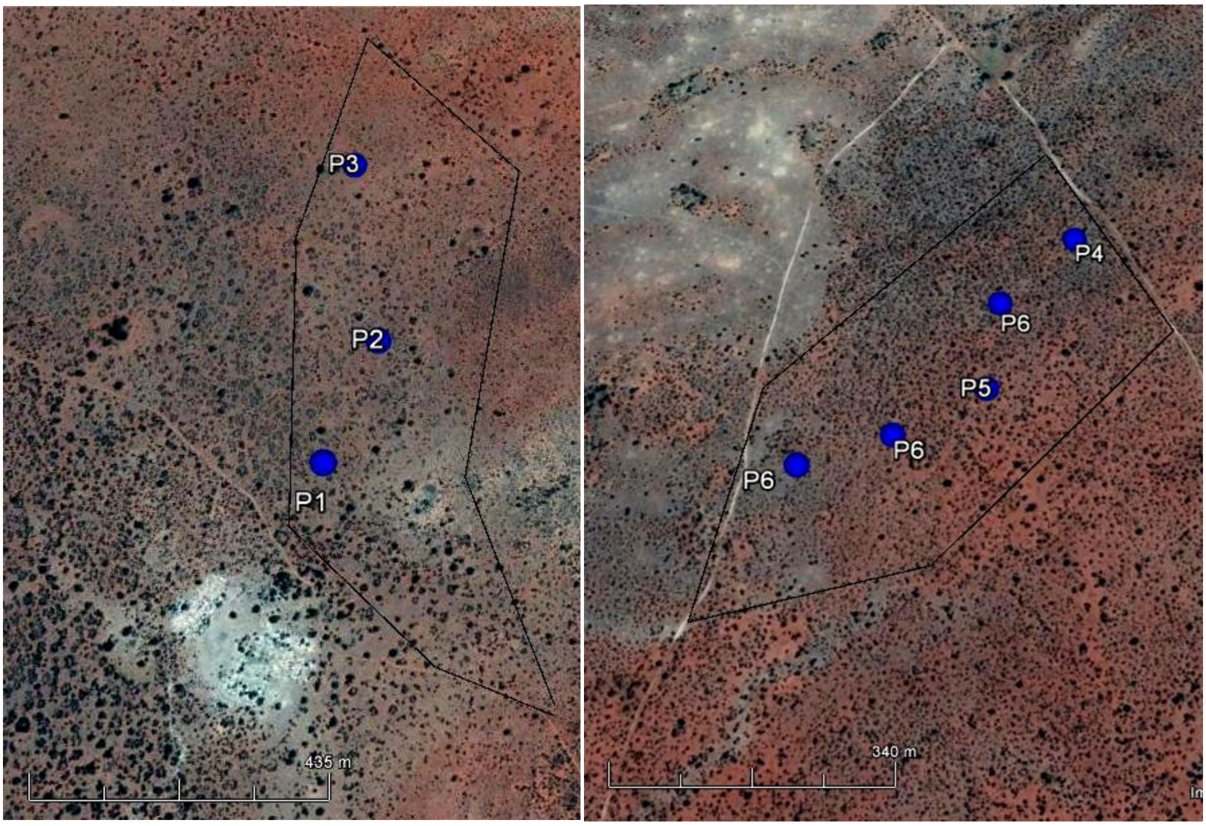

Figure 2.9: Location of soil profiles on the sandy site (P1, P2, P3) and the rocky site (P4, P5, P6*). *Several attempts to dig profile 6 with all the same result – very shallow (< 0.2 m) soil depth.

Figure 2.10: Soil profiles 1 (left), 2 (middle), and 3 (right) on the sandy site (Photos: IJ Stehn)

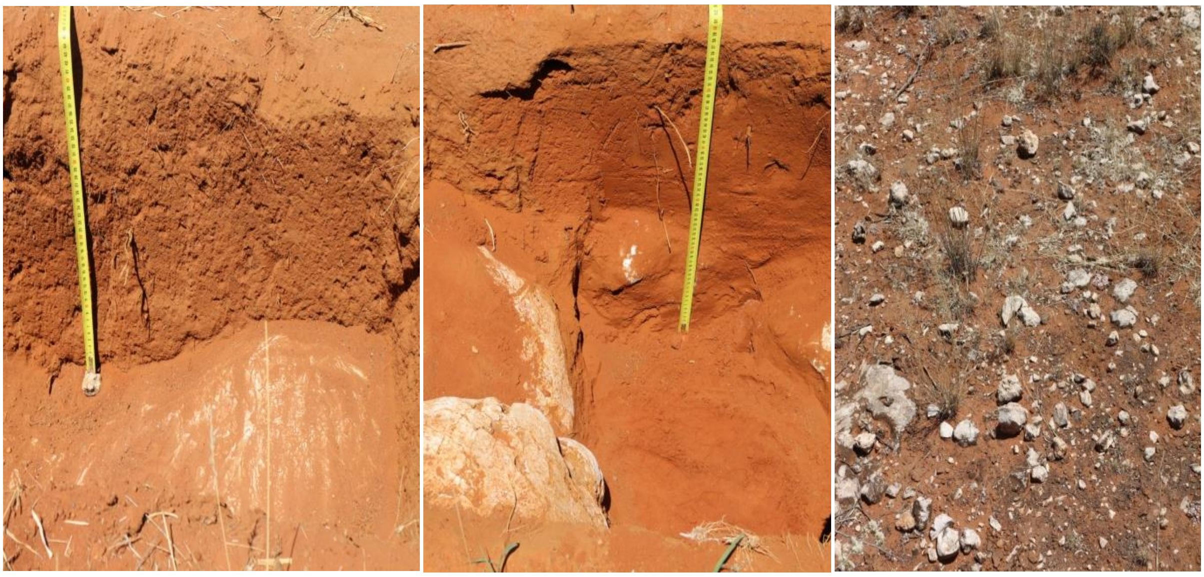

Figure 2.11: Soil profiles 4 (left), 5 (middle) and 6 (right) on the rocky site (Photos: IJ Stehn)

Table 2.1: Full description of the three soil profiles on the sandy experimental site (Le Roux *et al.* 2013; Le Roux 2015)

	Profile 1	Profile 2	Profile 3
Master Horizons & Thickness	A: 0 – 350 mm B_1: 350 – 680 mm B_2: >680	A: 0 – 300 mm B: 300 – > 830 mm	A: 0 – 400 mm B : 400 – > 1120 mm
Topsoil Horizon	Orthic A	Orthic A	Orthic A
Subsoil Horizons	Red Apedal B Soft Carbonate	Red Apedal B	Red Apedal B
Signs of Wetness	B_2	Absent	Absent
Structure	Apedal	Apedal	Apedal
Texture (Field test)	A & B_1: 0 – 6 % clay, medium sand	A & B: 0 – 6 % clay, medium sand	A & B: 0 – 6 % clay, medium sand
Mottles	A & B_1: Few (< 2%), grey Fine (Ø < 5 mm) B_2: Common (2 -20%), Yellow & grey Medium (Ø5–15 mm)	A & B: none	A & B: none
Rocks	A: None B_1: Few (< 20%) Ø 2 -25 mm B_2: Few (< 20%) Ø 2 -25 mm	A: Few (<20%) Ø 2–25 mm B: none	A: Very few (<5%) Ø 2–25 mm B: none
Transition of horizons	A – B_1: Diffuse B_1 – $B_{2:}$: Clear	Diffuse	Diffuse
Soil Form	**Kimberley**	**Hutton**	**Hutton**

Table 2.2: Full description of the three soil profiles on the rocky experimental site (Le Roux *et al.* 2013; Le Roux 2015)

	Profile 4	Profile 5	Profile 6
Master Horizons & Thickness	A: 0 – 320 mm B: > 320 mm	A: 0 – 390 mm B_1: 390 – 600 mm B_2: > 600 mm	A: 0 – 60 mm B: > 60 mm
Topsoil Horizon	Orthic A	Orthic A	Orthic A
Subsoil Horizons	Hardpan Carbonate	Red Apedal B Hardpan Carbonate	Hardpan Carbonate
Signs of Wetness	Absent	Absent	Absent
Structure	A: Apedal B_2: Massive	A & B_1: Apedal B_2: Massive	A: Apedal B: Massive
Texture (Field test)	A: 7 - 10 % clay, medium sand	A: 7 – 10 % clay, medium sand B_1: 0 – 6 % clay, medium sand	A: 7–10 % clay, medium sand
Mottles	None	A: Few (< 2%) Grey Fine (Ø < 5 mm) B_1: Few (< 2%) Grey Fine (Ø < 5 mm)	None
Rocks	A: Common (20 – 50%) Ø 2 – 100 mm	A: Common (20 – 50%) Ø 2–100 mm B_1: Common (20 – 50%) Ø 2–100 mm	A: Abundant (20 – 50%) Ø 2 – 100 mm
Transition of Horizons	Clear	A – B_1: Diffuse B_1 –- B_2: Clear	Clear
Soil Form	**Coega**	**Prieska**	**Coega**

2.2.3 Vegetation at the experimental sites

According to the vegetation map of Rooipoort Nature Reserve, as compiled by Bezuidenhout (2009), the sandy and the rocky sites both fall within the *Ziziphus mucronata* – *Tarchonanthus camphoratus* Shrubland (3.2) (see Figure 2.5). However, for the purpose of this study, further substantial vegetation differences between the two main experimental sites (sandy vs rocky) were established. This was done by determining:

- the species composition and dry matter production of the grass layer in each site,
- the woody plant density (plants ha^{-1}), and
- the woody plant layer competitiveness in terms of ETTE ha^{-1} (Evapotranspiration Tree Equivalents) (1 ETTE = the leaf volume equivalent of a 1.5 m single-stemmed tree = 500 cm^{3} (Smit 1989a, 2014)).

2.2.3.1 Procedure

The survey was done at the end of the growing season in May/June 2018. All measurements were repeated for six transects (100 m) on the sandy and rocky experimental sites. For the determination of the species composition of the grass layer in each experimental site, a point technique based on frequency of occurrence according to the nearest plant method (Everson & Clarke 1987; Smit & Rethman 1999) was used. 100 points at 1 m intervals along a 100 m measuring tape (line transect) were recorded. The measuring tape was placed in random straight lines to ensure proportional sampling of canopied and uncanopied areas. At each survey point two observations were recorded: (1) closest grass species within 15 cm radius around the point, irrespective of its perenniality, and (2) the nearest perennial grass species within 15 cm radius around the point. If no grass species could be recorded for either observation on bare soil, it was recorded as “bare”. In cases where a large rock was hit, those points were recorded as “rock”.

A harvest technique (Grunow *et al.* 1980) was applied to determine the above-ground herbaceous dry matter (DM) yield of the herbaceous plants. For this, ten quadrates (0.25 m^{2}) were randomly thrown along each 100 m transect. The rooted herbaceous plants within each quadrate were clipped to stubble height and dried at 70°C to constant mass and weighed. In addition, all woody plants rooted within the 100 m x 2.5 m belt transect were measured following the BECVOL 3 – model procedures (Smit 2014). This procedure is described in more detail in chapter 9 of this study.

2.2.3.2 Results

The grass species composition for the sandy and rocky sites is presented in Table 2.3. On the sandy site, *S. pappophoroides* was the most dominant grass species, while on the rocky site *E. lehmanniana* and *S. pappophoroides* were the most abundant grass species. While *Aristida stipitata* was absent on the rocky site, *Aristida adscensionis, Enneapogon desvauxii* and *Fingerhuthia africana* were absent on the sandy site. Furthermore, the total calculated herbaceous DM yield for the sandy site was 590.7 kg ha^{-1} while the dry matter yield of the rocky site was lower at 469.0 kg ha^{-1}.

On the sandy site, the tree stratum was dominated by *Z. mucronata* (buffalo thorn) and *V. tortilis* (umbrella thorn), with isolated *V. erioloba* (camelthorn) trees. *S. mellifera* (black thorn) became more dominant on the southern end of the site. The shrub stratum was dominated by *T. camphoratus* (camphor bush) and *G. flava* (velvet raisin). The average woody plant density at this site was calculated as 2320 plants ha^{-1} and 5696 ETTE ha^{-1} (Figure 2.12).

Figure 2.12: Vegetation at the sandy site (Photos: IJ Stehn)

The rocky site was dominated by *Z. mucronata* and shrubs, *T. camphoratus* and *G. flava*. *V. erioloba* and *S. mellifera* were absent on this site. Higher average woody plant density, at 4000 plants ha^{-1} and 8688 ETTE ha^{-1} was recorded in the rocky site compared to the sandy site (Figure 2.13).

Figure 2.13: Vegetation at the rocky site (Photos: IJ Stehn)

The third (burnt) experimental site is located within the *Tarchonanthus camphoratus* – *Acacia mellifera* Shrubland (5.1) (Bezuidenhout 2009). The woody stratum was dominated by isolated *V. tortilis,* while the shrub stratum was dominated by *T. camphoratus* and *S. mellifera. S. pappophoroides* and *H. contortus* were the most abundant grass species.

Table 2.3: Percentage grass species composition based on frequency of occurrence in the sandy and rocky experimental sites

Experimental site	Species	Percentage (%) Nearest plant*	 Nearest perennial plant**
Sandy site	*Aristida congesta*	1.8	-
	Aristida diffusa	0.2	0.2
	Aristida meridionalis	0.7	0.7
	Aristida stipitata	3.2	-
	Cenchrus ciliaris	0.2	0.2
	Cymbopogon pospischilii	0.5	0.8
	Enneapogon cenchroides	0.3	-
	Eragrostis lehmanniana	23.0	24.2
	Eragrostis trichophora	0.5	0.5
	Heteropogon contortus	0.3	0.3
	Schmidtia pappophoroides	58.0	60.0
	Stipagrostis uniplumis	1.7	1.7
	Bare patches	9.7	11.5
Rocky site	*Aristida adscensionis*	0.2	-
	Aristida congesta	2.2	-
	Aristida diffusa	6.7	6.8
	Aristida meridionalis	0.5	0.5
	Cenchrus ciliaris	-	0.2
	Cymbopogon pospischilii	4.2	4.2
	Enneapogon cenchroides	3.7	-
	Enneapogon desvauxii	1.8	-
	Eragrostis lehmanniana	37.0	38.2
	Fingerhuthia africana	0.3	0.3
	Heteropogon contortus	1.8	1.8
	Schmidtia pappophoroides	25.0	25.2
	Stipagrostis uniplumis	2.5	2.8
	Bare patches	14.0	19.3
	Rock	0.7	0.7

* first recording **second recording

CHAPTER 3

Literature Review

3.1 Description of the genus *Tarchonanthus*

The genus *Tarchonanthus* is very closely related to the genus *Brachylaena.* *Tarchonanthus* consists of six species occurring in Saudi Arabia, Yemen, East Africa and southern Africa (Beentje 1999a), namely, *Tarchonanthus trilobus, Tarchonanthus minor, Tarchonanthus obovatus, Tarchonanthus camphoratus, Tarchonanthus littoralis* and *Tarchonanthus parvicapitulatus.* Before 2002, *Tarchonanthus* consisted of only two species, namely, *T. trilobus* and *T. camphoratus* complex*,* including the other five species which were treated as one complex species. Due to differences in distribution, palatability, synflorescences, flowering times and leaf form, Herman (2002) divided the complex *Tarchonanthus camphoratus* and identified five different species:

3.1.1 Tarchonanthus minor

T. minor grows on hills, rocky ridges and mountain slopes in Lesotho, Free State, Eastern, Western and Northern Cape. Its leaves are relatively small and narrowly elliptic, with a smooth leaf margin. *T. minor* flowers from August to December (spring to early summer) and has dense synflorescences arranged in a spike form.

3.1.2 Tarchonanthus littoralis

T. littoralis occurs along the coast on littoral dunes, hillsides and riverbanks of southern KwaZulu-Natal, the Eastern Cape and the Western Cape. Its dark green leaves are large oblanceolate or elliptic to narrowly elliptic with a finely toothed upper margin and have a long petiole. *T. littoralis* flowers mainly in late summer (December to July with a peak in February and March).

3.1.3 Tarchonanthus obovatus

T. obovatus is a single-stemmed tree (< 2 m) which is endemic to the Northern Cape where it mainly grows on rocky outcrops, hillsides or flats with a lime or ironstone base in sandy soil. It has obovate to elliptic leaves with an entire leaf margin. The seeds are covered by pure white hairs. Flowering time for *T. obovatus* peaks during autumn and early winter (March to May). Furthermore, this species is readily browsed by game and domestic livestock.

3.1.4 Tarchonanthus parvicapitulatus

T. parvicapitulatus grows on riverbanks, hills, mountain slopes in the bushveld, forest and valleys of the Northern Cape, North-West Province, Gauteng, Mpumalanga and KwaZulu-Natal, as well as Swaziland and Zimbabwe. Its oblanceolate to obtuse leaves are finely toothed towards the leaf tip. *T. parvicapitulatus* flowers in autumn and winter (March to October and peaks April to June) and has synflorescences, which tend to be more open than in the other species with much smaller flower clusters.

3.1.5 Tarchonanthus camphoratus

T. camphoratus grows in semi-arid habitats, such as the woodland, savanna and grassland, on mountainous slopes, rocky hills, riverbanks or flats and grows on a variety of soils, ranging from sand, loam, gravel, calcrete, and quartzite to dolomitic soils.

This multi-stemmed shrub can grow approximately 1 – 9 m high. It has a relatively rounded crown with branches growing from ground level (Figure 3.1). Its simple alternate leaves are dicolourous. The upper surface of the young leaf is grey-green and hairy but becomes glabrous with increasing age, while the lower greyish surface is felted with prominently raised veins. The leaves are narrowly elliptic to slightly oblanceolate with an entire leaf margin.

T. camphoratus is dioecious, with male and female flowering parts that occur on separate plants. Synflorescences occur on terminal panicles and are creamy white. Flowering time is in autumn and winter from March to August. The fruit are clustered small nutlets which are enveloped by cream – to – yellowish hair.

In addition to the above description of Herman (2002), Schleicher *et al. (*2011) reported that under semi-arid conditions *T. camphoratus* rarely exceeds 2 – 3 m. Van Wyk *et al.* (2011) noted that the leaves have a strong camphor smell when bruised.

3.2 The value of *Tarchonanthus camphoratus*

There are many medicinal as well as economic uses for *T. camphoratus.* The Herero and Damara in Namibia, as well as the Bushmen and Zulus in South Africa used *T. camphoratus* leaf infusions and roots to relief respiratory complaints, such as asthma, whooping cough and bronchitis (Hutchings *et al.* 1996; Von Koenen 1996). The smoke from green branches is inhaled to cure headaches while leaf infusions were also used to ease toothache, inflammation and plaque (Hutchings *et al.* 1996; Beentje 1999). Furthermore, *T. camphoratus* leaves were also rubbed on the body as an insect-repellent. While the Herero chewed fresh leaves, the Hottentot and Bushmen in South Africa smoked the leaves for a narcotic effect (Beentje 1999a).

Figure 3.1: Typical *Tarchonanthus camphoratus* shrub (Photo: IJ Stehn)

Economic uses of *T. camphoratus* include the use of the wood as firewood and for charcoal production, especially in Kenya (Young & Francombe 1991; Kiruki & Njung'e 2007). Moreover, shrubs are planted to manage erosion problem areas, due to their rather strong root system (Venter & Venter 2002). Durable fence poles, musical instruments and boats can be made from this species (Palgrave 2002).

Reports on the value of *T. camphoratus* as browse for livestock and game vary greatly. A possible reason for this variability is the fact that *T. camphoratus,* has previously (before 2002) been treated as a single complex species.

Palmer and Pitman (1972) as well as Venter and Venter (2002) reported that leaves are readily browsed from the shrub, as well as from the ground, by livestock and wildlife such as giraffe, eland, kudu, gemsbok, sable, black wildebeest, nyala, impala, springbok and grey duiker. Also, studies by Van der Merwe and Nel (1991) proposed that up to 30% crushed *T. camphoratus* coppice leaves and shoots can be used in the finishing diet of lambs without negatively influencing the growth rates or carcass weights of the lambs. They found the crude protein content of stems and leaves with browsable shoots to be 5.65% and 16.32% on a dry-mass basis, respectively. It is further suggested that *T. camphoratus* can be used as a potential fodder resource, especially during periodic droughts (Palmer & Pitman 1972; Van der Merwe & Nel 1991; Venter & Venter 2002). Ward *et al.* (2018) have observed goats browsing the leaves of *T. camphoratus* and suggested that as sodium shortages are often experienced by herbivores in arid environments (Scholes & Walker 1993), the goat's preference to *T. camphoratus* could be the elevated sodium ion concentrations in the leaves. They therefore propose that it might be advantageous to sustain some *T. camphoratus* in order to combat sodium shortages in this arid environment.

In contrast, Young and Francombe (1991), Palgrave (2002); Herman (2002), as well as Kiruki and Njung'e (2006) claimed that *T. camphoratus* is only browsed as a last resort during times of severe drought, when forage shortages occur. During a study in Kenya, Pratt and Knight (1971) found variations in browse preference to *T. camphoratus* between different goat herds, possibly due to differences in adaption period and breed.

Furthermore, *T. camphoratus* is relatively resistant to defoliation by either fire or cutting, as it is known to regenerate vigorously (Pratt 1966; Young & Francombe 1991; Coetzee *et al.* 2008). Defoliation by cutting or burning increased *T. camphoratus* populations (plants per area) primarily by sub-dividing shrub crowns and by the development of root suckers (Pratt 1966). This may either be a desirable or undesirable characteristic. In the case of sustained wood production for firewood or charcoal production, fast re-sprouting after cutting or burning would be a desirable characteristic. However, in cases where bush-thickening by *T. camphoratus* has become a concern, this characteristic is undesirable and could make bush control programmes challenging.

3.3 Bush-thickening

Strictly speaking, bush-thickening is the densification by an indigenous woody plant species in its natural environment (Joubert *et al.* 2008; Harmse *et al.* 2016), while bush encroachment is the increase of woody plant abundance by an indigenous species which does not naturally occur in this environment. In most cases, however, these terms are used interchangeably and both refer to the global phenomenon, mostly associated with the savanna and grassland biomes (O'Connor *et al.* 2014), in which the vegetation structure shifts from a grass-dominated state towards a woody-plant-dominated state (Ward 2005; Joubert *et al.* 2008). Considering worldwide concerns over climate change and deforestation, bush-thickening may be regarded favourably in terms of carbon sequestration and increased forestation. However, this state of transition has serious consequences for the ecosystem's health, functioning and service provision. Even though countless efforts have been made, the causes and mechanism of bush-thickening remain debated upon. Similarly, prevention strategies or economically sensible treatment methods are still not entirely successful.

3.3.1 Possible causes of bush-thickening

Bush-thickening can be attributed to a range of global and local factors, as well as their interactions and compounded effects. Despite being a worldwide phenomenon, each bush-thickened area has a unique set of driving factors varying with climate, soil, involved species, historic land use and ecological history (Bond & Midgley 2012; O'Connor *et al.* 2014; Archer *et al.* 2017), thus making generalisations complicated.

a) Increased carbon dioxide

Increased carbon dioxide concentrations in the atmosphere and climate change are two global drivers, which are suspected as contributing factors in the proliferation of woody plants. Atmospheric carbon dioxide levels have risen exponentially during the last century and are currently at approximately 412 ppm, which is 48% higher than pre-industrial levels (Buis 2019). Elevated carbon dioxide influences plant growth. C_3 woody plants, *Vachellia karroo* and *Vachellia nilotica,* which were subjected to elevated carbon dioxide concentrations in a greenhouse experiment, have resulted in significantly higher above-ground biomass, stem length, root starch accumulation and root dry mass, as well as better herbivory defences such as tannins and spines (Kgope *et al.* 2010; Quirk *et al.* 2019). However, responses to elevated carbon dioxide concentrations remain species- (Morgan *et al.* 2004; Kgope *et al.* 2010; Bond & Midgley 2012; Buitenwerf *et al.* 2012; Quirk *et al.* 2019) and ecosystem-specific (Morgan *et al.* 2004; Buitenwerf *et al.* 2012).

According to Bond and Midgley (2012), arid as well as humid savannas are effected by a carbon-dioxide-driven increase in woody plants, but by differing mechanisms and to differing degrees. Increased carbon dioxide concentrations indirectly induce enhanced plant water-use efficiency, due to decreased stomatal conductance and therefore reduced transpiration (Polley *et al.* 1999; Morgan *et al.* 2004; Quirk *et al.* 2019), thereby prolonging available soil moisture (Morgan *et al.* 2004), which is especially important for water-limited ecosystems. This also improves seedling survival and woody plant growth (Bond & Midgley 2012; Stevens *et al.* 2016). However, Buitenwerf *et al.* (2012) argued that, because no significant increase in tree density, across all treatments on a semi-arid site in the Kruger National Park, could be established over more than 50 years of consistent burning regime, there is insufficient evidence that rising carbon dioxide concentrations drive bush-thickening in semi-arid savannas.

Humid savannas maintain higher herbaceous layer production and are thus more prone to regular veld fires. In these areas, an increase in woody plant density is probably directly influenced by elevated carbon dioxide levels, which result in increased photosynthesis and therefore increased growth (Bond & Midgley 2012). Furthermore, Kgope *et al.* (2010) have proven that clipped (to simulate herbivory or fire) plants were even more sensitive to higher carbon dioxide concentrations by showing significantly better growth of above-ground parts, probably facilitated by higher starch accumulations and larger root systems of the plants before the disturbance factor was applied.

In addition, Buitenwerf *et al.* (2012) found significant increases in woody plant density across all treatment plots subjected to the same burning regime for longer than 30 years in the mesic savanna of the Kruger National Park and in the Eastern Cape, suggesting that a global factor such as elevated carbon dioxide could be the driver. Stevens *et al.* (2016) confirmed this from a study conducted across the rainfall gradient with multiple land-uses and sites, that neither land-use nor rainfall provided sufficient evidence as the cause of bush-thickening.

In contrast, C_4 grasses*,* which are suspected to be replaced by competitor C_3 grasses and woody plants, have also been shown to increase water-use efficiency, photosynthesis and biomass at increased carbon dioxide concentrations (Morgan *et al.* 2004; Quirk *et al.* 2019). Furthermore, evidence exists that C_3 woody plants substitute C_3 and C_4 grasses, while C_3 grasses do not necessarily replace C_4 grasses in the ecosystem (Van Auken 2009; Belayneh & Tessema 2017), thus questioning the hypothesis of increased atmospheric carbon dioxide concentrations driving bush-thickening.

b) Climate change

Climate change in terms of precipitation variability and temperature is only weakly linked as a global driver of bush-thickening (Van Auken 2009). Woody seedling recruitment is most successful in wet cycles (Wiegand *et al.* 2005; Kraaij & Ward 2006; Joubert *et al.* 2008; Ward *et al.* 2014), as was shown for *S. mellifera,* which required at least two consecutive favourable rainfall seasons for successful recruitment (Joubert *et al.* 2013). Dry cycles limit woody plant growth, recruitment and seed production. However, decreases in perennial grass sward during dry years may result in increased woody seedling establishment in the following wet year, due to decreased competition (O'Connor *et al.* 2014). Furthermore, it was shown that rainfall frequency, not amount, played a major role in the successful establishment of *S. mellifera* (Ward 2005). Sankaran *et al.* (2005) and Graw *et al.* (2016) indicated a strong positive relationship between the average annual precipitation and the potential of areas to become bush-thickened. Moreover, with climate change, warmer temperatures and a decrease in frost events are expected. Frost may topkill or result in the mortality of many woody plants (Wakeling *et al.* 2012) and thus the absence of frost events, together with warmer temperatures, which encourage woody tree growth and seedling establishment (Stevens *et al.* 2014), would promote bush-thickening, but there is very little evidence to support this speculation (Buitenwerf *et al.* 2012; O'Connor *et al.* 2014; Ward *et al.* 2014; Venter *et al.* 2018).

c) Fire suppression

Local factors that may be contributors to bush-thickening include fire suppression and herbivory (increased grazing pressure and decreased browsing pressure) (Teague & Smit 1992; O'Connor *et al.* 2014). According to Scholes and Archer (1997), fire is a fundamental driver of the savanna structure. While natural fires were widespread in southern Africa during the 19th century, fire suppression became a common practice since the early twentieth century (O'Connor *et al.* 2014). In arid and semi-arid savannas (where this study was conducted), however, fires are uncommon, because fuel loads seldom support high intensity fires and is considered less important in maintaining an open savanna (Teague & Smit 1992; Sankaran *et al.* 2005; Kraaij & Ward 2006; Joubert *et al.* 2012; O'Connor *et al.* 2014;). Joubert *et al.* (2012) reported that, even though infrequent, fires in arid savannas are pivotal in preventing the shift from open savannas to thickets, as they result in significant seedling mortality, and suggested that, in contrast to humid savannas where fire frequency is important, arid savanna fires should be timed with seedling establishment. In mesic savannas, suppression of occasional hot fires by human intervention or by high herbivory pressure results in successful woody seedling establishment and allows young woody plants to grow out of the detrimental 'fire-trap' and thus accounts for bush-thickening (Roques *et al.* 2001; Van Auken 2009; O'Connor *et al.* 2014; Belayneh & Tessema 2017; Venter *et al.* 2018; Turpie *et al.* 2019). Rapid growth rates, as driven by increased carbon dioxide levels and warmer temperatures with decreased fire frequencies, allow woody plants to escape the flame zone more rapidly and further intensify the bush-thickening problem (Bond & Midgley 2012).

d) Herbivory

The loss of browsing herbivores and a substantial increase in grazing herbivores may contribute to bush-thickening (O'Connor *et al.* 2014). The loss of especially mega-herbivores (for example, elephants) may have led to an increase in woody cover. They consume very large amounts of woody plant material, uproot, pollard and bark-strip trees, thus causing mortality, decreasing growth rate and increasing vulnerability to fire in woody plants (O'Connor *et al.* 2007; Stevens *et al.* 2016). Furthermore, smaller browsers, mainly concentrate feeders, such as impala, dik-dik, and even sheep, browse on woody plant seedlings and coppices. Browsers can therefore act as a bottleneck for seedling establishment and growth, but their effect depends on the browsers present as well as their feeding patterns (O'Connor *et al.* 2014).

Prolonged heavy grazing and selective grazing of perennial grasses on the other hand, reduces the productivity of the grass sward. Thereby a competitive advantage for woody plant seedlings is created and fuel loads are decreased, consequently suppressing fires (intensity and frequency), resulting in successful woody seedling establishment, survival and unhindered growth and promoting bush-thickening (Roques *et al.* 2001; Smit 2004; O'Connor *et al.* 2014; Belayneh & Tessema 2017; Venter *et al.* 2018; Turpie *et al.* 2019). In a 52-year seasonal grazing trial in the Limpopo Province, woody plant cover had increased in continuously grazed camps as well as all camps seasonal grazed camps. However, camps grazed heavily during the growing season of each year showed the fastest increase in woody plant cover (Smit & Rethman 1992). Ward and Esler (2011) confirmed significantly higher *S. mellifera* seedling recruitment where grass competition was removed by clipping. Kraaij and Ward (2006) and Ward *et al.* (2014) dispute this and could not establish significant differences in recruitment between heavy grazed and not grazed areas, but suggest that, if heavy grazing pressure coincides with good rainfall, seedling recruitment will be more successful, provided seedlings are not consumed or trampled. Coetzee *et al.* (2007) demonstrated that overgrazing facilitated recruitment of *T. camphoratus* seedlings and therefore drives bush-thickening by this species. Roques *et al.* (2001) reported that the key factor driving bush-thickening in a study conducted in north-eastern Swaziland was heavy grazing resulting in low fire frequency.

e) Soil properties

Soil characteristics, including nutrient availability, texture and depth, also influence woody cover (Sankaran *et al.* 2008; Van Auken 2009; Mills *et al.* 2013, 2017). According to Sankaran *et al.* (2008) woody cover decreases with increasing soil clay percentage. Higher plant-available water as well as increased water infiltration and deep percolation favours deep rooted woody plants, while shallow rooted grasses are favoured with increasing clay content (Dye & Spear 1982; O'Connor *et al.* 2014). Furthermore, woody cover and soil nitrogen content are negatively correlated (Kraaij & Ward 2006; Sankaran *et al.* 2008). Nitrogen enrichment increases the competitive advantage of the herbaceous layer and retards woody seedling growth and survival of especially leguminous species with low nitrogen requirements, while other woody species thrive under these conditions (Kraaij & Ward 2006; Van Auken 2009). Importantly, soil characteristics determine much of a landscape's response to disturbance factors such as fire and herbivory (O'Connor *et al.* 2014; Turpie *et al.* 2019).

It is clear, that there are multiple factors with complex interactions triggering bush-thickening, which may even change over time, all leading to a challenging task for ecologists and landowners to effectively address the problem with economic and ecological consequences and no simple solution.

3.3.2 Consequences of bush-thickening

The impacts of bush-thickening are ecosystem, climate, soil and species specific (Eldridge *et al.* 2011, 2013; Archer & Predick 2014). Depending on their density and the landowners' needs, woody plants may be seen advantageous or disadvantageous.

Once woody plants reach a certain threshold density, they pose a major threat to the livestock industry, by decreasing fodder availability for domestic grazers and increasing the occurrence of pseudo-droughts. Woody species suppress palatable grasses and herbaceous species (Ward 2005; O'Connor *et al.* 2014) causing a significant decline in their biomass, density and cover, resulting in lower grazing capacity (De Klerk 2004; Van Auken 2009; Archer & Predick 2014; Ward *et al.* 2014; Haussmann *et al.* 2016; Venter *et al.* 2018). Richter *et al.* (2001) reported a drop in grazing capacity from 10 ha LSU^{-1} at 400 tree equivalents ha^{-1} to 42 ha LSU^{-1} at 2 500 TE ha^{-1} in the Molopo Thornveld. Contrarily, woody plants below certain critical densities (300 – 500 TE ha^{-1}) may actually benefit grass production (Bosch & Wyk 1970; De Klerk 2004). Smit and Swart (1994) recorded significantly higher herbaceous production (especially *Panicum maximum*) under leguminous *Senegalia erubescens* than under non-leguminous woody plants and uncanopied zones. Similar results were reported by Tessema and Belay (2017), who found significantly higher herbaceous biomass yields and plant abundance under *Vachellia robusta* compared to *Ziziphus spina-christi*, *Balanites aegyptiaca* and uncanopied areas.

Furthermore, bushes at very high density reduce accessibility and visibility (Bezuidenhout *et al.* 2015). These bush-thickened areas are therefore less attractive, which is especially problematic for the tourism and hunting sector (Bezuidenhout *et al.* 2015; Haussmann *et al.* 2016; Arbieu *et al.* 2017). Dense, bush-thickened areas are less aesthetic and animals are more difficult to spot, which, amongst others, increase chances for unsuccessful hunts or wounded animals and hunters struggle to find and retrieve hunted animals in the thickets. Furthermore, livestock handling in these dense thickets is also complicated (Archer & Predick 2014).

Bush-thickening also threatens biodiversity (De Klerk 2004). According to Archer and Predick (2014), species richness may increase, decrease or remain unchanged with increasing woody plant density depending on the species' habitat preferences. Botanical diversity is especially threatened where woody plants almost form a monoculture and herbaceous species become very limited (De Klerk 2004; Archer & Predick 2014). Bush-thinning operations may reverse this trend. However, in some cases controlled woody species are only replaced by another undesirable woody species or herbaceous weeds (Archer & Predick 2014; Haussmann *et al.* 2016). The effect of bush-thickening on wildlife diversity varies with functional group and taxa (Archer & Predick 2014). Mammal species adapted to woodlands (such as kudu, black rhinoceros and duiker) may increase with increasing woody plant cover, while mammal species preferring open grassland (such as cheetah, springbok, warthog and zebra) decrease (De Klerk 2004, Archer & Predick 2014; Stolter *et al.* 2018). While birds, reptiles and arthropods generally follow the same trend as mammals, it is notable that vultures (for example, Cape Griffons) in particular are extinct in very dense thickets in Namibia, as they struggle to find food and do not have sufficient space for landing and take-off (Joubert & Zimmermann 2002).

Moreover, bush-thickening is likely to reduce groundwater recharge and stream flow, even though research is still very limited (Acharya *et al.* 2018; Groengroeft *et al.* 2018). Decreased water infiltration, with increased interception, evapotranspiration and surface-runoff, as well as water uptake from greater soil depths by woody plant roots resulting from higher woody plant densities (Smit & Rethman 2000; Groengroeft *et al.* 2018), allow less deep percolation and less water reaching the groundwater (Le Maitre *et al.* 2016; Groengroeft *et al.* 2018; Geißler *et al.* 2019). Bush control may favour groundwater recharge to some extent, but has not been entirely successful and strongly depends on soil properties, herbaceous cover, bush control method and topography (Archer & Predick 2014; Acharya *et al.* 2018).

Air quality is also affected by bush-thickening. According to Archer and Predick (2014), the absence of a herbaceous layer and the structure of woody vegetation contribute to air-flow turbulence near the bare soil surface, leading to increased wind erosion and production of dust. This can have adverse effects on human health.

Bush-thickening may favour the global carbon budget; however, very few studies have quantified this yet (Archer *et al.* 2017). Carbon sequestration, the rate whereby atmospheric carbon dioxide is captured as plant and soil organic matter, as well as its quantity, are expected to rise as a result of bush-thickening. Turpie *et al.* (2019) concluded from a study conducted by Hudak *et al.* (2003) in South Africa that the total woody carbon pool may rise by 20 t C ha^{-1} and 100 t C ha^{-1} in sandy semi-arid and clay loam mesic savannas respectively, until a threshold woody plant density is reached. Self-thinning of shrubs may decrease carbon stocks again (Turpie *et al*. 2019). In addition, carbon stocks are sensitive to soil texture, rainfall, age and type of plants (Hudak *et al.* 2003) and effectively depend on the net productivity of woody plants (Archer & Predick 2014; Archer *et al.* 2017). Soil organic carbon is known to be higher under tree canopies compared to intercanopy/treeless areas and increase with increasing tree size (Belsky *et al.* 1993; Smit & Swart 1994; Mills & Fey

2004; Hagos & Smit 2005; Ward *et al.* 2018). Dlamini *et al.* (2019) found that on average carbon stocks and soil organic carbon were 117% - 148% higher on bush-thickened soils of the Limpopo Province of South Africa, except where other disturbance factors such as overgrazing, wildfires and erosion result in declined soil organic carbon (Turpie *et al.* 2019).

Furthermore, it has to be noted that bush-thickening also provides a renewable resource which creates new economic opportunities (Smit 2004; Birch *et al.* 2016). Charcoal production has not only become one of Namibia's fastest growing industries, but is also used as a tool to manage bush-thickening species, amongst others, *S. mellifera, Dichrostachys cinerea* and *Vachellia reficiens* (Birch *et al.* 2016; Namibia Charcoal Association 2018). Firewood, wood briquettes, wood chips and wood pellets, as well as animal fodder ("boskos"), fence poles and biochar, are all products using woody biomass to our advantage (Smit 2004; Turpie *et al.* 2019).

Another positive attribute of woody plants is their function to create so-called "nutrient hotspots" (van Auken 2009). The importance of trees in soil enrichment, especially on nutrient-poor sandy soils compared to fine-textured soils with a high nutrient status, is of substantial significance (Campbell *et al.* 1994; Hagos & Smit 2005). Bush clearing operations would lead to a nutrient loss from the soil; thus bush clearing impact studies highlight the importance of bush thinning or selective bush clearing instead of total clearing (Joubert & Zimmermann 2002; Smit 2005; Birch *et al.* 2016).

In conclusion, the consequences of bush-thickening are primarily negative, with only very few positive effects and thus largely reducing the ecosystem service value (Turpie *et al.* 2019). It is therefore essential that — depending on the state of the vegetation — bush control measures, either preventative, adaptive or reactive have to be implemented.

3.3.3 Managing bush-thickening

Our incomplete understanding of savanna ecosystem functioning and its dynamics, as well as the complexity of the causes of bush-thickening, make it very difficult to find long-term sustainable management solutions for the problem (Smit 2004; O'Connor *et al.* 2014). There are several approaches and methods by which bush-thickening can be managed. However, before deciding on a management plan, its economic and ecological feasibility should be considered (Smit 2004). Furthermore, it is important to realise that the outcome and success after woody plant removal may differ between bush control methods and approach, veld types, soil properties, history, species and time after removal (Dye & Spear 1982; Teague & Smit 1992; Richter *et al.* 2001; Bezuidenhout *et al.* 2015; Haussmann *et al.* 2016). The single biggest problem of most bush control measures is re-encroachment, often resulting in a state that is worse than before the treatment (Smit *et al.* 2015).

The reactive and preventative methods that are most commonly used include mechanical or manual woody plant removal, chemical treatment, prescribed fire regimes and biological control, with each having its advantages and restrictions. These control methods are either used singly, successively or in combination (Archer & Predick 2014). The selection of the specific method to use depends on a number of factors, including bush-thickening species, growth form and their density as well as the terrain, available resources and urgency at which restoration should take place (Campbell 2000).

Chemical control is either done by hand or by aerial application and mainly applied where extensive areas need treatment, woody plant cover is too dense or largely unpalatable to browsers, where mechanical means are impractical or too expensive and browsers ineffective (De Klerk 2004; Harmse *et al.* 2016). Herbicides containing photosynthesis-inhibiting tebuthiuron as active ingredient are most popular amongst farmers in southern Africa (Bezuidenhout *et al.* 2015; Harmse *et al.* 2016). The herbicide is either applied in granular, pellet or liquid form onto the soil surface, where it is taken up by the roots after the rain or via foliar or stem application (De Klerk 2004). Stem applications are often done after manual or mechanical control was practised to prevent woody plant from regrowing. Disadvantages of chemical control include active ingredients may persist in the soil for as long as 15 years (Bezuidenhout *et al.* 2015), non-target woody plants (20 – 50 m away) may also die, dosage is dependent on tree size, soil clay and soil organic matter, time-consuming and labour intensive (in case of hand and stem application) (De Klerk 2004). Occasionally controlled woody species are replaced by other undesired pioneer woody plant species, such as in northern Namibia where the unpalatable *Pechuel-loeschea leubnitziae* replaced *S. mellifera* on chemically treated sites (Smit *et al.* 2015; Haussmann *et al.* 2016). Advantages of chemical control include its persistence may control seedling establishment, large areas can be treated relatively fast and cost effectively and the soil is undisturbed (De Klerk 2004).

Mechanical woody plant control is done with the aid of heavy machinery including bulldozers, tractors and custom-built bush-cutting machines, whereas manual woody plant control involves felling woody plants with axes, chainsaws or handheld saws (De Klerk 2004). In the case in which bulldozers are used and woody plants are uprooted, considerable soil disturbance is caused, which creates a favourable environment for woody seedling establishment, particularly *D. cinerea,* resulting in a state of bush-thickening worse than before in five to six years (Zopke 1986, as cited by De Klerk 2004; Pienaar 2006). Where woody plants are cut above the soil surface either by mechanical or manual means, it is not unusual that the woody plants coppice. Coppice regrowth from the collar region of woody plants is well documented (Smit 2003; Luoga *et al.* 2004). In Limpopo it has been shown that *Combretum apiculatum* and *Senegalia erubescens* trees that were cut and not treated will regrow to their original leaf biomass within five years, but with significantly lower wood biomass (Smit 2003a). While, De Klerk (2004) claimed that 100% coppicing of *D. cinerea* can be expected and most *S. mellifera* will also resprout, farmers claimed that season of cutting may play a role in whether a woody plant will coppice or die. Coppice regrowth will also result in plants that are structurally different from the original plant, with single-stemmed trees that grow into multi-stemmed shrubs (Smit 2003). For this reason, it is crucial that cut stems are treated with herbicide immediately after cutting to prevent coppicing (De Klerk 2004, Pienaar 2006, Ndhlovu *et al.* 2011). However, if woody plants are cut ≥ 10 cm below the soil surface they will not regenerate, except for *D. cinerea.* This method is very time-consuming and labour intensive (De Klerk 2004). Ndhlovu *et al.* (2011) found that grazing capacity increased by 110% within four to six years post-clearing in the *Prosopis* invaded Nama-Karoo, while Mapuma (2000) surveyed an increase of up to 700% in the first four years after mechanical clearing in the mesic bushclump savanna of the Eastern Cape.

Fire and herbivory can also be used as a management tools for bush-thickening. As explained earlier (section 3.3.1), occasional fires in arid savannas are crucial for preventing dense thickets developing from open savanna systems, because these fires primarily result in high (97 – 99%) seedling mortality and topkill saplings (Joubert *et al.* 2012). It is suggested that, for arid and semi-arid savannas, fire treatment should coincide with seedling establishment. However, once bush-thickening has already occurred, fuel loads are generally too low to produce high-intensity fires that can damage the woody plants and many savanna plants are resistant to fire due to their strong coppicing ability. Trollope (1980) suggests that browsers should follow-up the fire treatment, as coppice is at reachable heights and more palatable. However, Joubert *et al.* (2012) have observed that *S. mellifera* coppice are not readily browsed due to their hard thorns, but other woody species, such as *D. cinerea,* are readily browsed. The effectiveness of using herbivores is therefore depended on the woody species. Fire, as well as herbivory is better used as a preventative or follow-up strategy than as a curative strategy. It must further be noted that, using fire as a management tool, could impact the woody layer composition, because species not resistant to fire are replaced by fire-resistant species, such as *T. camphoratus* (Kiruki & Njung’e 2007; Mudongo *et al.* 2016).

Occasionally, stem burning or fire-girdling is practiced to control individual woody plants, but, because it is very labour-intensive and time-consuming, it is seldom used over large areas. It involves making a hot fire around the stem base (De Klerk 2004). For fire girdling to be most effective it needs to be done as close as possible to the ground, with high fire intensity for a certain minimum time (about six minutes) and during the active growing season of the woody plant (Donaldson 1967; Strohbach 1998). Correctly treated *S. mellifera* resulted in 100% mortality (Donaldson 1967; Strohbach 1998) while the majority of *D. cinerea, Terminalia prunioides* and *Terminalia seilcea* coppiced readily and follow-up treatment, for example with browsers, was necessary (Strohbach 1998).

Moreover, it is not only the method used to remove woody plants, but also the approach which plays a role in the effectiveness of the intervention. One of two approaches is followed: (1) total, non-selective clearing of all woody plants, or (2) selective clearing or tree thinning of only a predetermined percentage of a certain species. The outcome of these approaches is a different vegetation structure with one mimicking an open grassland while the second approach aims to gain the most from the positive woody plant attributes (their direct use, browse provision, soil enrichment and positive effect on herbaceous layer) and use competitive and facilitative interactions to progressively develop into a stable savanna systems (Joubert & Zimmermann 2002; Smit 2004). Harmse *et al.* (2016) reported from a study conducted in the Kalahari that grass dry matter yield was 280% and 200% higher in non-selectively cleared and selectively cleared sites, respectively, compared to bush-thickened sites. However, they found a more favourable species composition and significantly higher forage quality in the selectively cleared sites compared to the non-selectively cleared sites. Furthermore, non-selectively cleared sites had higher seedling recruitment which increases the risk for re-thickening. The main aim of woody plant removal is increased herbaceous productivity, but also long-term stability (perennial palatable grass layer and open savanna structure), decreased soil erosion and the preservation of soil fertility (Smit 2004). It has been suggested that a more stable savanna environment can be created by maintaining or restoring savanna structure (protecting/restoring large trees), since large trees are able to suppress the establishment and survival of new tree seedlings in their near vicinity (Smit 2004). It is clear that selectively cleared or thinned sites achieve more of these aims than non-selectively cleared sites, especially when considering that non-selectively cleared sites require follow-up treatments faster and probably at higher expenses than selectively cleared sites (Smit 2004; Harmse *et al.* 2016).

No matter where and which woody plant control programme is implemented, woody plant removal is not a once-off intervention. Instead, follow-up treatments and maintenance interventions will be necessary to prevent rapid re-thickening by aggressive and invasive woody species and this must be planned and budgeted for (Smit 2004; Pretorius *et al.* 2008; Smit *et al.* 2015; Archer *et al.* 2017). The intervals between follow-up treatments will in part be determined by the success of the initial intervention, environmental conditions (for example, rainfall) (Joubert *et al.* 2013), the specific problem species and implementation of effective veld management practices that allow for adequate rest periods (Joubert *et al.* 2014), as well as the applied stocking rates of browsers and grazers (Joubert *et al.* 2014; Smit 2004). In the end, it is unlikely that long-term restoration success will be achieved without a proper understanding of the specific woody plant species, as well as the ecological processes involved in the savanna ecosystem following drastic bush clearing or thinning operations (Smit 2004; Smit *et al.* 2015).

CHAPTER 4

Effect of *Tarchonanthus camphoratus* on the soil-nutrient status

4.1 Introduction

During the last few decades and still continuing today, large areas of the southern African savanna are cleared of woody plants in an effort to manage bush-thickening and regain grazing potential. Often entire areas are non-selectively cleared of their woody plants, without paying much attention to the potential positive attributes that especially large woody plants could have in maintaining long-term ecological stability and supporting biological diversity in the savanna ecosystem (Smit 2004).

In semi-arid savannas, water is a key limiting factor influencing mainly the duration of forage production, while soil nutrients influence the forage growth rate (Scholes 1990). Many savannas have nutrient-poor weathered soils (Turpie *et al.* 2019); therefore, compounded limitations of water and nutrients are not uncommon in arid and semi-arid savannas, as was shown by Ludwig *et al.* (2004), as well as Kraaij and Ward (2006). Woody plant canopies alter microclimates (for example, temperature and light intensity), as well as soil physical (for example, bulk density and soil moisture) and chemical properties (for example, nutrients and pH). These may be favourable or unfavourable for the herbaceous plants growing underneath their canopies (Belsky *et al.* 1989; Wang *et al.* 2009; Holdo & Mack 2014; Ward *et al.* 2018) depending on the net outcome of facilitative and competitive effects of woody plants (Ludwig *et al.* 2001).

Even though weathering parent material determines much of a soil's nutrient-status at first, biological activities further form and preserve localised nutrient-rich patches, especially on nutrient poor soils (Scholes 1990). Woody plants may therefore act as such biological agents, forming islands underneath their canopies that differ in nutrient status from the uncanopied areas. In the arid and semi-arid savanna, soil enrichment under woody plant canopies has been reported extensively, and differs by woody plant species, age and soil nutrient (Hagos & Smit 2005; Wiegand *et al.* 2005; Treydte *et al.* 2007; Holdo & Mack 2014). Ward *et al.* (2018) found higher soil-nutrient concentrations under the canopies of large shrubs of non-leguminous *T. camphoratus* and leguminous *S. mellifera* compared to under canopies of small shrubs and the open grassland in the Kimberley Thornveld of the Northern Cape. Furthermore, they reported that sodium and pH differed significantly between the species.

This study aimed to quantify soil-nutrient concentrations (soil enrichment) under the canopies of *T. camphoratus* and also those of a co-occurring bush-thickening species, *S. mellifera,* compared to the open grassland. In addition, differences in soil enrichment by *T. camphoratus* that grow on deep sandy soil and shallow rocky soil were also investigated. These aims were achieved by testing the following hypotheses:

a) Savanna trees are responsible for soil enrichment and the soil-nutrient concentrations under the canopies — especially close to the main stem — of *T. camphoratus* and *S. mellifera* will be higher compared to the uncanopied area.
b) The various canopied and uncanopied subhabitats on the shallow rocky soil will have a slightly higher soil-nutrient status than the same subhabitats on deep sandy soil, due to expected leaching of nutrients on the deep sandy soil.
c) Soil-nutrient concentrations under *S. mellifera* and *T. camphoratus* will be similar in sandy soil, except for soil nitrogen which is expected to be higher under *S. mellifera* canopies, due to nitrogen fixation associated with leguminous tree species.

4.2 Literature review

Scholes (1990) described that, even though soil parent material determines the primary soil fertility; biological activities form and preserve localised nutrient-rich patches in savanna ecosystems. The soil's capacity to supply suitable nutrients to plants, amongst other variables, determines plant species composition, vegetation structure, woody plant abundance (Mills *et al.* 2013a, 2013b, 2017), herbaceous layer production, chemical composition (forage quality) (Jackson & Ash 1998; Moyo *et al.* 1998; Treydte *et al.* 2007) as well as the degree and type of herbivory (Augustine & Mcnaughton 2006). For example, Treydte *et al.* (2007) found that grass leaves originating from under the tree canopy, where soils are more fertile, had up to 25% higher nitrogen and phosphorous content compared to grass leaves originating from the uncanopied zones. This highlights the importance of woody plants in soil enrichment, especially on nutrient-poor sandy soils (Ludwig *et al.* 2004; Hagos & Smit 2005).

The sources and mechanisms which lead to the so-called "nutrient hotspots" under the woody plant canopy are poorly understood (Johnson & Lehmann 2006; Mlambo & Nyathi 2008), probably due to the complexity of interactions between many possible factors.

One of the major sources of elevated nutrient status under the tree canopy is the accumulation of leaf litter (Bosch & Wyk 1970; Belsky *et al.* 1989; Aweto & Dikinya 2003; Mlambo & Nyathi 2008), including leaves, twigs, flowers and pods or other reproductive parts (Witkowski 1991; Hagos & Smit 2005). Smit and Swart (1994) proposed that structural differences between leaves, such as those of microphyllous and broad-leaved trees, may result in different leaf quantities reaching the soil immediately under the tree canopy, as the latter are more subject to wind dispersal. Decreased nutrient-leaching under trees (Belsky *et al.* 1989), as well as improved decomposition activity due to soil moisture retention and more favourable temperatures (Gutirrez *et al.* 1993), may favour soil enrichment in the canopied zone.

Another mechanism which may contribute towards elevated nutrient levels under tree canopies and especially in the close vicinity of the stem include stemflow and throughfall, containing dust (i.e. mineral) deposits that accumulated on the leaves (Muoghalu 2003; Johnson & Lehmann 2006), as well as bark-shedding (Belsky *et al.* 1989).

The role of leguminous trees in semi-arid environments as a nitrogen-enrichment mechanism under the tree canopy is still uncertain. Numerous studies reported no significant differences in soil nitrogen status under the canopies of leguminous and non-leguminous woody plants (Belsky *et al.* 1989; Smit & Swart 1994; Treydte *et al.* 2007; Ward *et al.* 2018), thus questioning the role of leguminous woody plants in nitrogen enrichment. Bernhard-Reversat and Poupon (1980) found no root nodules indicating active nitrogen-fixation on adult *Senegalia senegal* and hypothesised that older leguminous woody plants lose the ability to fix nitrogen. Furthermore, Hartwig (1998) suggested that leguminous nitrogen fixation is strongly reduced under high ambient temperatures, soil water shortages, low plant-available phosphorus and plant defoliation (high browsing pressure), all prevailing conditions in arid and semi-arid savannas. Herbaceous leguminous plants growing under the canopy may possibly be more efficient in nitrogen fixation and non-leguminous herbaceous plant litter may also be a source of soil nutrients under woody plants (Hartwig 1998; Hagos & Smit 2005).

Furthermore dung from large mammals using the trees’ shade as hiding and resting places, as well as bird droppings and nesting material, may contribute to increased nutrient levels under trees (Belsky *et al.* 1989; Kellman 1979). However, Belsky *et al.* (1993) questioned why then the lowest nutrient levels exited towards the canopy edge where most bird nests were positioned.

The degree of nutrient enrichment varies with woody plant age, species, specific soil nutrient and rainfall (Kellman 1979; Scholes & Archer 1997; Treydte *et al.* 2009; Wang *et al.* 2009; Tessema & Belay 2017; Ward *et al.* 2018). Furthermore, some soil-nutrient concentrations decline with soil depth and distance from the stem (Bernhard-Reversat 1982; Ludwig *et al.* 2004; Hagos & Smit 2005).

Campbell *et al.* (1990) found an 88% correlation between the soil-nutrient index and tree-canopy area in their study conducted on nutrient-poor soil in Mozambique. Likewise, Wiegand *et al.* (2005) demonstrated in their study in the arid Khomas Hochland savanna of Namibia that soil under large trees had significantly higher organic carbon and nitrogen than soil under small trees. Furthermore, Bernhard-Reversat (1982) also found a steep declining gradient for organic carbon and nitrogen content with increased depth and increased distance from the tree trunk, which also supports the idea that tree age plays a role in the nutrient status of soils. The area closest to the stem is exposed to the sources and mechanisms of nutrient enrichment the longest (since seedling). It is therefore concluded that nutrient enrichment is a very slow process (Bernhard-Reversat 1982; Scholes & Archer 1997).

Different tree species affect different soil nutrients to different degrees:

a) Soil organic matter and organic carbon

Most studies confirm a higher soil organic matter content in the canopy zone compared to the uncanopied open grassland zone (Smit & Swart 1994; Mills & Fey 2004; Hagos & Smit 2005; Wiegand *et al.* 2005; Treydte *et al.* 2007; Wang *et al.* 2009). In a study conducted by Smit (2003) in the Mopane savanna of South Africa, the organic carbon percentage in the soil under *Salvadora australis* was significantly higher than under *Colophospermum mopane.* Similarly, in Sahelian Niger, soil organic carbon under *Faidherbia albida* was significantly higher than under *Piliostigma reticulatum* (Diallo *et al.* 2019). Abule *et al.* (2005) found higher organic carbon under the canopy of *Vachellia tortilis* compared to *Balanites aegyptiaca* under medium grazing treatment, while there was no difference in organic carbon between the same two species under a heavy grazing treatment in Ethiopia. Similarly, the organic carbon content was significantly higher under *Vachellia robusta* than under *Ziziphus spina-christi* and *B. aegyptiaca* (Tessema & Belay 2017).

In contrast to the above mentioned, soil organic carbon content did not differ significantly under the canopies of *Combretum apiculatum* and *Peltophorum africanum*, both growing in semi-arid south-eastern Botswana, but was 55% and 47% higher than in the uncanopied areas (Aweto & Dikinya 2003). Smit and Swart's (1994) study also yielded no significant difference in organic carbon in the soils collected from the canopy zones of *C. apiculatum* and *Senegalia erubescens,* similar to Belsky *et al.* (1989), who investigated the differences between *V. tortilis* and *Adansonia digitata* in Kenya*.*

It is therefore clear that not all tree species affect soil organic matter content in the same way. The degree to which soil organic matter is influenced differs, amongst others, by tree species as well as grazing treatment.

b) Soil Nitrogen (N)

Leguminous plants harbour nitrogen-fixing *Rhizobium* bacteria in their root nodules, which are able to convert atmospheric nitrogen (N_2) into ammonia (NH_3), which is further converted into plant-available ammonium (NH_4^+) (Hartwig 1998). It would thus be expected that soils under leguminous trees have higher nitrogen concentrations compared to soils originating from under non-leguminous trees. However, varying results are found.

Total nitrogen percentage and mineralisable nitrogen is often closely correlated to the soil organic matter content. Therefore, nitrogen concentrations under woody plants are usually higher than in the open grassland zones (Smit & Swart 1994; Ludwig *et al.* 2004; Mills & Fey 2004; Abule *et al.* 2005; Hagos & Smit 2005; Wang *et al.* 2009; Holdo & Mack 2014; Ward *et al.* 2018). Similar to soil organic matter, soil nitrogen levels also tend to follow a decreasing gradient with distance from the tree trunk (Garcia-Moya & McKell 1970; Hagos & Smit 2005). Soil under the canopies of *C. mopane* had a lower total nitrogen percentage than soil originating from the canopy zone of *S. australis* (Smit 2003b). Likewise, the ammonium (NH_4^+) concentration under *P. reticulatum* was significantly higher than under *F. albida, Annona senegalensis* and *Combretum aculeatum* (Diallo *et al.* 2019). Contrasting with the studies on *Prosopis juliflora,* where total available nitrogen was about 15 times more under the canopy than in the inter-canopy zone, *Juniperus occidentalis* seemed to leave plant-available nitrogen almost unaffected (Tiedemann & Klemmedson 1995). Tessema and Belay (2017) had found definite higher levels of total nitrogen under the leguminous *V. robusta* compared to the non-leguminous *Z. spina-christi* and *B. aegyptiaca.* Garcia-Moya and McKell (1970) found that the nitrogen content of the soil was not only related to the species but also to root distribution.

In contrast to the above-mentioned findings, Smit and Swart (1994) did find a difference in total soil nitrogen percentage under non-leguminous *C. apiculatum* and leguminous *S. erubescens* canopies, but this difference was statistically non-significant. Furthermore, Belsky *et al.* (1989) found no significant differences in mineralisable nitrogen between soils from the canopy zones of leguminous *V. tortilis* and non-leguminous *Adansonia digitata.* Treydte *et al.* (2007) found up to 30% higher soil nitrogen under tree canopies compared to the uncanopied areas and also no significant difference between leguminous and non-leguminous species in northern South Africa; however, no canopy effects on soil nitrogen could be found in their Tanzania site. Similarly, Ward *et al.* (2018) reported no significant differences in soil nitrogen concentration between *T. camphoratus* and *S. mellifera* in the Northern Cape Province of South Africa.

c) Soil phosphorus

Phosphorus is a highly immobile anion in soils and its plant availability is highly sensitive to soil pH (Havlin *et al*. 2014). Reports about the phosphorus concentrations under tree canopies of various tree species and between canopied and uncanopied zones vary greatly.

Phosphorus neither differed significantly between *S. erubescens* and *C. apiculatum* trees on sandy Hutton soil in the mixed bushveld of South Africa (Smit & Swart 1994) nor did phosphorus levels differ significantly between the canopied and uncanopied zones (Smit & Swart 1994; Hagos & Smit 2005; Wiegand *et al.* 2005; Holdo & Mack 2014). Belsky *et al.* (1989) observed a similar decreasing gradient of phosphorus concentration from canopy centre to the end of the canopy zone as Hagos and Smit (2005) and Klemmedson and Tiedermann (2000), under *V. tortilis* and *A. digitata,* but found no significant difference in the phosphorus concentration between soils under *V. tortilis* and *A. digitata*. Significantly higher phosphorus concentrations under *V. robusta* compared to *Z. spina-christi* and *B. aegyptiaca* were found in a study conducted in the semi-arid savanna of Ethiopia (Tessema & Belay 2017). Comparably, in west Africa, Diallo *et al.* (2019) reported significantly higher phosphorous concentrations under *F. albida* than under *A. senegalensis* and *C. aculeatum.* Furthermore, significantly higher plant-available phosphorus in the canopied area of *S. mellifera* than in the open grassland was found by Ward *et al.* (2018), and similar results were obtained by Ludwig *et al.* (2004).

d) Soil potassium (K)

Potassium concentrations were generally higher under the tree canopies than in the open grassland (Belsky *et al.* 1989; Smit & Swart 1994; Aweto & Dikinya 2003; Ludwig *et al.* 2004; Ward *et al.* 2018). Smit and Swart (1994) also found that potassium concentrations were higher under the canopies of non-leguminous *C. apiculatum* than under the canopies leguminous *S. erubescens.* Similarly, soil under *S. australis* had a notably higher potassium concentration than soil under *C. mopane* (Smit 2003b). Furthermore, Tessema and Belay (2017) also found significantly higher potassium concentrations under *V. robusta* and *Z. spina-cristi* compared to *B. aegyptiaca.* Soils from the canopy zone of *P. reticulatum, F. albida* and *A. senegalensis* showed no differences in extractable potassium, but were significantly higher in extractable potassium than soils collected under *C. aculeatum* (Diallo *et al.* 2019). Ward *et al.* (2018) could not establish differences in soil potassium concentrations between *T. camphoratus* and *S. mellifera.*

e) Soil calcium (Ca)

Similar to the previous elements, extractable calcium also seemed to be in higher concentration in the canopied zone than in the uncanopied zone (Belsky *et al.* 1989; Smit & Swart 1994; Aweto & Dikinya 2003; Hagos & Smit 2005; Ward *et al.* 2018). The extractable calcium was higher under *S. australis* than under *C. mopane* (Smit 2003b). Diallo *et al.* (2019) reported significantly lower calcium levels under *A. senegalensis* than under *F. albida* and *C. aculeatum.* Contrasting with this, neither Smit and Swart (1994) nor Ward *et al.* (2018) reported significant differences in calcium concentrations between soil under the canopies of their study species, *C. apiculatum* and *S. erubescens, T. camphoratus* and *S. mellifera,* respectively. Moreover, calcium concentrations declined faster with distance from the trunk under *A. digitata* than under the *V. tortilis* canopy (Belsky *et al.* 1989).

f) Soil magnesium (Mg)

Smit (2003b) reported that the soil under *C. mopane* had a significantly lower magnesium concentration compared to soil under *S. australis.* Similar to organic carbon, phosphorus, calcium and pH, soil exchangeable magnesium was highest under *F. albida* and significantly less under *A. senegalensis* (Diallo *et al.* 2019). Comparable with potassium, Smit and Swart (1994) also found that soil magnesium concentrations were higher under *C. apiculatum* than under *S. erubescens.* However, Aweto and Dikinya (2003) could not establish significant differences in soil magnesium levels between *C. apiculatum* and *P. africanum,* even though the levels were double under the canopy than in the open grassland. Magnesium concentrations at the trunk of *V. tortilis* and *A. digitata* were very similar to those in the open grassland (Belsky *et al.* 1989). Furthermore, significantly lower magnesium concentrations under *V. tortilis* compared to concentrations under *A. digitata* was about the only notable difference in nutrient-status between these two tree species. Contrasting with the other elements, magnesium increased with distance from the trunk up to a threshold level (Belsky *et al.* 1993).

g) Soil sodium (Na)

Similar to all above-mentioned elements, sodium concentrations under *S. australis* were also found to be higher than under *C. mopane* (Smit 2003b). In contrast, no differences in sodium between study species or between the canopied and uncanopied zones were found by Smit and Swart (1994), as well as Aweto and Dikinya (2003). Studies on *S. mellifera* further supported this result (Hagos & Smit 2005). However, Ward *et al.* (2018) reported significantly higher soil sodium concentration under *T. camphoratus* canopies than under the *S. mellifera* canopies or open grassland. Significantly lower sodium concentrations were recorded under the canopies of shrub species *A. senegalensis* and *C. aculeatum* compared to tree species *F. albida* and *P. reticulatum* in Sahelian Niger (Diallo *et al.* 2019).

h) Soil pH

Different plants have different pH tolerances but even more important is the role which pH plays in terms of soil-nutrient solubility and therewith availability to plants (Havlin *et al.* 2014). Most macronutrients such as calcium, magnesium, potassium, phosphorus and nitrogen, as well as sulfur and boron, are insoluble at too low pH, while many micronutrients, such as iron, zinc, copper, cobalt and manganese, are very soluble at low pH and even reach toxic levels. On the other hand, in slightly to moderately alkaline soils, all macronutrients (except phosphorus) and molybdenum are readily available, while most micronutrients are insoluble, which may result in plant deficiency. Furthermore, it is important to realise that pH influences the occurrence of soil microorganisms such as bacteria, and thus plays a role in the functioning of microorganism-driven soil processes such as decomposition, mineralisation, immobilisation and nitrification and therefore also influence the availability of nutrients in the soil (Bohn *et al.* 2001). For these reasons, soil nutrients cannot be discussed without also mentioning soil pH.

The soil pH is influenced by the presence of trees as well as by the specific tree species present. A higher pH under *S. australis* than *C. mopane* was reported (Smit 2003b). On the sandy Hutton soil in the mixed bushveld of South Africa, the pH was higher under the trees compared to the open grassland area (Smit & Swart 1994). Diallo *et al.* (2019) reported higher soil pH under woody plant canopies and found that soil under *C. aculeatum* had a significantly lower pH (5.4) than the soil under *F. albida, A. senegalensis* and *P. reticulatum* (5.64 – 5.68).

In contrast, the pH under *S. mellifera* was slightly acidic, which was explained by the high leaching potential of the sandy soils (Hagos & Smit 2005). Similarly, the pH was almost unaffected by the canopy of *V. robusta* and *Z. spina-christi,* but *B. aegyptiaca* had the highest pH (> 8.0) under its canopy among all studied species and in comparison to the area outside the canopy (Tessama & Belay 2017). Moreover, the average pH under *V. tortilis* was slightly less (6.1) than the average pH under *A. digitata* (6.5) (Belsky *et al.* 1993).

4.3 Procedure

4.3.1 Soil sampling

To investigate the influence of *T. camphoratus* on the soil-nutrient status in its immediate surroundings, ten *T. camphoratus* shrubs of approximately similar size (1.5 – 2 m height) were randomly selected on both the sandy and the rocky site for soil sampling (a total of 20 shrubs). For comparison purposes, a further ten large (> 2 M height) *S. mellifera* shrubs were chosen on the sandy site only, as no *S. mellifera* occur on the rocky site. In order to exclude possible influences from nearby shrubs, only free-standing shrubs were used and shrubs with bird nests were also avoided. Furthermore, the low branching and dense growth form of the shrubs make them unsuitable as resting areas for large mammals. It is thus expected that differences in soil chemical properties are a result of the shrubs alone and not due to nutrient import from dung and urine by large mammals such as antelope resting under the tree canopies.

Soil sampling was done in three identified subhabitats (Smit & Swart 1994), namely:

A. close to the stem (< 0.25 m from stem),
B. in the middle between the stem and the canopy edge, and
C. in the uncanopied zone (open).

Due to the high density of *T. camphoratus* shrubs and their extensive root systems (D. Ward personal communication[1]), the sample from the uncanopied zone was taken at approximately half way distance between two adjacent shrubs, but possibly still in the *T. camphoratus* root zone (Figure 4.1). This amounted to a total of 60 soil samples for *T. camphoratus* and 30 samples for *S. mellifera*.

In each subhabitat, four topsoil samples to a depth of 200 mm at 90 degree angles to each other were taken using a soil auger and bulked. This was done to avoid the influence of direction to the shrub to influence the analyses (Tiedemann & Klemmedson 1973; Belsky *et al.* 1989; Ward *et al.* 2018). The bulked samples were thoroughly mixed and a subsample was taken for laboratory analyses. Sampling took place in May 2018.

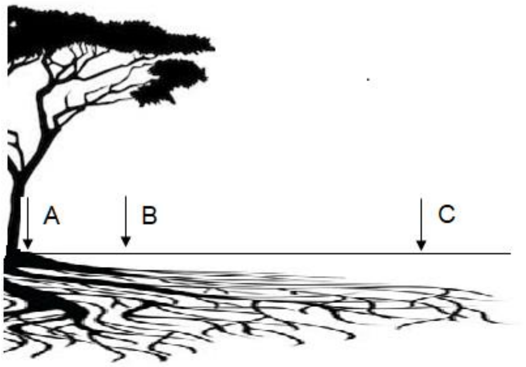

Figure 4.1: Layout for soil sampling: (A) at the stem, (B) canopy middle, (C) uncanopied area

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[1] David Ward: Kent Education – dward21@kent.edu

4.3.2 Soil chemical analyses

Soil analyses were done following the standards of the Non-Affiliated Soil Analysis Work Committee (1990) at the University of the Free State. Samples were dried and sieved through a 2 mm sieve to remove gravel and large plant parts. Soil pH, exchangeable cations (calcium, potassium, sodium, and magnesium), plant-available phosphorus, percentage nitrogen and organic carbon were analysed. Soil pH (H_2O) was determined with a 1:2.5 soil-to-water suspension using a pH-meter with a combined glass-calomel electrode, while carbon and nitrogen percentages were determined by dry oxidation using a CHNS analyzer (Elementar-Analysensysteme GmbH, Hanau, Germany). Using the HCl test no inorganic carbon was detected in the soil; thus, it is accepted that total carbon is approximately equal to organic carbon. Plant accessible phosphorus was extracted using the Olsen method with 0.5 N sodium hydrogen carbonate ($NaHCO_3$) corrected to pH 8.5 and the concentration determined by using a Thermo Spectronic Hexios γ colorimeter. Lastly, the exchangeable cations (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}) were extracted using a 1 N ammonium acetate (NH_4OAc) solution and then determined by means of an atomic absorption spectrophotometer. Soil analyses were done in duplicate and averages used for data analysis. Concentrations of P, K^{+}, Ca^{2+}, Mg^{2+}, Na^{+} were converted to mg kg^{-1} whereas organic carbon and nitrogen concentrations were given as percentages. Soil analyses took place in August 2018.

4.3.3 Statistical analysis

The ten samples from each subhabitat in each site were considered as replications. Thus the means for all tested soil variables in each subhabitat per site were used for statistical analyses. Data were tested for normality using Shapiro-Wilk ($p > 0.05$) (Shapiro & Wilk 1965) and homogeneity of variance using the Levene's test ($p > 0.05$) (Levene 1960) and necessary transformations were performed where necessary. Potassium, calcium, total nitrogen and organic carbon percentage were log-transformed. One-way ANOVA was applied to test for each, subhabitat, species and soil type influence on each soil nutrient. Where necessary, Tukey´s (HSD) *post hoc* test was performed to detect significant differences ($p < 0.05$). Because magnesium in the canopy middle subhabitat on the rocky site was non-normally distributed and could not be transformed, the non-parametric Mann-Whitney U test was used to test for significant ($p < 0.05$) differences of all possible combinations. All analyses were conducted using IBM SPSS version 25 (IBM Corp., Armonk 2017) and results are presented as mean ± 1 SE.

4.4 Results

4.4.1 Soil pH

The pH (H_2O) was slightly alkaline on the rocky soil and slightly acidic to slightly alkaline for *T. camphoratus* and *S. mellifera* on the sandy soil. (Figure 4.2). The pH on the rocky soil was significantly ($p < 0.05$) higher (more alkaline) than on the sandy soil for all three subhabitats (stem: $F_{1;18} = 8.265$, $p = 0.01$; canopy middle: $F_{1;18} = 5.784$, $p = 0.03$; open: $F_{1;18} = 30.463$, $p < 0.001$) of *T. camphoratus*. Furthermore, there were significant differences in pH (H_2O) between the *T. camphoratus* subhabitats on the rocky ($F_{2;27} = 4.999$, $p = 0.014$) and the sandy sites ($F_{2;27} = 10.312$, $p < 0.001$), as well as the *S. mellifera* subhabitats ($F_{2;27} = 7.763$, $p = 0.002$). The pH in the stem subhabitat of *T. camphoratus* and *S. mellifera* was significantly ($p < 0.05$) lower compared to the pH in the canopy middle in both soil types. There were no significant soil pH differences ($p > 0.05$) between *T. camphoratus* and *S. mellifera* in all three subhabitats on the sandy site.

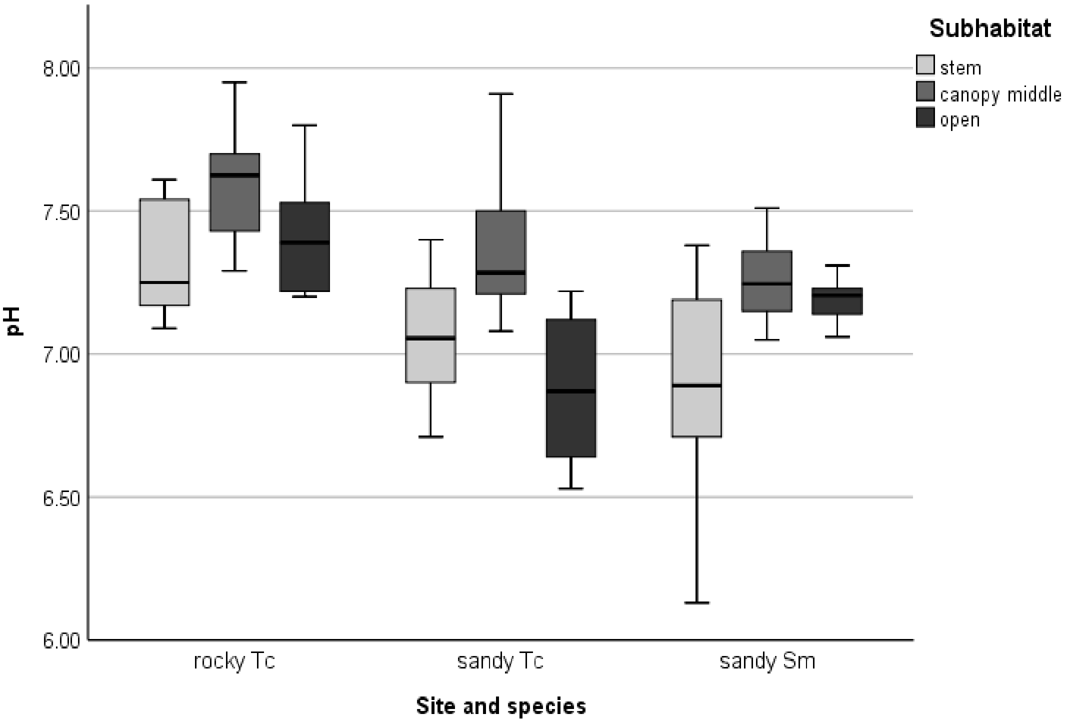

Figure 4.2: Boxplots of pH (H_2O) according to soil type and shrub species for three subhabitats (stem, canopy middle and open grassland). The horizontal lines represent the median; the box spans show the first and third quartile. The whiskers are the non-outlier range. Tc = *T. camphoratus;* Sm = *S. mellifera*

4.4.2 Exchangeable cations

While soil type did not significantly ($p > 0.05$) influence potassium ion concentration in any *T. camphoratus* subhabitat, the calcium ion concentration was significantly higher on the rocky soil compared to the sandy soil in all three subhabitats (stem: $F_{1;18} = 16.472$, $p = 0.001$; canopy middle $F_{1;18} = 16.951$, $p = 0.001$; open: $F_{1;18} = 23.918$, $p < 0.001$). Significant differences in sodium ion concentration ($F_{1;18} = 6.242$, $p = 0.022$), as well as magnesium ion concentration ($F_{1;18} = 6.929$, $p = 0.017$), were established between the stem subhabitats of the rocky and the sandy sites.

Furthermore, subhabitat differentiation had highly significant influences on the potassium ion concentration around *T. camphoratus* on the rocky site ($F_{2;27} = 21.245$, $p < 0.001$) and sandy site ($F_{2;27} = 21.984$, $p < 0.001$), as well as around *S. mellifera* ($F_{2;27} = 14.224$, $p < 0.001$). In both soil types and woody plant species, soil potassium ion concentrations closest to the stem and in the canopy middle were significantly higher ($p < 0.001$) than in the open grassland subhabitat, while no significant differences existed between the two canopied subhabitats (Figure 4.3 a).

Similarly, calcium ion concentration around *T. camphoratus* on the rocky site ($F_{2;27} = 10.561$, $p < 0.001$) and sandy site ($F_{2;27} = 19.015$, $p < 0.001$), as well as around *S. mellifera* ($F_{2;2} = 8.047$, $p = 0.002$) were significantly affected by the different subhabitats. On the rocky site the calcium ion concentration in the soil closest to the *T. camphoratus* stem (mean ± SE = 475.23 ± 27.005) and in the canopy middle (436.17 ± 44.254) were significantly higher ($p < 0.001$ and $p = 0.007$, respectively) than in the open grassland subhabitat (306.81 ± 18.068). On the sandy site, a significant ($p = 0.02$) calcium ion concentration decrease occurred from the stem subhabitat (339.51 ± 20.838) to the canopy middle subhabitat (279.36 ± 12.111) and further decreased significantly ($p = 0.005$) towards the open grassland subhabitat (233.98 ± 17.048). Soil calcium ion concentration in the stem subhabitat around *S. mellifera* were significantly higher ($p = 0.001$) than in the open, but neither of the two subhabitats differed significantly to the canopy middle subhabitat (Figure 4.3 b).

Sodium ion concentrations in the soil were unaffected by subhabitat differentiation around *S. mellifera* and *T. camphoratus* on both sites. The only small but nevertheless significant difference ($p = 0.007$) occurred between the canopy middle (4.723 ± 0.096) and open grassland (4.30 ± 0.078) subhabitats around *T. camphoratus* in the sandy soil (Figure 4.4).

Soil magnesium concentrations also differed non-significantly between the subhabitats around *S. mellifera* ($F_{2;27} = 2.454$, $p = 0.105$) and *T. camphoratus* on the sandy soil ($F_{2;27} = 1.866$, $p = 0.174$). However, around *T. camphoratus* in the rocky soil, magnesium ion concentrations at the stem (95.17 ± 2.876) and the canopy middle (90.31 ± 2.492) were significantly higher ($p < 0.001$) than in the open grassland (71.22 ± 2.57) (Figure 4.5).

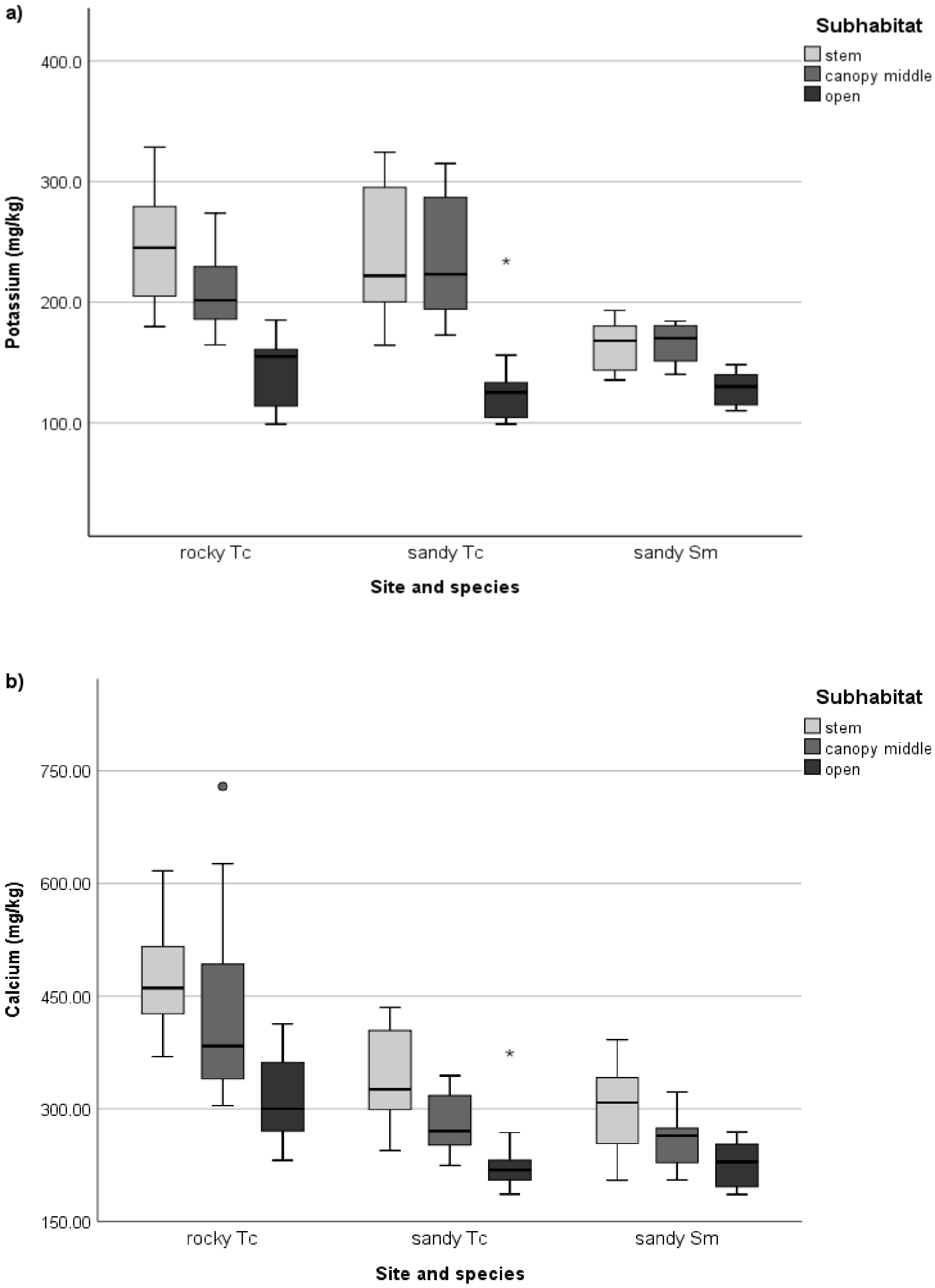

Figure 4.3: Boxplots representing a) potassium ion concentration and b) calcium ion concentration (mg kg^{-1}) according to soil type and shrub species for three subhabitats (stem, canopy middle, and open). The horizontal lines represent the median; the box spans show the first and third quartile. The whiskers are the non-outlier range, whilst dots/stars are outliers. Tc = *T. camphoratus,* Sm = *S. mellifera*

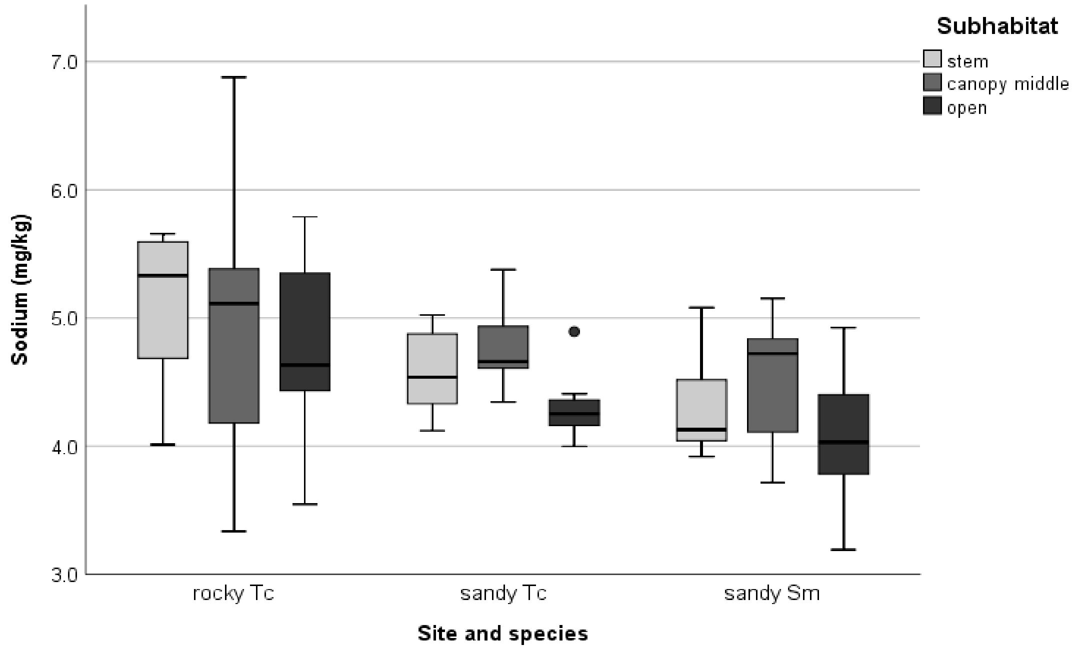

Figure 4.4: Boxplots representing sodium ion concentration (mg kg^{-1}) according to soil type and shrub species for three subhabitats (stem, canopy middle, and open). The horizontal lines represent the median; the box spans show the first and third quartile. The whiskers are the non-outlier range, whilst dots/stars are outliers. Tc = *T. camphoratus,* Sm = *S. mellifera*

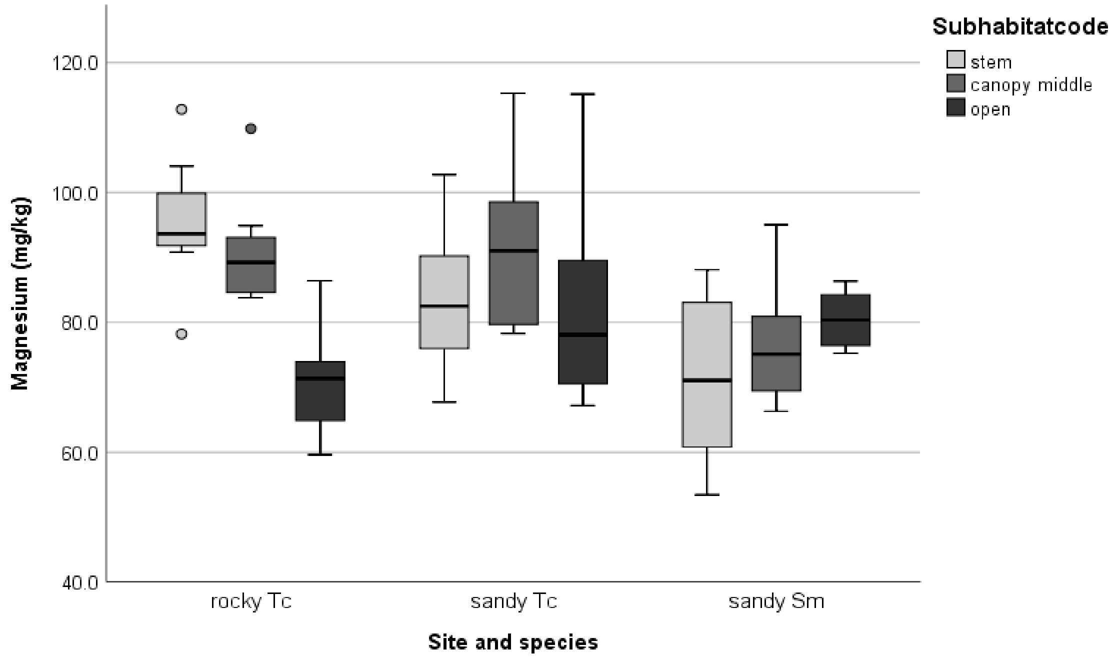

Figure 4.5: Boxplot representing magnesium ion concentration (mg kg^{-1}) according to soil type and shrub species for three subhabitats (stem, canopy middle, and open). The horizontal lines represent the median; the box spans show the first and third quartile. The

whiskers are the non-outlier range, whilst dots/stars are outliers. Tc = *T. camphoratus,* Sm = *S. mellifera*

Moreover, species did not significantly ($p > 0.05$) influence sodium and calcium ion concentrations on the sandy site in any of the three subhabitats. However, potassium ion concentrations at the stem ($F_{1;18} = 18.285$, $p < 0.001$) and canopy middle ($F_{1;18} = 19.620$, $p < 0.001$) were found to differ highly significant for species, with higher values recorded under *T. camphoratus*. Similar, magnesium ion concentrations differed significantly for species, at the stem ($F_{1;18} = 5.365$, $p = 0.033$) and canopy middle ($F_{1.18} = 9.604$, $p = 0.006$). For both, soil potassium and magnesium, no significant differences ($p > 0.05$) between the species could be recorded for the open grassland subhabitat.

4.4.3 Plant-available phosphorus

Plant-available phosphorus differed non-significantly ($p > 0.05$) between the different soil types (rocky soil vs sandy soil) for all three subhabitats around *T. camphoratus.* Significant differences were established between the *T. camphoratus* subhabitats on the sandy soil ($F_{2;27} = 6.395$, $p = 0.005$), with plant-available phosphorous at the stem being significantly higher (7.86 ± 1.203) than in the canopy middle (4.17 ± 0.671) and in the open grassland (3.77 ± 0.699) subhabitat. However, no significant differences were established between the subhabitats of *T. camphoratus* on the rocky soil ($F_{2;27} = 2.013$, $p = 0.153$) and *S. mellifera* ($F_{2;27} = 0.391$, $p = 0.680$). Furthermore, species did not significantly influence plant-available phosphorus in any of the tested soil subhabitats (Figure 4.6).

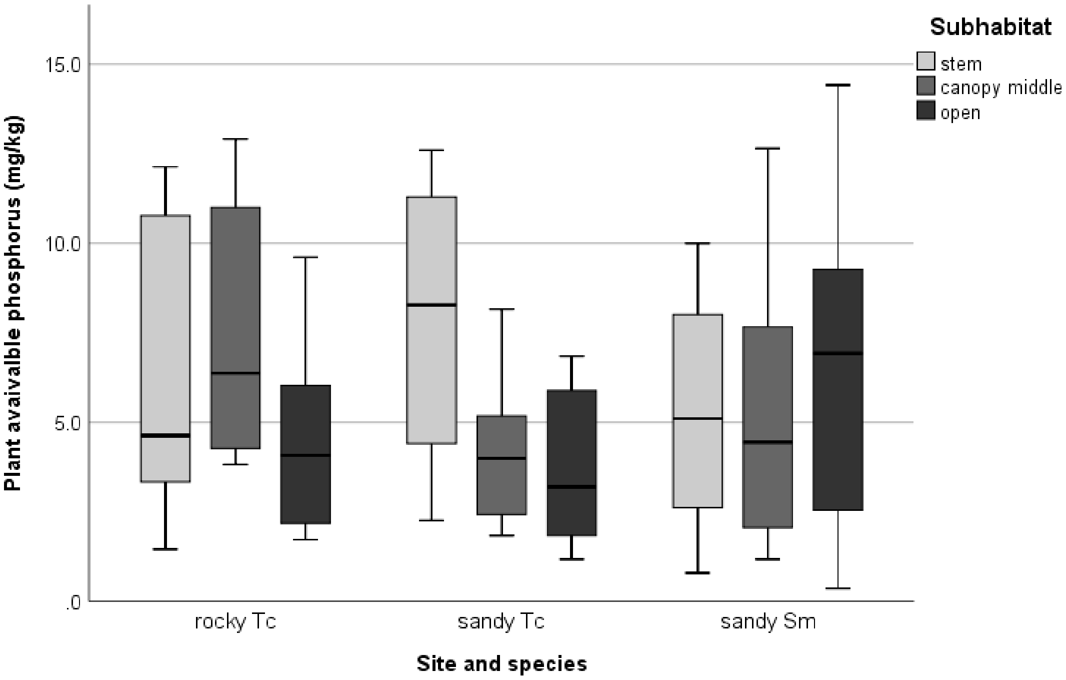

Figure 4.6: Boxplot representing plant-available phosphorus (mg kg^{-1}) according to soil type and shrub species in three subhabitats (stem, canopy middle and open grassland). The

horizontal lines represent the median; the box spans show the first and third quartile. The whiskers are the non-outlier range. Tc = *T. camphoratus;* Sm = *S. mellifera*

4.4.4 Soil nitrogen, organic carbon and carbon : nitrogen ratio

Soil type had a significant influence ($p < 0.05$) on the nitrogen and organic carbon percentages. Significantly higher soil nitrogen percentages were recorded for the stem ($F_{1;18} = 9.184$, $p = 0.007$) and canopy middle subhabitats ($F_{1;18} = 17.249$, $p = 0.001$) of *T. camphoratus* growing in the rocky soil compared to those growing in sandy soil. However, soil nitrogen percentages did not differ significantly between the soil types in the open grassland subhabitat ($F_{1.18} = 2.446$, $p = 0.135$) (Figure 4.7). Organic carbon percentages were significantly higher in the rocky than the sandy soil for all three subhabitats (stem: $F_{1.18} = 13.735$, $p = 0.002$, canopy middle: $F_{1.18} = 45.138$, $p < 0.001$, open: $F_{1.18} = 21.066$, $p < 0.001$) (Figure 4.8). Carbon : nitrogen ratios differed non-significantly ($p > 0.05$) between the soil types for all three subhabitats (Figure 4.9).

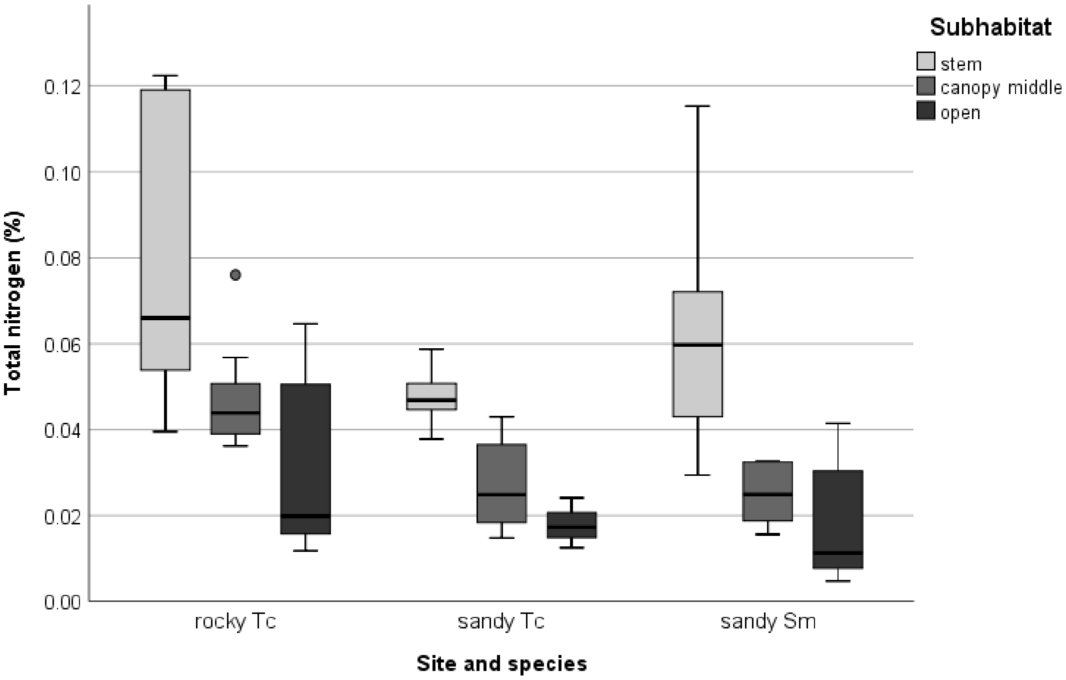

Figure 4.7: Boxplot representing soil nitrogen (%) according to soil type and shrub species in three subhabitats (stem, canopy middle and open grassland). The horizontal lines represent the median; the box spans show the first and third quartile. The whiskers are the non-outlier range, whilst dots/stars are outliers. Tc = *T. camphoratus*; Sm = *S. mellifera*

Soil nitrogen and organic carbon percentage decreased significantly ($p < 0.05$) with increased distance from the stem for both soil types and woody plant species. Soil nitrogen was on average approximately 163% higher in the stem subhabitat of *T. camphoratus* than in the open grassland subhabitat in both, the rocky and the sandy soil and 260% higher in the soil closest to the stem of *S. mellifera* than in the open grassland (Table 4.1). Similarity, soil organic carbon around *T. camphoratus* was found to be 169% and 132% higher around the stem than in the open grassland in the rocky and sandy soil, respectively. For *S. mellifera* the soil organic carbon was 177% higher at the stem than in the open grassland. However, carbon : nitrogen ratios were non-significant between the subhabitats of *T. camphoratus* on both soils (sandy: $F_{2;27} = 2.688$, $p = 0.086$; rocky: $F_{2;27} = 1.258$, $p = 0.3$), but differed significantly between the stem and open grassland subhabitat of *S. mellifera* ($F_{2;27} = 4.866$, $p = 0.016$). In addition, there were no significant differences ($p = 0.05$) between the species, *T. camphoratus* and *S. mellifera* in any of the three subhabitats for soil nitrogen, soil organic carbon or the carbon : nitrogen ratio.

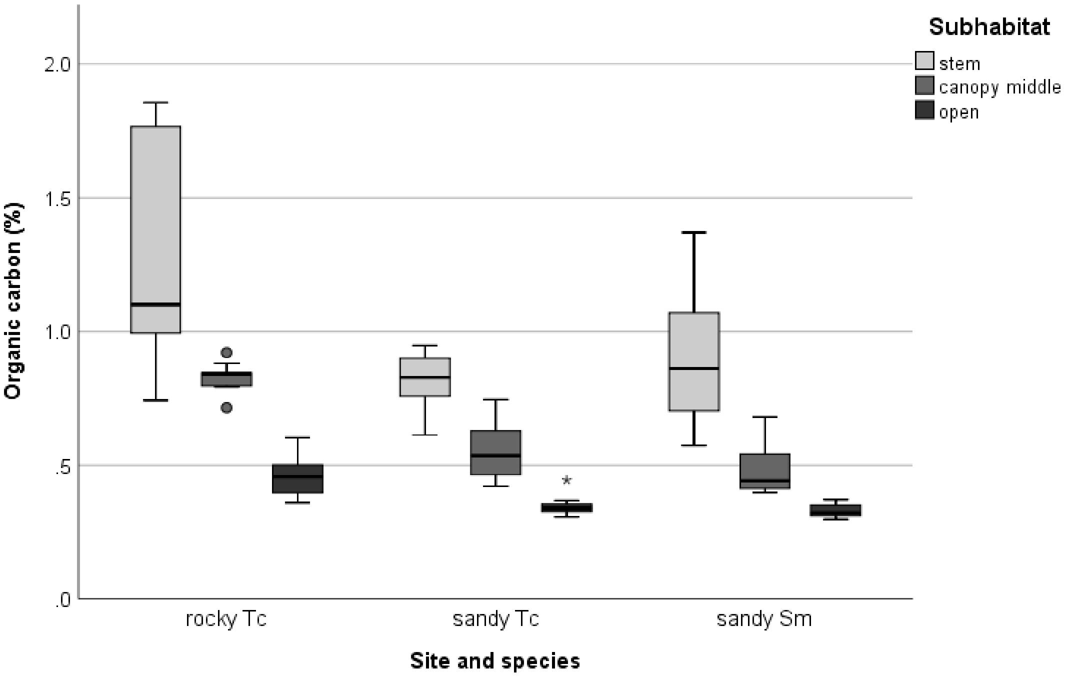

Figure 4.8: Boxplot representing soil organic carbon (%) according to soil type and shrub species in three subhabitats (stem, canopy middle and open grassland). The horizontal lines represent the median; the box spans show the first and third quartile. The whiskers are the non-outlier range, whilst dots/stars are outliers. Tc = *T. camphoratus;* Sm = *S. mellifera*

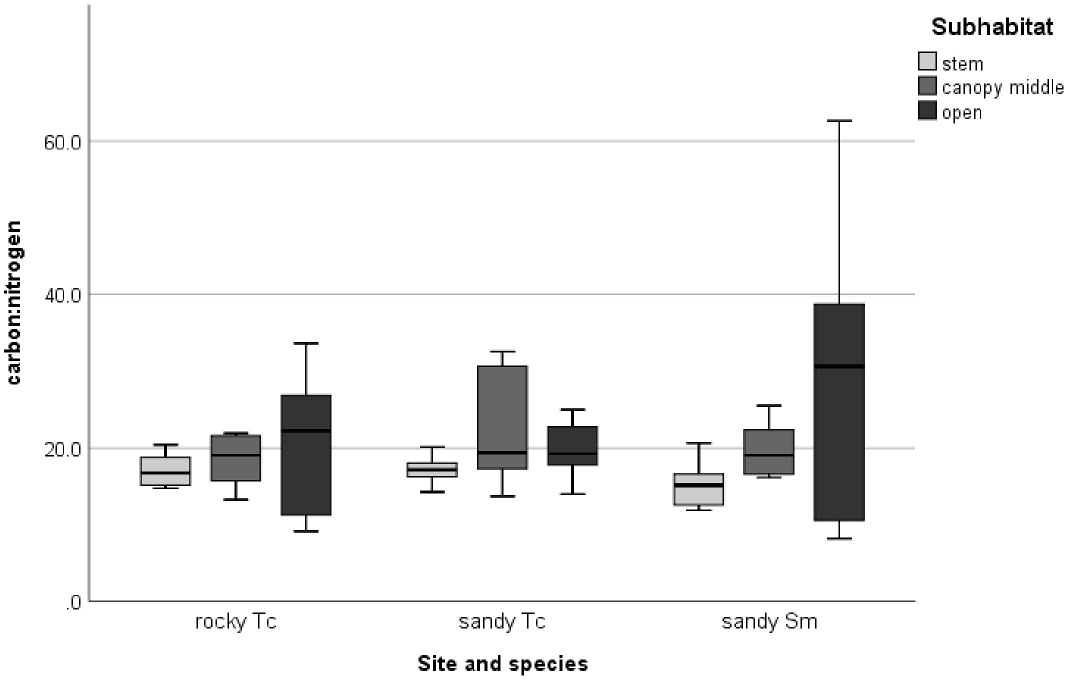

Figure 4.9: Boxplots representing carbon : nitrogen ratio (C;N) according to soil type and shrub species in three subhabitats (stem, canopy middle and open grassland). The horizontal lines represent the median; the box spans show the first and third quartile. The whiskers are the non-outlier range. Tc = *T. camphoratus;* Sm = *S. mellifera*

4.5 Discussion

The soil-nutrient status is partly determined by weathering of the parent material. However, the interaction of chemical and physical processes as well as biological activities, especially organic matter, principally control plant nutrient availability (Scholes 1990; Archibold 1995; Havlin *et al.* 2014), which lead to specific vegetation composition, structure and productivity (Hagos & Smit 2005). Marked differences in soil-nutrient status between the uncanopied subhabitat and the two canopied subhabitats were found for study species, *T. camphoratus* and *S. mellifera,* confirming the development of “nutrient hotspots” under the woody plant canopy (accepting hypothesis A). Despite the consensus with many studies that also demonstrated soil enrichment by woody plants, dissimilarities were established.

4.5.1 Soil pH

As a major determinant of plant nutrient availability, soil pH controls the weathering rate of parent material, the solubility of compounds, quantity of ions stored on the cation exchange sites and microorganism activity in the soil (Bohn *et al.* 2001). In agreement with findings of Hagos and Smit (2005) a lower soil pH in the stem subhabitat of *S. mellifera* compared to the uncanopied subhabitat was found. It did differ, however, from similar studies

Table 4.1: Mean ± SE of all tested soil variables for two soil types (sandy and rocky) and two species (*T. camphoratus* and *S. mellifera)* in three subhabitats

Site	Rocky			Sandy			Sandy		
Species	*T. camphoratus*			*T. camphoratus*			*S. mellifera*		
Subhabitat	stem	canopy middle	open	stem	canopy middle	open	stem	canopy middle	open
pH (H_2O)	7.32 ± 0.06	7.59 ± 0.06	7.41 ± 0.06	7.04 ± 0.07	7.35 ± 0.08	6.88 ± 0.08	6.89 ± 0.11	7.26 ± 0.52	7.20 ± 0.02
K^+ (mg kg^{-1})	244.37 ± 15.19	208.82 ± 9.98	143.47 ± 8.99	239.42 ±17.61	237.97 ± 16.50	132.96 ± 12.424	164.12 ± 6.65	165.86 ± 5.50	129.29 ± 4.68
Ca^{2+} (mg kg^{-1})	475.22 ± 27.01	436.17 ± 44.25	306.80 ±18.07	339.51 ± 20.84	279.36 ± 12.11	233.98 ± 17.048	305.92 ± 19.21	260.48 ± 11.24	226.79 ± 9.04
Mg^{2+} (mg kg^{-1})	95.17 ± 2.88	90.31 ± 2.49	71.22 ± 2.57	83.52 ± 3.37	91.47 ± 3.69	81.28 ± 4.609	71.47 ± 3.97	77.02 ± 2.86	80.55 ± 1.33
Na^+ (mg kg^{-1})	5.10 ± 0.18	4.91 ± 0.33	4.80 ± 0.22	4.58 ± 0.10	4.72 ± 0.10	4.30 ± 0.078	4.26 ± 0.1137	4.52 ± 0.15	4.09 ± 0.16
P (mg kg^{-1})	6.30 ± 1.25	7.53 ± 1.11	4.52 ± 0.79	7.86 ± 1.20	4.17 ± 0.67	3.77 ± 0.699	5.14 ± 0.99	5.08 ± 1.19	6.39 ± 1.35
N (%)	0.08 ± 0.01	0.05 ± 0.00	0.03 ± 0.01	0.05 ± 0.00	0.03 ± 0.00	0.02 ± 0.001	0.06 ± 0.01	0.03 ± 0.00	0.02 ± 0.00
OC (%)	1.29 ± 0.27	0.829 ± 0.02	0.47 ± 0.03	0.81 ± 0.03	0.548 ± 0.00	0.35 ± 0.012	0.91 ± 0.08	0.48 ± 0.03	0.33 ± 0.01
C:N	17.0:1 ± 0.60	18.4 :1 ± 0.98	20.8:1 ± 2.70	17.2:1 ± 0.49	22.0:1 ± 2.21	19.9 ± 1.127	15.5:1 ± 0.93	19.8:1 ± 1.10	30.9:1 ± 6.06

(Smit & Swart 1994; Ward *et al.* 2018) in other savanna areas, which reported a higher soil pH under woody plant canopies compared to uncanopied areas. Yan *et al.* (1996) reported that soil organic matter decomposition increased cation concentrations, which increase base saturation, release ammonium ions and organic anions which all consequently increase soil pH. While all these decomposition processes are recognised by Singh and Gupta (1977) and McCauley *et al.* (2017), they further reported that the formation of humic acid from organic matter breakdown, nitrification of ammonium, as well as nitrate leaching, reduce pH and thus conclude that the net effect on soil pH depends on the rate at which the decomposition processes occur and the fate of the nitrates, as well as the quality and quantity of organic matter. This may in part explain the differences in findings for this study and between other studies. In contrast to the findings of Ward *et al.* (2018), no differences in soil pH could be established between the species, *T. camphoratus* and *S. mellifera*.

4.5.2 Exchangeable cations

The cations, potassium, calcium and magnesium are macronutrients and therefore essential to plant growth and health (Havlin *et al.* 2014). Potassium functions in enzyme activation, water movement control and ATP (energy-carrier) production and is the second most absorbed macronutrient (Havlin *et al.* 2014). Absorbed in lower quantities, calcium and magnesium are considered secondary macronutrients. Calcium is a structural component of plant cell walls and plays a vital role in cell permeability and cation and nitrate uptake, while magnesium is a chlorophyll constituent and structural component of ribosomes (Havlin *et al.* 2014). A study conducted by Ward *et al.* (2018) in the same bioregion, found significantly higher potassium ion concentration and slightly higher magnesium ion concentration under the woody plant canopy than in the uncanopied area, but no differences in calcium concentrations. This study confirms these findings for potassium and for magnesium on the rocky soil only; however, it contradicts the results of calcium. Hagos and Smit (2005), on the other hand, also found significantly higher calcium concentrations under the canopies of *S. mellifera,* as well as a decreasing gradient of potassium, calcium and magnesium ion concentration with distance from the stem.

The significantly ($p < 0.05$) higher calcium concentration in all three subhabitats in the rocky soil is probably linked to the high abundance of calcrete sedimentary rocks (see section 2.2.2) which undergo weathering processes and therewith release calcium, magnesium and iron ions into the soil (King n.d.).

Sodium is not readily leached, not required by most plants, and high concentrations increase the osmotic potential of soil solution, thus making water unavailable to plants (Bohn *et al.* 2001). It is probable therefore that many studies, including this study, report no significant differences in sodium ion concentration between the canopied and uncanopied areas (also refer to Smit & Swart 1994; Hagos & Smit 2005; Ward *et al.* 2018).

Contrasting with Ward *et al.* (2018), this study did not establish significant differences in sodium ion concentration between *T. camphoratus* and *S. mellifera,* but found significant differences between the species in potassium and magnesium ion concentration of the canopied subhabitats. Cation concentration in the uncanopied subhabitats was unaffected by species, which, in view of the horizontal redistribution of nutrients (Dye & Spear 1982; Belsky *et al.* 1993; Ravi *et al.* 2010), suggests that both species utilise cations from the surrounding topsoil in a similar way.

4.5.3 Plant-available phosphorus

Phosphorus is an important constituent of the cell nuclei and is essential for cell division, especially root growth as well as energy transfer and storage. Havlin *et al.* (2014) and Bohn *et al.* (2001) further explain that decomposed organic matter is the major source of plant-available phosphorus. Reports on the influence of woody plants on plant-available phosphorus differ widely. While some studies (Belsky *et al.* 1989; Ludwig *et al.* 2004) reported elevated phosphorus levels under woody plant canopies, others (Smit & Swart 1994; Hagos & Smit 2005; Wiegand *et al.* 2005) reported no effect of woody plants on phosphorus levels. Similar to the findings of Ward *et al.* (2018), both scenarios were found during this study, which were clearly associated with soil type and tree species. Subhabitat differentiation had a significant ($p < 0.05$) influence under *T. camphoratus* on plant-available phosphorus on the sandy site, but there were no significant differences ($p > 0.05$) on the rocky site and under *S. mellifera.* Differences between phosphorus extraction methods used in chemical analyses (White 2019) in connection with different soil types could account for some of the variation between study findings.

4.5.4 Soil nitrogen, organic carbon and carbon : nitrogen ratio

Nitrogen is the most abundantly absorbed macronutrient in plants and is vital for plant growth (Havlin *et al.* 2014). Soil organic carbon is an indicator of soil organic matter (Pribyl 2010), which is important because it is a major plant nutrient source. It also acts as an energy source for soil microbes, increases cation-exchange capacity, buffers soil pH and improves soil structure, water infiltration and water-holding capacity (Bohn *et al.* 2001). In agreement with several other studies conducted on nutrient-poor soils (Smit & Swart 1994; Hagos & Smit 2005; Ward *et al.* 2018), total nitrogen and organic carbon percentages in the soil were significantly higher under the woody plant canopies than in the open grassland and decreased with distance from the stem. The decreasing gradient of nitrogen and organic carbon content away from the main stem can be explained by the effect of a growing canopy, with the soil under the tree canopy closest to the main stem being affected the longest and having additional nutrient supply from stem flow and bark shedding (Belsky *et al.* 1993) (also see section 4.2). This also highlights the importance of large woody plants in the ecosystem, because increasing plant age/size has an increasing positive effect on soil nutrients. Similar to the results of Ward *et al.* (2018), higher total nitrogen and organic carbon concentrations were found in the rocky soil compared to the sandy soil. A possible reason for the decreased nitrogen levels in the sandy soil could be an increased leaching potential of the highly soil-mobile nutrient (Bohn *et al.* 2001) to deeper soil depths on the sandy soil and increased plant densities (see section 2.2.3). Thus, increased leaf litter and decreased wind (as shrubs act as wind breaks) to blow away organic matter could possibly be the reason for increased organic carbon in the rocky soil.

Against expectations (rejecting hypothesis C), total nitrogen percentage did not differ significantly ($p > 0.05$) in the soil under the two species, despite *S. mellifera* being a leguminous woody plant, that is able to fix nitrogen through symbiotic nitrogen fixing *Rhizobium* bacteria on its roots. Similar results were found by Smit and Swart (1994) and Ward *et al.* (2018). It has been suggested that older plants lose their nitrogen-fixing ability (Bernhard-Reversat & Poupon 1980) which thus indicates that age rather than woody plant size played the bigger role. Prevailing conditions in the semi-arid savanna are often outside the tolerance range of nitrogen-fixing *Rhizobium* bacteria (Hartwig 1998). Nitrogen fixation may therefore be limited to younger plants or restricted to times when environmental conditions are more favourable.

The carbon : nitrogen ratio of the soil together with climatic factors is a major determinant for the rate of soil organic matter decomposition. A narrow ratio indicates fast nutrient release, while a wider ratio indicates nutrient immobilisation by soil microorganisms (Manzoni *et al.* 2008; Havlin *et al* . 2014). Even though non-significant ($p > 0.05$), it is notable that soil carbon : nitrogen ratios in the stem subhabitat of both species were lower than those in the open grassland, indicating faster nutrient release in this subhabitat.

4.6 Conclusion

This study confirms that both *T. camphoratus* and *S. mellifera* play important roles in soil enrichment (in line with hypothesis A), regardless of the soil type in which they grow. However, the extent to which each soil nutrient is affected differs. Subhabitat differentiation significantly ($p > 0.05$) influenced soil potassium and calcium concentrations, as well as total nitrogen and organic carbon percentages in 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 in the rocky soil only, while plant-available phosphorus only differed between subhabitats under *T. camphoratus* in sandy soil. Furthermore, soil potassium and magnesium concentrations were the only nutrients which were influenced by species, thus rejecting the hypothesis that leguminous *S. mellifera* would significantly increase nitrogen concentrations, depending on the age of the woody plant. Soil pH, calcium concentration, nitrogen and organic carbon percentage were significantly influenced by soil type, thus partly confirming the hypothesis that soil-nutrient status on the rocky soil will be higher than on the sandy soil.

Even though the results of this study correspond with the results of several similar studies, some differences have been established. This is true, not only for studies on different woody species and soil types, but also for a study by Ward *et al.* (2018), who studied the same species in the same bioregion. It appears that the extent to which woody plants influence soil chemistry is very specific for each nutrient element, soil type and tree species, as well as environmental conditions.

In view of bush clearing or thinning operations, this study clearly demonstrates that *T. camphoratus,* as well as co-occurring *S. mellifera,* positively influence the nutrient status of the nutrient-poor soils they grow in and are thus important biological agents which will ensure higher soil-nutrient status on a landscape level. It is therefore recommended that bush-control operations in areas with densities too high to allow sufficient herbaceous production should follow a selective thinning approach and must therefore retain a proportion of the larger shrubs of both shrub species. In this way, the positive attributes of woody plants, such as soil enrichment, provision of browse and ecosystem stability are maintained (Smit 2004).

CHAPTER 5

Phenology

5.1 Introduction

Global climate change is a suspected factor contributing to bush-thickening in savannas around the world. Plant phenology, defined as the study of the timing of characteristic periodic events, such as leaf-budding, flowering and leaf senescing in the life cycle of plants as influenced by environmental factors such as climate (Trollope *et al.* 1990), may therefore react strongly to the expected temperature rise and rainfall pattern change.

However, environmental factors such as day length (Archibald & Scholes 2007; Sekhwela & Yates 2007; Di Lucchio *et al.* 2018), air temperature and soil moisture availability (Hall-Martin & Fuller 1975; Janecke & Smit 2011) only partially govern plant phenology . Inherent characteristics differing between plant species, plant age, vegetation type (Guy *et al.* 1979; Dekker & Smit 1996; Archibald & Scholes 2007) soil fertility, soil depth and herbivore use (Milton 1987; Makhado *et al.* 2020) also affect the phenology of a woody species. The extent of phenological response to influencing factors is species and individual dependent (Makhado *et al.* 2020).

The importance of plant phenology is often underestimated. Through its response to favourable and unfavourable environmental conditions, phenology studies aid in the prediction of the effects of global warming, biodiversity and natural habitat loss (Pettorelli *et al.* 2005). They further help understand population dynamics of woody plant species and the determine factors hindering recruitment (Joubert *et al.* 2013). In addition, the phenology of woody plants affects browse availability throughout the year (Sekhwela & Yates 2007), which in turn influences the foraging ecology of herbivores (Milton 1987).

The transition from a grass dominant to a woody-plant dominant state is determined by the recruitment and survival success of a woody species (Joubert *et al.* 2008). Understanding the importance of phenology and having good knowledge about factors influencing different phenophases is therefore essential for the effective management of bush-thickening species.

In this study, the phenology of the most dominant woody species on the sandy soil and the rocky soil was characterised in order to identify influencing climate variables and establish the importance of the focus species, *T. camphoratus,* as a possible browse source in a habitat of primarily winter deciduous species. Phases in the growth of *T. camphoratus* which are particularly important to the plant's survival and reproduction success (active growth, flowering and seed development) were also identified. The following hypotheses were tested:

- *a)* Temperature, day length and rainfall are correlated with the phenology (leaf-carriage score, leaf-budding, leaf-yellowing and flowering) of *T. camphoratus, Grewia flava Ziziphus mucronata,* and *S. mellifera.*
- b) The leaf carriage of the woody species differs between plants growing in shallow rocky and deep sandy soil.
- c) Monthly leaf carriage between female and male *T. camphoratus* shrubs differs.
- d) The leaf carriage of *T. camphoratus* varies little throughout the year, while the leaf carriage of *G. flava, Z. mucronata* and *S. mellifera* shows large seasonal variation, having no or only dry leaves during some periods of the year.

5.2 Literature review

5.2.1 The effect of climate change on phenology

Day length, temperature and soil moisture have been identified as major environmental cues affecting plant phenology. Van Rooyen *et al.* (1986) reported that, in *Berchemia zeyheri* and *Olea europaea* subsp. *africana* growth activity only started once a certain ambient temperature was reached together with increased day length, while rainfall only became an influencing factor later in the growing season. Janecke and Smit (2011) as well as Butler (2017) found a strong correlation between minimum temperature and leaf phenology and a moderate correlation between rainfall and leaf phenology of some woody plants in the central Free State, but differences occurred between species. Phenological studies of different species belonging to the family of Asteraceae in Uganda revealed that annual rainfall primarily influenced flowering while seasonal rainfall influenced fruiting (Mbatudde *et al.* 2007). Smit (2001) found that *C. mopane* at lower tree densities retained their leaves longer, flushed earlier and had comparatively younger leaves towards the end of the dry season than trees at higher tree densities. It was hypothesised that this was triggered by decreased competition and thus higher soil moisture availability.

According to Cleland *et al.* (2007), shifts in plant phenology (for example, earlier leaf-budding) in response to changing global climate may have a marked influence on the survival and reproductive success of a species and may therefore determine its presence or absence in the future. For example, Joubert *et al.* (2013) found that pod production of *S. mellifera* in central Namibia was strongly correlated with the rainfall of the preceding season, such that seed production in the season following a low rainfall year was virtually absent. It was also reported that flowers were dropped if temperature extremes or a lack of rain occurred during flowering time (Van Rooyen *et al.* 1986). Furthermore, early flushing species such as *Vachellia karroo* and *Diospyros lycioides* (Janecke & Smit 2011) were at risk of dropping their first flush due to delayed spring rains or late frost occurrences. Even though re-flushing does occur, it is at great energy expense, which could be detrimental in the long term (Archibald & Scholes 2007; Cleland *et al.* 2007). Milton (1987) found that reproductive plant parts are more sensitive to environmental change than vegetative plant parts. As a result, timing of the reproductive phase is critical for optimal seed production (Cleland *et al.* 2007). Prolonged fodder shortages due to droughts or delayed leaf emergence due to late rainfall may strongly influence the survival and reproduction rates of animals (Sekhwela & Yates 2007).

On the other hand, increased temperature and fewer frost occurrences prolong the growing season with earlier leaf-flushing and later leaf fall. Evidently, climate changes primarily affect the timing of different phenophases (Sekhwela & Yates 2007) and alter ecosystem processes such as carbon and water uptake as well as fodder supply (Archibald & Scholes 2007; Cleland *et al.* 2007). This has ecological and economic consequences because structure, function and regeneration of the plant communities as well as quality and quantity browse are affected (Williams *et al.* 1999).

5.2.2 Phenology and the availability of browse

The seasonal variation in phenology of especially winter-deciduous woody plants is responsible for the notable variation in available browse throughout the year, consequently, altering food preferences, habitat selection and the distribution of browsing herbivores (Hall-Martin & Fuller 1975; Milton 1987; Owen-Smith & Cooper 1988; Dekker & Smit 1996; Styles & Skinner 1997; Sekhwela & Yates 2007; Janecke & Smit 2011; Butler 2017; Makhado *et al.* 2020). Fodder availability for browsers is especially limited towards the end of the dry season, after leaf senescence until leaf-flushing and varies between geographical locations. In the central Free State, this critical period was identified as July/August to mid-October (Janecke & Smit 2011), while Smit (2001) noted that, in the Mopani veld of the Northern Province, high rates of kudu mortality were observed between September and October, before the start of the rainy season. In the Sengwa Wildlife Research area of Zimbabwe, browse was most limited between October and November (Guy *et al.* 1979).

The value of a woody species as browse fluctuates with season according to its phenology, which results in availability and palatability changes. During critical periods, browsers are often forced to feed on less palatable and lower quality feed. Thus species including evergreen woody plants, dry forbs and succulents, less preferred during the wet season become increasingly important (Milton 1987; Owen-Smith & Cooper 1988). For example, Butler (2017) found that, while kudu primarily browsed on deciduous woody plants after leaf-flushing had occurred, evergreen woody plants of the study area were highly preferred during the dry period. Furthermore, Styles and Skinner (1997) reported from a study conducted in the Northern Tuli Game Reserve of Botswana that the chemical composition and palatability of *C. mopane* leaves varied with the season and the corresponding phenophase. They found that young *C. mopane* leaves were most nutritious and decreased in nutritional value with increasing age. However, these very young leaves were also the most unpalatable due to the presence of highly condensed tannins and the palatability of especially mature leaves changed throughout the year.

As mentioned by Smit (2001) and Abule *et al.* (2007), the quantity of browse available at peak biomass is probably less important than the consistency of browse throughout the year. This highlighted the importance of less palatable woody species such as *C. mopane,* with longer leaf carriage periods relative to other woody species in the area (Dekker & Smit 1996).

5.3 Procedure

5.3.1 Trial layout and phenology scoring

On each of the two soil types, deep sandy and shallow rocky, twenty *T. camphoratus* shrubs of different height classes and ages were randomly selected and permanently marked (a total of 40 shrubs). In order to investigate the importance of *T. camphoratus* in providing browse during the dry period of the year in an environment of primarily deciduous vegetation, a further ten shrubs each of *Grewia flava* and *Ziziphus mucronata* were marked on each soil type (a total of 20 shrubs per species). Due to their high abundance on the sandy soil, ten S*enegalia mellifera* were also marked. The GPS coordinates for each shrub were logged. In the week of the 20th day of each month, starting in March 2018 and continuing until February 2020, the phenological leaf carriage for each marked shrub was subjectively scored. Scoring was done as follows: 0 = no leaves, 1 = 1 – 15% of full leaf carriage, 2 = 16 – 40% of full leaf carriage, 3 = 41 – 70% of full leaf carriage, 4 = 71 – 90% of full leaf carriage, and 5 = 91 – 100% of full leaf carriage, where full leaf carriage is considered the maximum abundance of leaves that a tree/shrub can carry. This score was further subdivided into a proportional estimate of leaves in each of the following phenophases: BL = budding leaves, IL = immature leaves, ML = mature leaves, YL = yellowing leaves and DL = dry senescing leaves retained on the shrub. Therefore, a score of 4 might consist of 3 ML and 1 YL. This method was in accordance with Dekker and Smit (1996), Smit (2001), as well as Janecke and Smit (2011).

In addition, the presence of flowers and fruits, as well as the stage in which the majority of them occurred, was recorded. Five flowering stages and three fruiting stages were identified, namely, latent flowers, early flowering, full flowering, late flowering and dry flowers retained on the shrub, as well as unripe, ripe and dropping/dry fruits.

5.3.2 Statistical analyses

For each species, monthly median values were calculated for each phenophase, flowering and fruiting stage. This was done due to the non-parametric nature of the data. The phenophase median values were subsequently summed to calculate the monthly leaf-carriage score ranging between zero (no leaves) and five (about 100% leaf carriage) for each species.

A correlation analysis between leaf-carriage scores of all focal plants over the 24-month period and various climate variables was done per species using Spearman's correlation analysis**.** Correlations involving budding and yellowing leaves were performed using Pearson's correlation coefficients. Climate variables were calculated from hourly data collected at the mobile weather station located at the Rooipoort Nature Reserve homestead (see section 2.1.3). It must be noted that, due to technical issues with the mobile weather station resulting in missing weather data, hourly data collected by Weather SA at the Kimberley Airport were used for the following dates: 25 September 2018 11:00 AM to 25 October 2018 6:00 PM and 13 November 2018 00:00 AM to 22 November 2018 08:00 PM. The following climate variables were calculated using daily average, maximum and minimum temperatures: the average, maximum and minimum temperature as well as the average maximum and average minimum temperatures of the 7, 14 and 28 days preceding the monthly observation date. The same calculations were repeated, however, with a 3-, 7-, 10- and 14-day delay before the monthly observation date. Similarly, the average, maximum and minimum day lengths were calculated for the 7, 14 and 28 days preceding the observation date and repeated for the same delay periods. Rainfall was summed for 7, 14 and 28 days, 6 and 9 months preceding the observation date and was also delayed with 3, 7, 10 and 14 days before the observation date. To avoid excessive skewness, all rainfall variables were square root transformed. Only the variable with the highest correlation was reported for each temperature, day length and rainfall.

In order to test whether soil type (site) has an influence on the phenology, monthly leaf-carriage scores of *T. camphoratus, G. flava* and *Z. mucronata* on the sandy and rocky sites were compared to each other using the non-parametric Mann-Whitney U test (i.e. *T. camphoratus*-sandy vs. *T. camphoratus*-rocky).

Lastly, monthly leaf-carriage scores of *T. camphoratus* were compared to each *S. mellifera, G. flava* and *Z. mucronata*. Comparisons were also performed using the Mann-Whitney U test, in order to identify the importance of *T. camphoratus* as a potential fodder source during critical periods. Differences in leaf-carriage patterns between female and male *T. camphoratus* were also tested using the Mann-Whitney U test. All analyses were performed with IBM SPSS Statistics for Windows, version 25 (IBM Corp., Armonk 2017).

5.4 Results

5.4.1 Climate and Phenology

Correlation analyses, testing the phenological response of the four most dominant species in the study area to various climatic variables with delay periods has shown the relationship between climate variables and phenology was species-specific.

Monthly leaf carriage of *T. camphoratus* had a moderate negative correlation with maximum temperature of the week prior to observation ($r = -0.597$, $p < 0.001$) and minimum day-length of the week prior to observation ($r = -0.571$, $p < 0.001$). Furthermore, the sum of rainfall of the six months prior to observation was very strongly correlated ($r = 0.800$, $p < 0.001$) with the leaf carriage of *T. camphoratus.* Leaf-flushing in *T. camphoratus* was moderately correlated with the minimum temperature of the four weeks prior to observation, with a 14-day delay ($r = 0.460$, $p< 0.001$) and sum of rainfall of the four weeks prior to observation ($r = 0.604$, $p < 0.001$), but very weakly correlated with the four-week minimum day length with 14 days' delay ($r = 0.243$, $p < 0.001$). The proportion of dry leaves on *T. camphoratus* was moderately negatively correlated with the four-week minimum temperature with 14 days' delay ($r = -0.627$, $p < 0.001$) and four-week sum of rainfall with seven days' delay ($r = -0.653$, $p < 0.001$), but only weakly correlated with the four-week minimum day length with 14 days' delay ($r = -0.372$, $p < 0.001$). *T. camphoratus* flowering was very weakly correlated with two-week sum of rainfall with ten days' delay ($r = 0.232$, $p < 0.001$) and correlations with temperature and day length were negligible ($r < 0.2$).

Monthly leaf-carriage scores of *G. flava, Z. mucronata* and *S. mellifera* were best correlated with the same climate variables, which are presented in Table 5.1. Minimum temperature of the four weeks prior to observation with a 14 days' delay was moderately correlated with monthly leaf carriage of *G. flava* and *Z. mucronata* and strongly correlated with *S. mellifera* leaf carriage. While minimum day length of the four weeks prior to observation with 14 days' delay was weakly correlated with leaf carriage of *G. flava* and *Z. mucronata,* a moderate correlation existed with *S. mellifera.* Furthermore, sum of rainfall of four weeks prior to observation with ten days' delay had a very strong positive correlation with the leaf carriage of all three deciduous species (Table 5.1).

However, leaf-flushing was moderately positively correlated with maximum temperature of two weeks prior to observation with 14 days' delay ($r = 0.699$, $p < 0.001$) in *G. flava* and strongly correlated with maximum temperature of the week prior to observation with 14 days' delay for *Z. mucronata* and *S. mellifera* (*Z. mucronata:* r = 0.751, p < 0.001 and *S. mellifera*: r = 0.794, p < 0.001). Minimum day length of four weeks prior to observation with 14 days' delay had the highest correlation with budding leaves of *G. flava* (r = 0.760, p < 0.001) and *Z. mucronata* (r = 0.798, p < 0.001), but for *S. mellifera* minimum day length of four weeks prior observation with seven days' delay (r = 0.841, p < 0.001) had the highest correlation. Sum of rainfall of the previous nine months (rainfall of the preceding season) had a strong negative correlation with budding leaves of *G. flava* (r = -0.742, p < 0.001), *Z. mucronata* (r = -0.769, p < 0.001) and *S. mellifera* (r = -0.793, p < 0.001).

Table 5.1: Summary of the best correlations between monthly leaf-carriage scores of *G. flava, Z. mucronata* and *S. mellifera* species and climate variables for 24 months from March 2018 to February 2020

	Minimum temperature of 4 weeks prior to observation with 14-day delay	Minimum day length of 4 weeks prior to observation with 14-days delay	Sum of rainfall of 4 weeks prior to observation with 10 days delay
G. flava	r = 0.698	r = 0.333	**r = 0.803**
	p < 0.001	p < 0.001	p < 0.001
Z. mucronata	r = 0.660	r = 0.275	**r = 0.770**
	p < 0.001	p < 0.001	p < 0.001
S. mellifera	r = 0.811	r = 0.496	**r = 0.868**
	p < 0.001	p < 0.001	p < 0.001

Highly significant (p < 0.001) moderate negative correlations existed between yellowing leaves and maximum temperature, as well as day length of the week prior to observation in *G. flava* (temperature: r = -0.501 and day length: r = -0.502) and *S. mellifera* (temperature: r = -0.619, day length: r = -0.585). Yellowing leaves in *Z. mucronata* had a strong negative correlation with both, maximum temperature of the week prior to observation with 14 days' delay (r = -0.756, p < 0.001) and maximum day length of four weeks prior to observation with seven days' delay (r = -0.745, p < 0.001). Correlations between yellowing leaves and rainfall were negligible for *G. flava* and *S. mellifera* (r < 0.3*)* but were moderate with sum of rainfall of two weeks with a seven-day delay. In addition, the relationship between flowering and the tested climatic variables was negligible (r < 0.2) for *G. flava, Z. mucronata* and *S. mellifera.*

5.4.2 Phenology of the four species

The woody species were classified into two main categories: (1) semi-deciduous, species which lost > 50% of its leaves, but seldom all leaves during the dry season, and (2) deciduous species which lost all leaves during the dry season and remained leafless for at least one month. *T. camphoratus* was classified a semi-deciduous while *G. flava, Z. mucronata* and *S. mellifera* were classified as deciduous.

a) *Tarchonanthus camphoratus*

During most of the study period there were budding and immature leaves present on *T. camphoratus* (Figure 5.1). From September to November 2019, following a below-average rainfall season, existing budding leaves died off, resulting in no living budding and immature leaves during these months. The active growth period of *T. camphoratus* occurred between December and May/June, because budding leaves seemed to be dormant the rest of the year. The first leaves were shed in July 2018 and June 2019 and continued until November of each year (Figure 5.2).

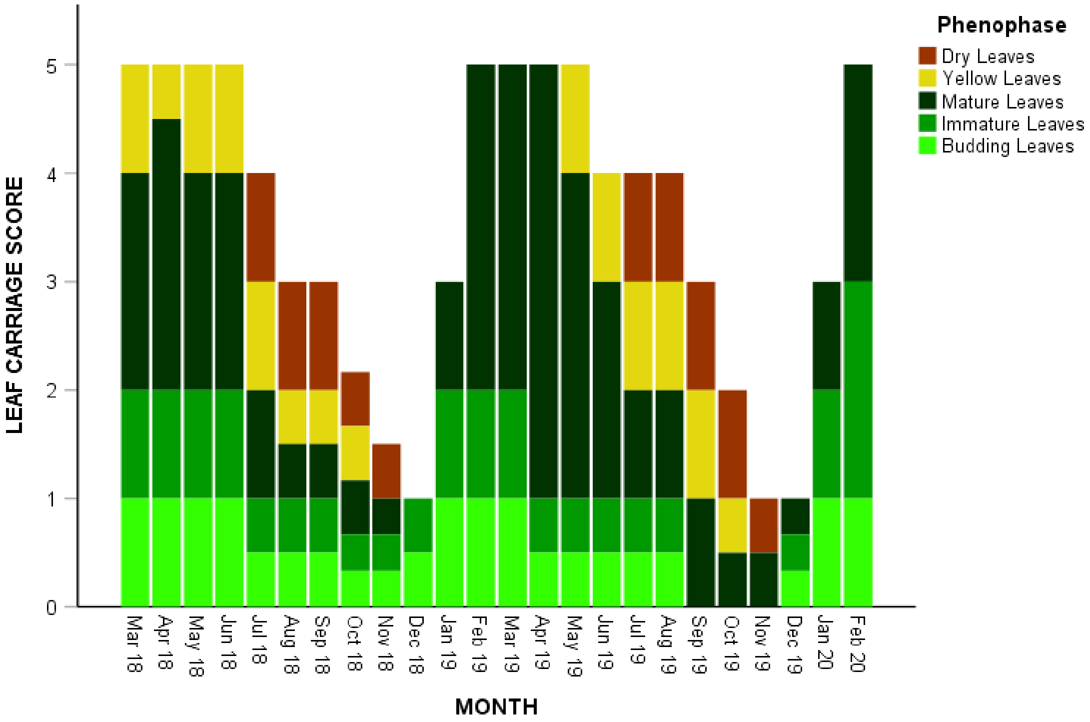

Figure 5.1: Leaf phenology of all *Tarchonanthus camphoratus* combined from March 2018 to February 2020 (n = 40)

Soil type significantly influenced the leaf-carriage score of all woody species, but this was often limited to a few months only. From August 2018 to December 2018, the leaf carriage of *T. camphoratus* growing in the rocky soil was significantly less ($p < 0.05$) compared to the leaf carriage of *T. camphoratus* growing in the sandy soil. However, in October 2019 and January 2020, the leaf-carriage score of *T. camphoratus* growing in the sandy soil (Figure 5.3 a) was significantly less ($p < 0.05$) compared to *T. camphoratus* growing in the rocky soil (Figure 5.3 b).

Sex also influenced leaf phenology of *T. camphoratus.* Male *T. camphoratus* had a significantly higher ($p < 0.05$) leaf-carriage score compared to female *T. camphoratus* from August to October 2018, and also in January 2019 and August 2019.

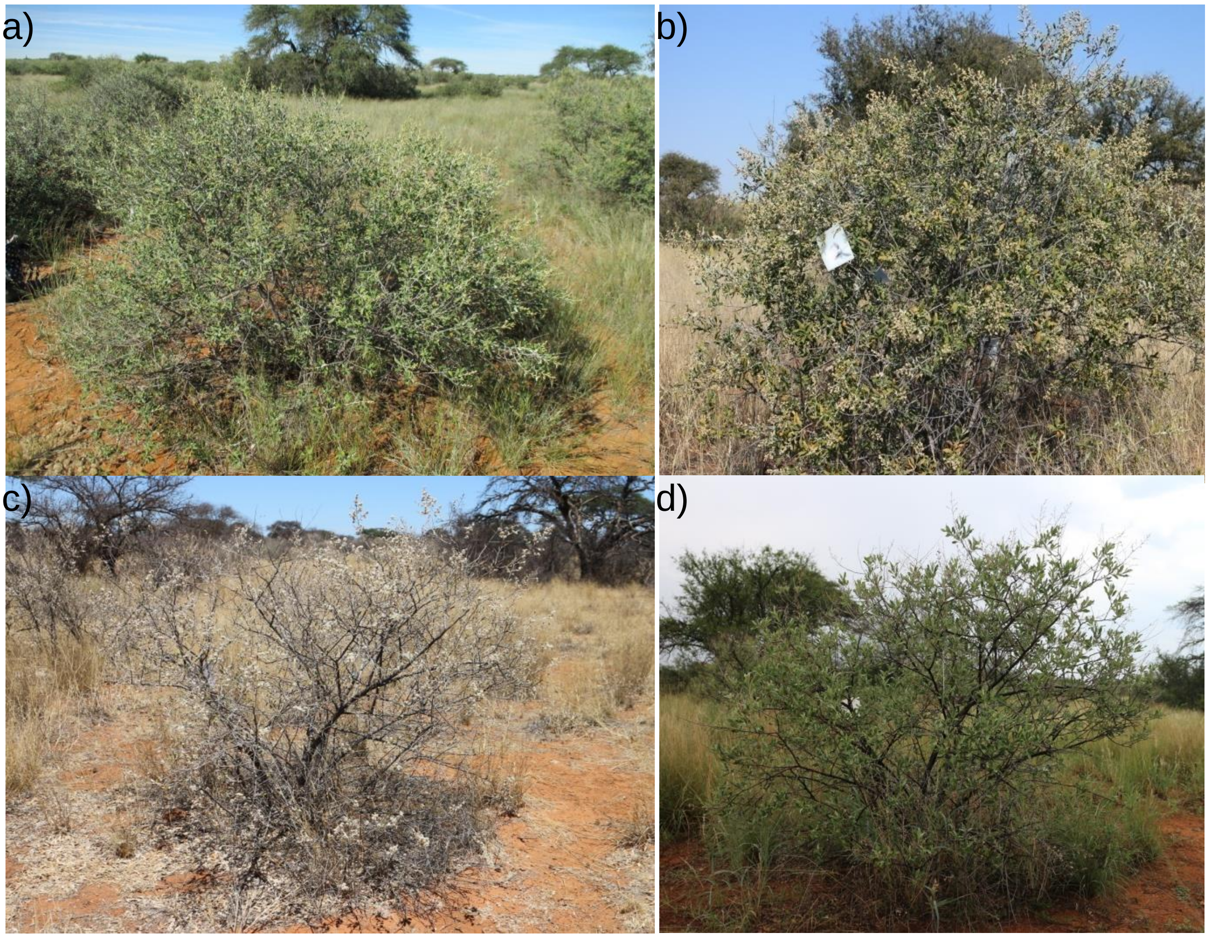

Figure 5.2: The leaf phenology of the same female *T. camphoratus* shrub in a) April 2018, b) July 2018, c) November 2019 and d) February 2020 (Photos: IJ Stehn)

Moreover, the monthly leaf carriage of *Z. mucronata, S. mellifera* and *G. flava* differed significantly ($p < 0.05$) from the monthly leaf carriage of *T. camphoratus.* Compared to *G. flava, T. camphoratus* had a significantly higher ($p < 0.05$) leaf carriage score from May to November each year, but in January the leaf-carriage score of *G. flava* was significantly higher ($p < 0.05$) than the leaf-carriage score of *T. camphoratus.* Similarly, compared to *S. mellifera* the leaf-carriage score of *T. camphoratus* was significantly higher ($p < 0.05$) from May to November 2018 and 2019 and significantly lower ($p < 0.05$) from December to February in the 2018/2019 and 2019/2020 season. *Z. mucronata* had significantly less ($p < 0.05$) leaves in May, June and August to October 2018, as well as in May and July to November 2019, but significantly more ($p < 0.05$) leaves from December to February in 2018/2019 and 2019/2020 compared to *T. camphoratus.*

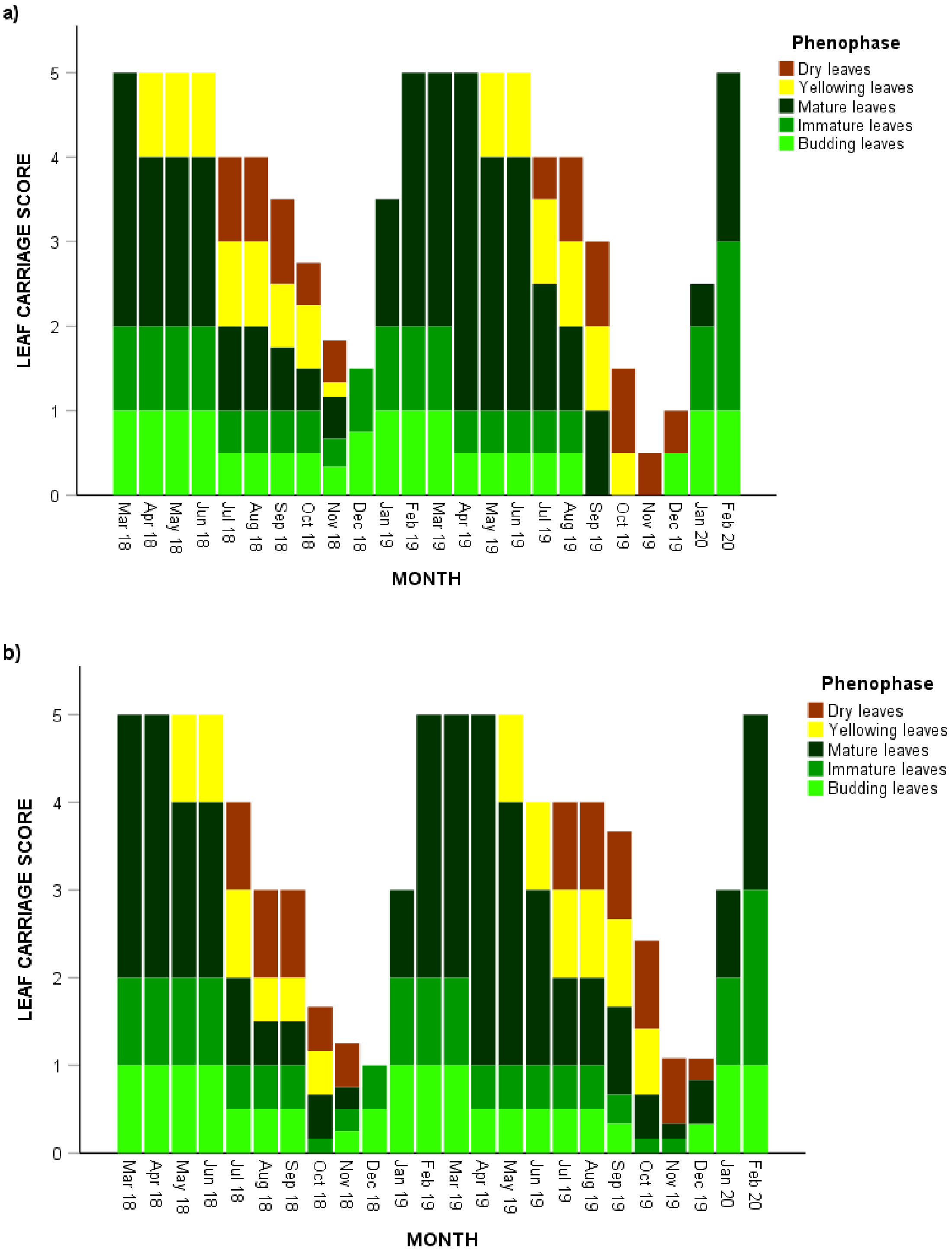

Figure 5.3: Leaf phenology of *Tarchonanthus camphoratus* growing in a) sandy soil and b) rocky soil from March 2018 to February 2020 (n = 20)

In March each year the first latent flowers appeared on *T. camphoratus* shrubs. *T. camphoratus* was in full flower between April and May each year, after which fruit development and ripening occurred on female shrubs until fruit shedding occurred from the end of August to November. Dry flowers were retained on male shrubs until they broke off or disintegrated, often until January of the next season. Die back of large parts or the entire reproductive shoot occurred after pollination in male plants and after fruit maturation in female shrubs.

b) *Grewia flava*

The first leaf buds of *G. flava* appeared in October 2018 and two months later the following year, December 2019. The active growing season started in October 2018 until March 2019 but was expected to be much shorter the following season, as it only started in December 2019. Leaf senescence started in May each year (Figure 5.4). From July onwards only dry leaves were retained on the shrubs but, while most shrubs were completely leafless for only one month in 2018 (September), the majority of *G. flava* were leafless for two months in 2019 (October and November). Furthermore, in 2018, *G. flava* growing in the rocky soil took two months longer (to start flushing leaves compared to *G. flava* growing in the sandy soil. The leaf-carriage score of *G. flava* growing in the sandy soil (Figure 5.5 a) was significantly higher ($p < 0.05$) in January 2019 and 2020 compared to the leaf-carriage score of *G. flava* growing in the rocky soil (Figure 5.5 b).

G. flava flowered between November/December and February. More flowers were produced during the 2018/2019 season compared to the 2019/2020 season. Fruits were present from February/March and were occasionally retained as dry fruits on the shrub until the new season's fruits appeared.

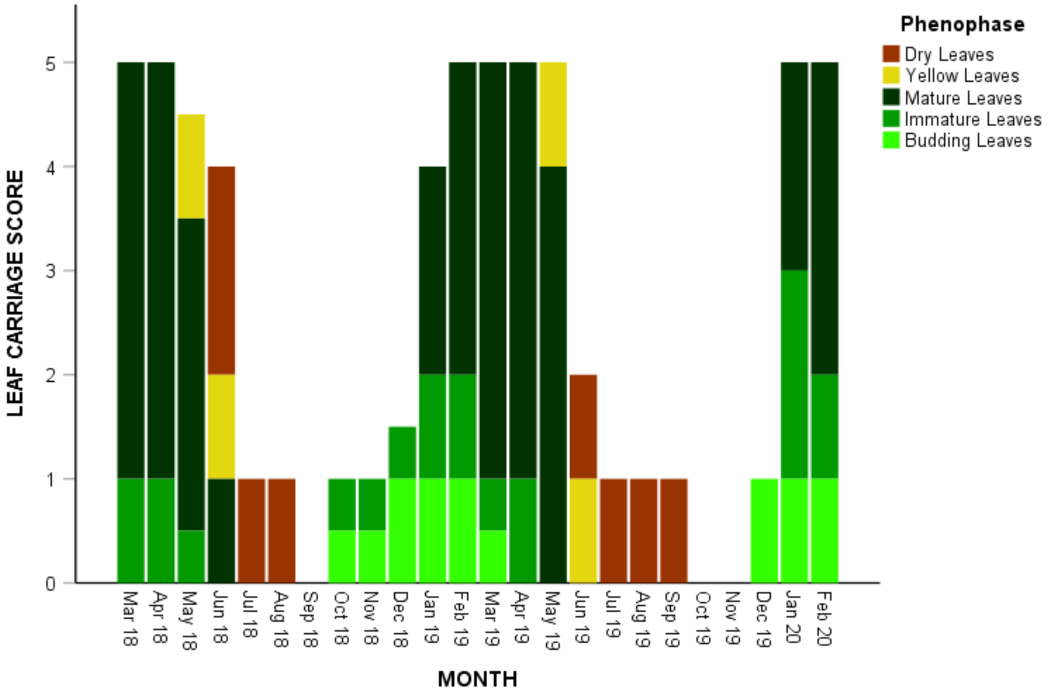

Figure 5.4: Leaf phenology of all *Grewia flava* from March 2018 to February 2020 (n = 20)

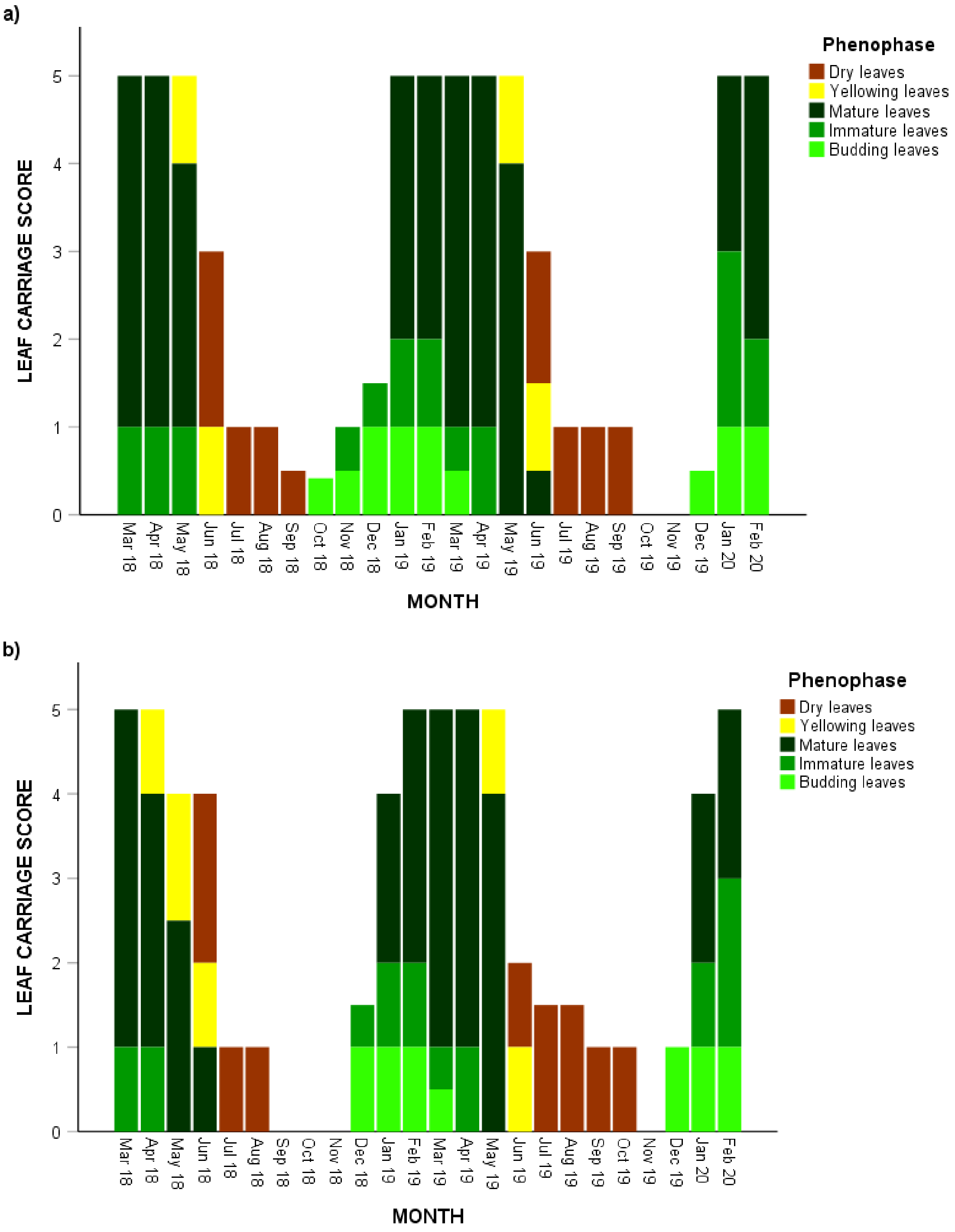

Figure 5.5: Leaf phenology of *Grewia flava* growing in the a) sandy and b) rocky soil from March 2018 to February 2020 (n = 10)

c) *Ziziphus mucronata*

The first leaf buds appeared during October 2018 and one month later during the second study season, in November 2019. The active growth season of *Z. mucronata* stretched from October 2018 to March 2019 and from November 2019, continuing through February 2020.

Full leaf carriage occurred in January during both seasons and leaf fall commenced in June. *Z. mucronata* was leafless during one month only in both study seasons, September 2018 and October 2019 (Figure 5.6).

Similar to *G. flava*, soil type also influenced the leaf-carriage score of *Z. mucronata* significantly. The leaf-carriage score of *Z. mucronata* growing in the sandy soil was significantly higher ($p < 0.05$) in November and December 2018, as well as December 2019 (Figure 5.7 a) compared to the leaf carriage score of *Z. mucronata* growing in the rocky soil (Figure 5.7 b). In 2019, the majority of *Z. mucronata* growing in the rocky soil retained their leaves one month longer, until October 2019, and started flushing leaves one month later, in December 2019, compared to *Z. mucronata* growing in the sandy soil.

Flowering in *Z. mucronata* took place between November 2018 and February 2019 but started only in December in 2019. Fruit production and ripening followed flowering and continued until July and dry fruits were often retained on the tree far into the next season.

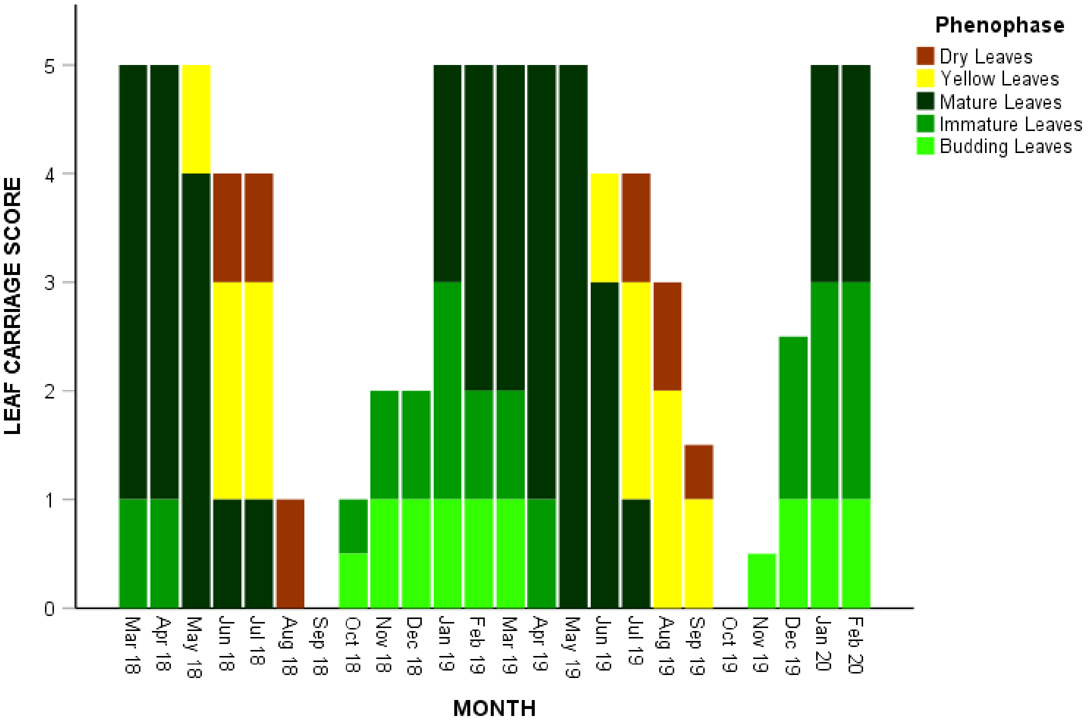

Figure 5.6: Leaf phenology of all *Ziziphus mucronata* from March 2018 to February 2020 (n = 20)

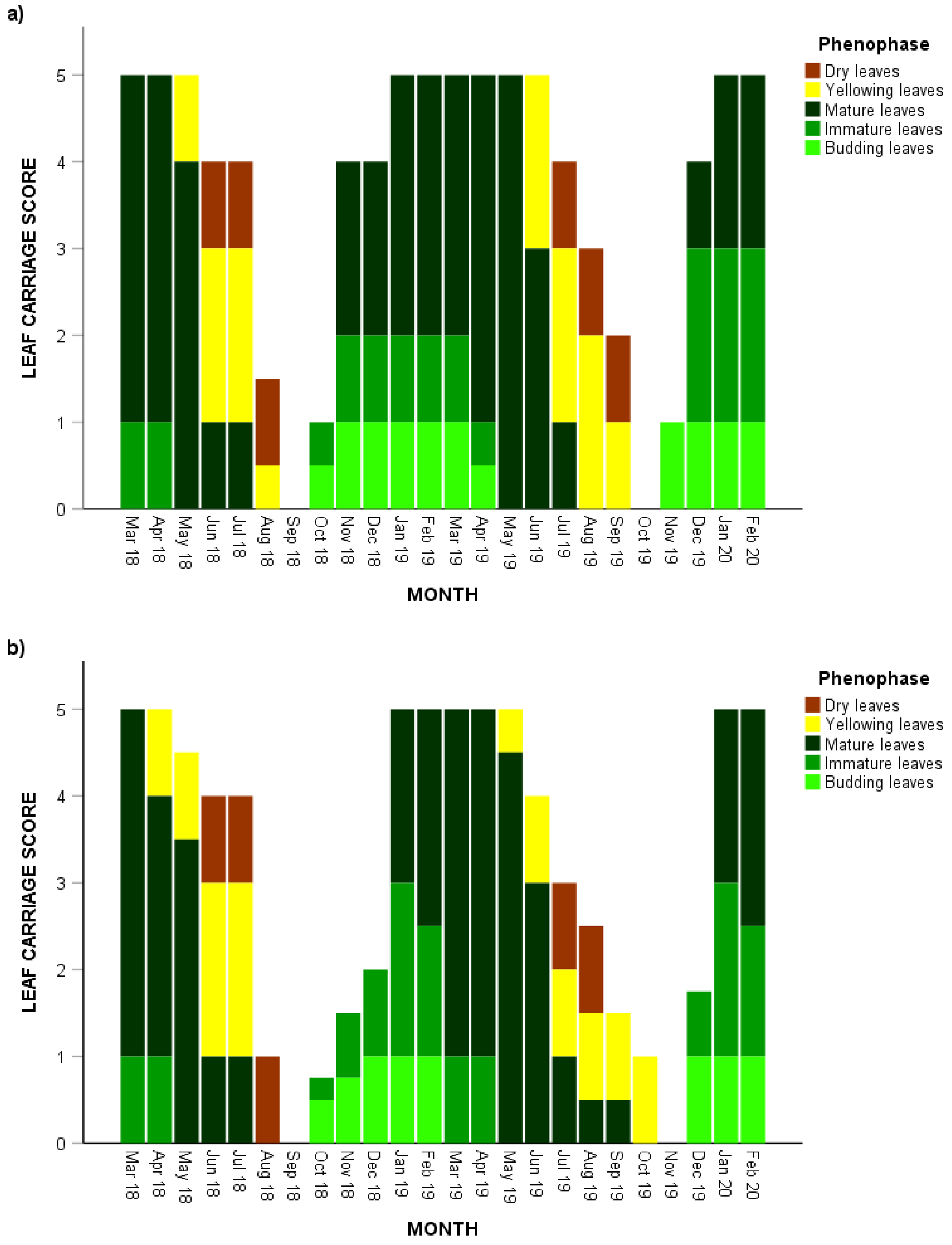

Figure 5.7: Leaf phenology of *Ziziphus mucronata* growing in the a) sandy soil and b) rocky soil (n = 10)

d) *Senegalia mellifera*

The first leaf buds of *S. mellifera* appeared in October 2018 and only one month later during the second study season, November 2019. Full leaf carriage only occurred from January in both seasons. The active growth season of *S. mellifera* occurred between

October/November and April. Leaves started to turn yellow in May during 2018 and 2019 and leaf fall commenced one month later, during June. In 2018, few dry leaves were retained on the shrubs when leaf-flushing started, and most *S. mellifera* were never completely leafless during that season. However, in 2019 *S. mellifera* was leafless for one month (October 2019) before leaf-flushing started (Figure 5.8).

S. mellifera flowered during September in 2018 and 2019, and fruit maturation occurred during October and November. By December all pods were dropped. In 2018, only 50% of the focal *S. mellifera* shrubs flowered but those that flowered produced many pods. In contrast, in 2019 all shrubs flowered but only 40% produced very few pods (< 10 pods per shrub).

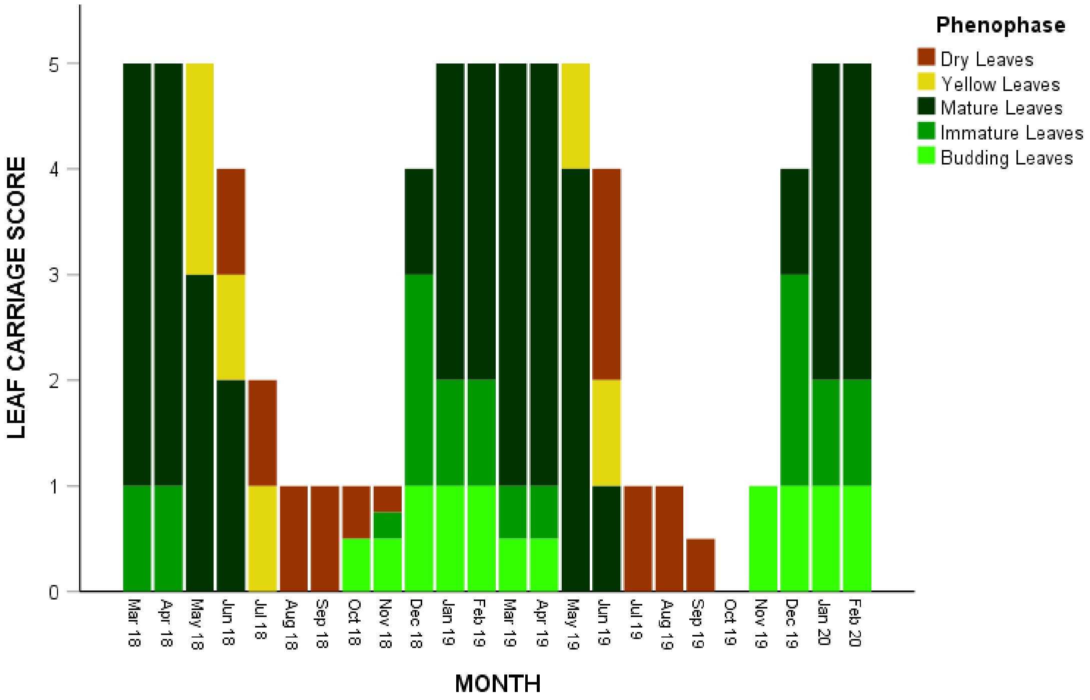

Figure 5.8: Leaf phenology of *Senegalia mellifera* from March 2018 to February 2020 on the sandy soil

5.5 Discussion

Plants in arid and semi-arid ecosystems tend to have a lagged response to changes in environmental conditions. Delayed response to precipitation may result from slow water infiltration to roots, increased time required by roots to become physiologically reactivated after long dry periods and time required for the acclimatisation of leaf physiology to environmental change (photoperiod, temperature and water availability) (Ogle & Reynolds 2004; Wu *et al.* 2015). For this reason, climate variables with delay periods proved to be useful in finding correlations with leaf-carriage score.

Temperature, day length and rainfall variables, which were best correlated with the overall leaf-carriage score, differed from the variables best correlated with the specific phenophases, leaf-flushing and leaf senescence. Different climatic variables triggering different growth phases has previously been reported (Cleland *et al.* 2007; Sekhwela & Yates 2007) and is possibly a result of a differential response of the woody plant in different growth stages (phenophases). Also differences in time frames (one to four weeks) and delay periods (no delay, 3, 7, 10 or 14 days) of climate variables between the species indicate that each species has its unique threshold temperature, day length or soil moisture requirement triggering endogenous activity.

In agreement with other phenology studies (Guy *et al.*1979; Milton 1987; Janecke & Smit 2011; Butler 2017) the response to climate variables is a species-specific trait. Similar to the observation made by Butler (2017), budding *T. camphoratus* leaves were present throughout the year (except during extreme drought), but they seemed to remain dormant from May until the start of the next active growing season in male and female plants. Development of these dormant budding *T. camphoratus* leaves only commenced after the first meaningful spring rains. The importance of soil water availability for leaf production in the plant family Asteraceae was demonstrated by Mbatudde *et al.* (2007) and was also highlighted by the moderate correlation of budding leaves with four-week sum of rainfall and very strong correlation of leaf carriage with sum of rainfall for six months. Taking into consideration the high dependence of *T. camphoratus* on soil water, and phenological observations of *T. camphoratus* conducted during normal and above-average rainfall years (Butler 2017), it would seem more sensible to classify *T. camphoratus* as a drought-deciduous shrub. Even though further research would be necessary to confirm this, leaves were probably only shed once soil water became limited and the extent of leaf shedding was probably dependent on the extent of water stress. This drought-avoidance strategy (Chaves *et al.* 2002; Ilyas *et al.* 2020) probably explains why *T. camphoratus* is often classified as an evergreen woody plant species in high rainfall areas and adds to the success of the species in a semi-arid environment.

The relationship between day length and leaf carriage of *G. flava, Z. mucronata* and *S. mellifera* was only weak to moderate. However, strong to very strong positive correlations existed between leaf carriage of *G. flava, Z. mucronata* and *S. mellifera* and minimum temperature and sum of rainfall of four weeks. Leaf-flushing in all three deciduous species occurred before the first meaningful rainfall (> 10 mm) of the season and had strong positive correlations with maximum temperature, day length and rainfall of the previous season (sum of nine-month rainfall). Below-average rainfall for the second season in a row during 2018/2019 may have resulted in the one- to two-month delayed leaf-flushing observed in all three deciduous species during 2019. It is therefore suggested that the ability to flush leaves in *G. flava, Z. mucronata* and *S. mellifera* is primarily dependent on the soil moisture availability at the end of winter, but if sufficient soil moisture is present, day length and temperature thresholds need to be exceeded before leaf-flushing can commence. Similar observations were made by Van Rooyen *et al.* (1986) who reported that, rainfall only influenced phenology after temperature and photoperiod threshold levels were reached. Furthermore, weaker correlations with rainfall and stronger correlations with temperature and day length indicate that leaf senescence of the deciduous species was primarily triggered by decreasing maximum temperatures and day length.

While *S. mellifera* flowered before leaf flush and fruit maturation were completed before the peak of the rainy season, *G. flava* and *Z. mucronata* flowered shortly after leaf flush and fruit maturation took place during the peak of the rainy season. In contrast, *T. camphoratus* flowered only after full leaf carriage was obtained, which coincided with the end of the wet season and early dry season and fruit maturation took place during the dry season in winter. Similar to observations by Hall-Martin and Fuller (1975), fruit maturation took longer compared to flowering in all four woody species. While no strong correlations between flowering and any climate variable could be identified, which could be ascribed to the non-sensitive non-parametric data collection method, Joubert *et al.* (2013) found that flowering and pod production of *S. mellifera* were strongly related to the rainfall of the previous season. Mbatudde *et al.* (2007) reported that flowering in the Asteraceae was dependent on annual rainfall.

The strong link between climate and phenology therefore confirmed hypothesis A. However, in line with hypothesis B, exogenous factors other than climate, such as soil type and soil depth also played a significant role. *T. camphoratus* on the sandy soil retained more leaves for longer in the dry season compared to *T. camphoratus* growing in the rocky soil. This could be attributed to higher water availability to shrubs in the sandy soil as a result of lower woody plant density reducing competition for soil water (Smit 2001), as well as greater soil depth which can be exploited by *T. camphoratus* roots (Casper & Jackson 1997). *G. flava* and *Z. mucronata* growing in the sandy soil often flushed slightly earlier compared to shrubs growing in the rocky soil. Thus shrubs growing in the sandy soil obtained higher leaf carriage earlier compared to shrubs growing in the rocky soil. A possible explanation is that threshold values triggering leaf flush were reached in both soil types at the same time. However, factors limiting growth rate, such as water and nutrient availability (Rugemalila *et al.* 2017), result in slower leaf production in shrubs on the rocky soil compared to the sandy soil.

Confirming hypothesis C, sex influenced leaf carriage of *T. camphoratus,* with female shrubs shedding more leaves between August and October and producing new leaves slower compared to male shrubs. Female shrubs invest more resources into reproduction compared to male shrubs (Amorim *et al.* 2011), resulting in a higher susceptibility to environmental stress factors, such as water-stress, and slower recovery in terms of leaf production in female shrubs compared to male shrubs (Espírito-Santo *et al.* 2003).

Leaf carriage was not constant throughout the year and varied considerably between species, seasons and years. Consistent with hypothesis D, all four species had significantly fewer leaves during the dry season compared to the wet season. In contrast to *G. flava, S. mellifera* and *Z. mucronata,* which were either leafless or retained only a few dry leaves at the end of winter and early spring*, T. camphoratus* maintained a significantly higher leaf carriage with significant amounts of mature green leaves. Janecke and Smit (2011) considered browse scarcity during the dry season as one of the most serious limitations for browsers in fenced areas. Even though *T. camphoratus* is considered rather unpalatable to browsers (Palgrave 2002), low availability of browse from palatable deciduous species during the dry period forced browsers and mixed feeders to feed on the less palatable semi-deciduous and evergreen species (Owen-Smith & Cooper 1988; Butler 2017). Therefore, *T. camphoratus* seemed to play a key role in terms of browse provision during the dry season in the study area, with very low abundance of other evergreen woody species. During November and December when the leaf carriage of *T. camphoratus* was at its lowest, deciduous woody species had already flushed. The critical period in terms of browse availability was, therefore, August to October and may be prolonged into November during drought years. This was in accordance with Janecke and Smit (2011), who reported that browse availability was most limned from August to middle October.

5.6 Conclusion

From this study, it was clear that climatic variables (temperature, day length and rainfall / soil moisture), soil type and sex influence leaf phenology. While a woody plant's response to some climatic variables is immediate (without delay), the response to other variables occurs with lag (delay). Furthermore, the best correlation with climatic variables varied by species as well as phenophase, suggesting species-specific threshold levels. Soil moisture was identified as the primary factor influencing the commencement of the active growth period in male and female *T. camphoratus*, while increasing temperatures and day length in combination with sufficient soil moisture triggered leaf-flushing in *S. mellifera, G. flava* and *Z. mucronata.* Leaf senescence was triggered by decreasing temperatures and day length. Leaf-carriage patterns differed between species and years.

In general, woody species growing in the sandy soil flushed slightly earlier and gained higher leaf carriage faster compared to woody species growing in the rocky soil. In *T. camphoratus,* male shrubs retained a higher leaf percentage in spring and early summer compared to female shrubs and produced higher quantities of leaves faster compared to female shrubs.

The winter-deciduous nature of three of the four most dominant woody plant species in the area (*S. mellifera, G. flava* and *Z. mucronata*) may result in a deficit of palatable browse between August and October/November. Thus, less palatable but drought-deciduous species such as *T. camphoratus* become an important fodder source to browsers and mixed feeders during the dry season and periods of drought. Where game is confined, it is therefore crucial that browser stocking rates are adapted to browse availability during the dry season or sufficient feed needs to be supplemented.

CHAPTER 6

Shoot growth and coppicing ability of *Tarchonanthus camphoratus*

6.1 Introduction

Woody plants form an integral component of savanna ecosystems (Ludwig *et al*. 2004). Human activities and environmental shifts have manifested imbalances in the woody and herbaceous plant proportion throughout savannas worldwide, threatening their productivity, stability and functioning (Turpie *et al.* 2019). Woody plants contribute towards soil enrichment (see chapter 4), habitat creation, herbaceous plant growth facilitation and fodder provision. The livelihood of many people is also dependent on woody plants as they use a wide range of woody plant species for fuelwood, charcoal production, construction timber, fencing and wood craft (Smit 2004).

Vegetation degradation, in the form of either deforestation (woody plant clearing) or bush-thickening, is a major problem concerning woody plants facing communal and commercial farmers in the southern African savanna (Strohbach 2001; Birch *et al*. 2016) and threatening the sustainability of their businesses. Understanding woody plant ecology in terms of their vegetative and reproductive growth is crucial for its conservation and effective management.

A key characteristic to the resilience and productivity of savannas is the ability of woody plants to regenerate quickly after disturbance by fire, browsing or cutting (Shackleton 2001; Smit 2003; Scogings *et al.* 2013). Depending on the management objectives and woody plant use, this attribute is either advantageous or disadvantageous. In cases where woody plants are harvested for fuelwood, charcoal production or as fodder, fast regrowth is indispensable for sustainable production and can even increase production if managed correctly, as coppicing is faster than growing new plants from seeds (Luoga *et al.* 2004). However, where woody plants are removed to increase gracing capacity, coppicing is undesirable.

By quantifying the shoot growth of healthy and mechanically cut *T. camphoratus* shrubs and investigating the periodicity of shoot elongation, as well as their response to mechanical cutting in different seasons, the aim of this study was to facilitate management decisions either in bush control programmes or sustainable woody product production. The following hypotheses were tested:

a) *T. camphoratus* shoot growth is correlated with environmental conditions such as temperature, day length and rainfall.
b) Shoot growth rates of male and female *T. camphoratus* shrubs differ.

c) *T. camphoratus* growing in deep sandy soil will have higher shoot growth rates than shrubs growing in shallow rocky soil.
d) Shrubs subjected to mechanical cutting during winter (dormant season) will coppice less vigorously compared to shrubs cut during summer (active growing season).
e) Coppice plants growing in the sandy soil will coppice more vigorously than coppice plants growing in rocky soil.

6.2 Literature review

6.2.3 Shoot growth

Changes in shoot mass are the most sensitive indicator of shoot growth, as this includes not only changes in shoot length and diameter but also changes in density (Rutherford & Panagos 1982). Closely coupled to phenology, the initiation, cessation and rate of shoot growth of undamaged and coppice plants is driven by the interaction of several factors. These factors include soil water availability (Rutherford & Panagos 1982; Milton 1988; Smit 2003), soil nutrients (Scholes 1990; Kaschula *et al.* 2005), temperature, day length (Rutherford & Panagos 1982; Van Rooyen *et al.* 1986; Milton 1987; Sekhwela & Yates 2007), browser damage or pruning (Milton 1988; Scogings *et al.* 2012; Moyo *et al.* 2015), plant species (Milton 1987; Kaschula *et al.* 2005), competition for growth resources (Smit 2001; Kiruki & Njung'e 2006), available carbohydrate reserves (Rutherford & Panagos 1982; Choeni & Sebata 2014), atmospheric carbon dioxide concentration (Kgope *et al.* 2010; Bond & Midgley 2012) and plant size/age (Luoga *et al.* 2004; Kaschula *et al.* 2005; Konstantinidis *et al.* 2006; Melesse & Zewotir 2020).

Shoot growth rates fluctuate throughout the season and the lifetime of woody plants. Milton (1987) has found that shoot elongation for *V. tortilis* was most rapid in the first two months of the growing season and the termination of shoot growth coincided with leaf fall. Similarly, Rutherford and Panagos (1982) found that shoot growth of *Ochna puchra* and *Burkea africana* started once the rate of temperature increases had reached a minimum threshold and corresponded to the previous season's rainfall. Furthermore, Schutz *et al.* (2009) found that, while photosynthesis in *V. karroo* coppices continued into the dry season, shoot growth was limited to a few months of the rainy season. Smit (2001) found that maximum shoot growth of *C. mopane* in the Northern Province of South Africa occurred between November and December. From a study conducted in Kenya, it was established that the maximum growth rate of *T. camphoratus* coppices occurred five to eight years after cutting (Kennedy 1998).

According to Scogings *et al.* (2012), elephant browsing on *Sclerocarya birrea caffra* had resulted in significantly longer and leafier shoots. In agreement with Milton (1988), who found that pruned *V. tortilis* produced more and leafier shoots than unpruned plants, Moyo *et al.* (2015) also reported increased shoot production of browsed *Terminalia sericea* coppice plants. However, all three authors agree that increased shoot production due to defoliation is only temporary and will diminish over time, if frequent defoliation continued and may in extreme cases lead to plant mortality as a result of depleted carbohydrate reserves.

Semi-arid savannas are water-limited ecosystems and thus soil water availability determines much of its productivity (Scholes 1990). Milton (1988), similar to Rutherford and Panagos (1982), found a positive correlation between rainfall and shoot production. In a study conducted in the Kruger National Park, Case *et al.* (2019) found that severe droughts (severe water stress) have resulted in declined growth rates of *D. cinerea* and *C. apiculatum* up to two years post-drought.

Inter-tree competition for growth resources, such as water and nutrients, plays an important role in determining shoot growth. *C. mopane* shoot growth in terms of length was significantly higher in plots of low tree-density compared to plots of high tree-density and, while no net growth after shoot die-back in the dry season was recorded for the high tree-density plots, positive net growth was recorded for low tree-density plots (Smit 2001). Kiruki and Njung'e (2006) reported from a study conducted in Kenya that reduced inter-tree competition may have resulted in the observed increased number of *T. camphoratus* stems per unit area in the plots with fewer trees.

In addition, young *Senegalia nigrescens* and *C. apiculatum* continued growing longer in the dry season compared to older mature plants (Novellie 1989). Research studying 673 046 trees belonging to 403 tree species worldwide, has shown that mass growth rates continuously increase with tree size and age for most trees. However, growth in terms of height decreased as trees reached their biological potential (maturity), and productivity, as well as growth efficiency (tree mass growth per unit of leaf mass) declined with increasing tree size and age (Stephenson *et al.* 2014).

6.2.2 Coppicing ability

Woody plants are often cut down or burnt in an attempt to manage bush-thickening, increase available browse at lower browsing heights or for the direct use of wood products (Smit 2003a). If these woody plants are not treated with arboricides, they regenerate rapidly, however, with varying coppicing vigour.

A key factor enabling woody plants to survive and recover rapidly and frequently after extreme defoliation is their ability to mobilise carbohydrates stored in their roots to support growth and respiration (Schutz *et al.* 2009). Allocation of growth reserves differs. Species are either quantity-driven (produce a large number of shoots), quality-driven (produce few large shoots) or intermediate (Kaschula *et al.* 2005; Choeni & Sebata 2014). Schutz *et al.* (2009) and Wigley *et al.* (2009) claimed that, while the root starch of coppicing *V. karroo* is drastically lowered initially, carbohydrate reserves are replenished within one to three years post-damage. Repeated defoliation can further delay replenishment (Schutz *et al.* 2011).

The availability of carbohydrate reserves in interaction with other factors, such as soil moisture availability (Milton 1988) and the plant's phenological state (Milton 1987), further explain variability in the coppicing ability of woody plants in response to the season in which a disturbance factor is applied (Luoga *et al.* 2004; Schutz *et al.* 2011). Top-killing or cutting woody plants, when their carbohydrate reserves are low, results in reduced coppicing vigour. Strohbach (1998) found that fire girdling in Namibia is most effective (i.e. highest mortality and lowest coppicing) during the active growing season of woody plants (January – April), because leaf-flushing and growth deplete carbohydrate reserves. Similarly, Milton (1988) found that pruning during summer yielded significantly less shoots than pruning during winter. However, Konstantinidis *et al.* (2006) argued that prevailing environmental conditions following defoliation were more important in determining coppicing ability than the physiological condition of the plant at the time of defoliation.

Coppicing ability is a species-specific trait. Smit (2003) reported from a study conducted in the Limpopo Province, that five growing seasons after cutting treatment was applied, leaf dry matter production of *C. apiculatum* was on average 875 g tree^{-1} compared to the 668 g tree^{-1} average leaf dry mass production of *S. erubescens*. Furthermore, Choeni and Sebata (2014) found that, five months after terminal shoots were cut, *V. karroo* grew 15 resprouts compared to only four resprouts grown on *Vachellia arenaria.* Kaschula *et al.* (2005) found that while *D. cinerea* produced a large number of smaller coppice shoots, *Combretum collinum* produced a small number of large coppice shoots. In addition, Shackleton (2000) found that the number of shoots per unit of stump area was ten times more for *Albizla harveyii* than *Plfiastigma thanningii* and concluded that there was an inverse relationship between potential height and number of shoots per stump area. The effect of plant size on coppicing ability was also reported by Konstantinidis *et al.* (2006), who found that the size of *Arbutus unedo* before a fire significantly affected the height and diameter of the coppice, especially two growing seasons later. In a study conducted on *V. karroo* in KwaZulu-Natal, Schutz *et al.* (2009) found a significant correlation between plant height before a fire and post-fire shoot production.

Cutting height is another factor determining the number as well as growth of coppice shoots. Up to a certain threshold, increased cutting height results in an increased number of shoots (Shackleton 2001). Smit (2003) reported that cutting height significantly affected the coppice height of *S. erubescens* but not *C. apiculatum* and leaf dry matter production five years post-cutting was also not affected significantly by cutting height. Increased cutting height increased shoot production in *D. cinerea, C. collinum* and *A. harveyi* (Kaschula *et al.* 2005). Witkowski and Garner (2008) found that cutting *Solanum mauritianum* below 18 cm from the soil surface resulted in 100% mortality, but guaranteed coppicing at cutting heights above 50 cm.

Similar to cutting height, an increased stump basal area may positively influence shoot production in some species. While in *D. cinerea* the number as well as the mean size of shoots increased with increased stump diameter, in *C. collinum* and *A. harveyi* only shoot numbers increased with increased stump diameter (Kaschula *et al.* 2005).

Other potential factors influencing coppicing ability include the percentage of stand removed (Smit 2003; Luoga *et al.* 2004), root:shoot ratio of coppice plants (Shackleton 2001) disturbance factor (fire, cutting or browsing), and harvesting technique, as well as soil and climate variables (Luoga *et al.* 2004; Kaschula, *et al.* 2005; Konstantinidis *et al.* 2006).

Therefore, the landowner's management objectives determine whether vigorous coppicing is desirable or not and which characteristics are to be exploited. In addition to reaching the goal of a sustainable and stable ecosystem, ecological and economic implications need to be considered.

6.3 Procedure

6.3.1 Shoot growth

Four healthy shoots were randomly selected on each of the 40 permanently marked *T. camphoratus* shrubs (see section 5.3.1) and permanently marked (a total of 160 shoots). Care was taken that these focal shoots all originated from different main stems and were distributed more or less evenly around the canopy in the top as well as the bottom parts of the canopy. In the third week of each month for a period of 24 months (April 2018 – March 2020), the length and base diameter of all focal shoots were measured. The shoots were measured in sections following the pathway, starting at the lowest end of the main focal shoot up to the apical bud of the upper most daughter shoot. A section was characterised by a relatively straight part of the shoot up to the upper most point of clear directional change, often at a bud scar, from where the next section was started. The number of daughter shoots branching off the measured shoot pathway was also counted. A similar method was used by Rutherford and Panagos (1982) and Smit (2001). Due to significant amounts of focal shoots, especially reproductive shoots, dying back each dry season and occasional browse and wind damage, a few new focal shoots had to be selected occasionally in order to replace the lost shoots. This was done to ensure continued data collection and the avoidance of missing/incomplete growth data.

6.3.2 Coppicing ability

Twenty healthy *T. camphoratus* shrubs of approximately the same size (± 1.5 m height) were randomly selected and permanently marked on each of the two soil types (a total of 40 shrubs). Similar sized shrubs were selected in order to limit possible variance which may occur due to difference in plant age (Smit 2003a). The canopy volume of all shrubs was measured according to the procedures of the BECVOL 3 – model (Smit 2014), after which ten shrubs on each soil type were felled at approximately 5 cm above the ground in late summer (March) and a further ten shrubs on each soil type in winter (June). According to Smith and Goodman (1986), as well as Smit (2001), the growth rate of the individual plant is dependent on the total canopy biomass in its surrounding; thus competition from surrounding shrubs may influence the coppicing ability. In an effort to limit this effect, relatively isolated shrubs were chosen, but leaving surrounding shrubs uncut, as would be the case in selective thinning practices. Immediately after felling, the base diameter of each stem was measured and used to calculate the total stem base area of each shrub.

Following felling, the total number of regrowing shoots on each coppice plant was counted once a month, in the third week of each month for a period of 24 months (summer treatment: April 2018 – March 2020; winter treatment: July 2018 – June 2020). In addition, five shoots, each originating from a different stump, were permanently marked on each coppice plant. The height and base diameter of each focal shoot were subsequently measured each month for a period of 24 months (Little & Gardner 2003).

Occasional browsing of regrowth by herbivores and insects was evident throughout the year, however, this occurred more frequently in the dry season from August to December. Due to significant browsing damage to coppices during September 2019, enclosures with 10 x 10 cm welded mesh (Figure 6.1) were put up around all coppice plants in October 2019 to prevent further damage.

Additional shrubs were felled on both soil types and allowed to coppice. Throughout the 24-month period their spatial canopy volume was measured and coppice plants were harvested for the development of regression equations relating the spatial canopy volume to the leaf and wood dry mass to fit the BECVOL 3 - model for *T. camphoratus* coppice (see chapter 9 for full procedures). At the end of the 24-month period, the canopy volume of each coppice plant in the late summer and winter treatment was determined according to the BECVOL 3 - model procedures, such that leaf and wood dry mass estimations could be calculated using the regression equations with the highest coefficient of determination developed from the harvested plants (see chapter 9).

Figure 6.1: Welded mesh enclosures put up around coppice plants (Photos: IJ Stehn)

6.3.2 Statistical analyses

For the calculations of shoot growth rates (diameter and length), only the actively growing daughter shoot measurements were considered. While the base diameter of the lower sections showed thickening throughout the study, the lengths of all lower sections remained constant and were therefore not analysed for this study. Shoot growth rate (mm day^{-1}) in terms of length were calculated as follows:

Shoot growth rate = $(L_x - L_{x-1})/(t_x - t_{x-1})$ with:

L_x = shoot length at xth observation

L_{x-1}= shoot length at previous observation

t_x = date of xth observation

t_{x-1}= date of previous observation

The same formula was used for the calculation of shoot growth rate in terms of diameter where L is replaced with D (shoot diameter). The number of daughter shoots on each focal shoot was standardised by calculating the number of shoots per centimetre of the total shoot length (all sections).

The same weather data as was used in the phenology study (see section 5.3.2) were used to test the correlation between climate variables and shoot growth rates of undamaged *T. camphoratus*.

All treatments were tested for normality by visual inspection of the histograms and Q-Q plots and homogeneity of variances using Levene's test ($p > 0.05$) (Levene 1960). The visual check for normality was preferred, because in large samples, as used in this case, the smallest deviation from normality is detected by the Shapiro-Wilk test ($p > 0.05$), but small deviations do not impact modelling. All rainfall measurements, including those without excessive skewness, as well as number of daughter shoots and daughter shoots cm^{-1}, were square root transformed.

Fifty percent of the data were used for correlations and the other 50% for modelling. Pearson correlation coefficients were calculated to test the link between different climate variables (temperature, day length, and rainfall) and shoot growth. To avoid co-linearity and excessive over-fitting one temperature variable, one day length variable and one rainfall variable were selected to be included in further modelling. This was done by identifying which options show the highest correlation with the target variables. R software was used for these analyses (R Core Team 2020) and *lmer4* (Bates *et al.* 2015) to perform linear mixed-effects analyses the relationship between environmental factors on shoot diameter and length growth rates, as well as shoots cm^{-1}. Soil type, temperature, daylight and rainfall were specified as fixed effects, while shrub and shoots on each shrub were specified as random intercepts (Harrison *et al.* 2018). Again, visual inspections of residual plots were used to test whether the main assumptions of the developed regression models appeared to hold. To test whether differences in shoot growth occur between sexes and soil type a one-way ANOVA was used.

The shoot density of the coppices was calculated as the number of shoots per basal stem area (shoots cm^{-2}) for each month, while diameter and height growth rates of coppices shoots were calculated similarly to the shoot growth rates of undamaged shrubs explained above. Proportional leaf and wood dry mass (DM) production of coppice plants was calculated as the ratio of leaf/wood DM of the coppice to the shrub's total leaf and wood DM before it was cut, in order to account for differences in the original size.

The independent sample t-test was used to test the effect of soil type (sandy vs. rocky) and cutting season (summer vs. winter) on the proportional leaf and wood DM production and coppice growth (shoot density, shoot diameter and height growth rate, shoot diameter, shoot height) for each of the 24 months. In months where normality and homogeneity of variance were not achieved the Mann-Whitney U test was applied. Treatment comparisons were done by using months since treatment (1 – 24) as an independent variable. Dead shoots which could not be replaced by new shoots were excluded from statistical analyses from the month they were observed as dead onwards, as well as shoots which suffered extreme browsing damage or had been remarked (as the original shoot broke off or died off) were excluded from analyses for the specific month in question only (Table 6.1). These data were analysed using IBM SPSS Statistics for Windows, version 25 (IBM Corp., Armonk 2017).

Table 6.1: The total number (n) and percentage (%) of shoots which were healthy or sustained damage during the 24-month study.

Shoots	n	%
Healthy	4502	93.8
Dead	199	4.1
Browsed	73	1.5
Remarked	26	0.5
Total	4800	100.0

6.4 Results

6.4.1 Shoot growth

A moderate correlation between length growth rate and diameter growth rate ($r = 0.456$, $p < 0.001$) existed. Shoot growth rates fluctuated throughout the year but growth occurred mainly between December and May (Figure 6.2 and Figure 6.3) and peaked during April 2019. The number of daughter shoots increased in two flushes, between November and January and between April and June (Figure 6.4). Shoot number, length and thickness remained relatively constant from June to August, but shoot die-back occurred between August and December, resulting in a great reduction in daughter shoots and shoot lengths, as well as a slight decline in shoot diameters. It was observed that especially shoots which bore flowers and/or seeds died off and only occasionally new daughter shoots emerged from the lower parts of these reproductive shoots during the following wet season. In contrast, shoots that did not bear reproductive organs stopped growing, but seldom died back during the dry period.

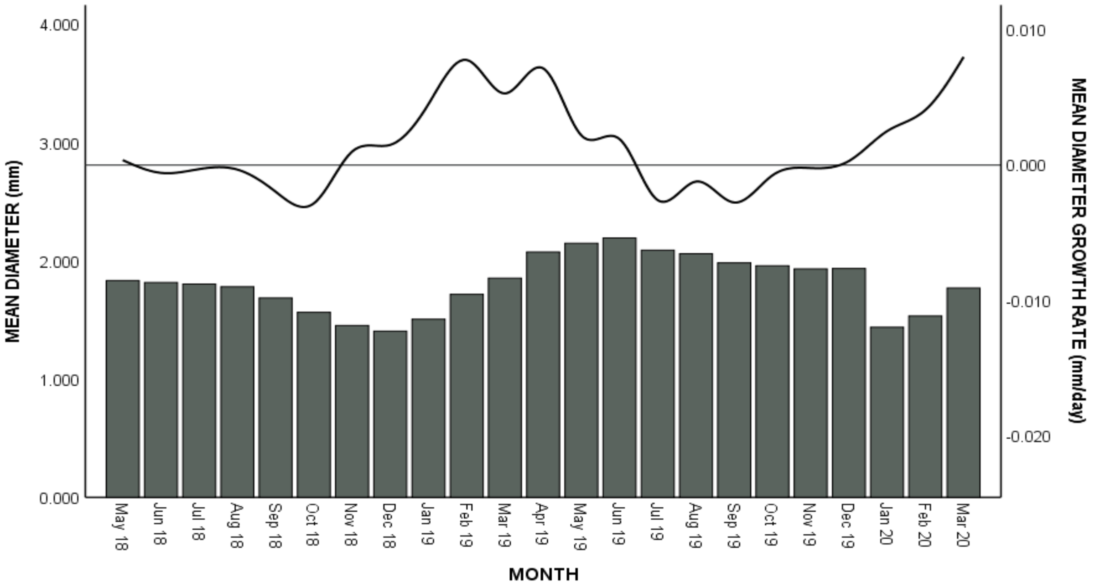

Figure 6.2: *T. camphoratus* mean shoot diameter (bars) and diameter growth rate (line) from May 2018 to March 2020

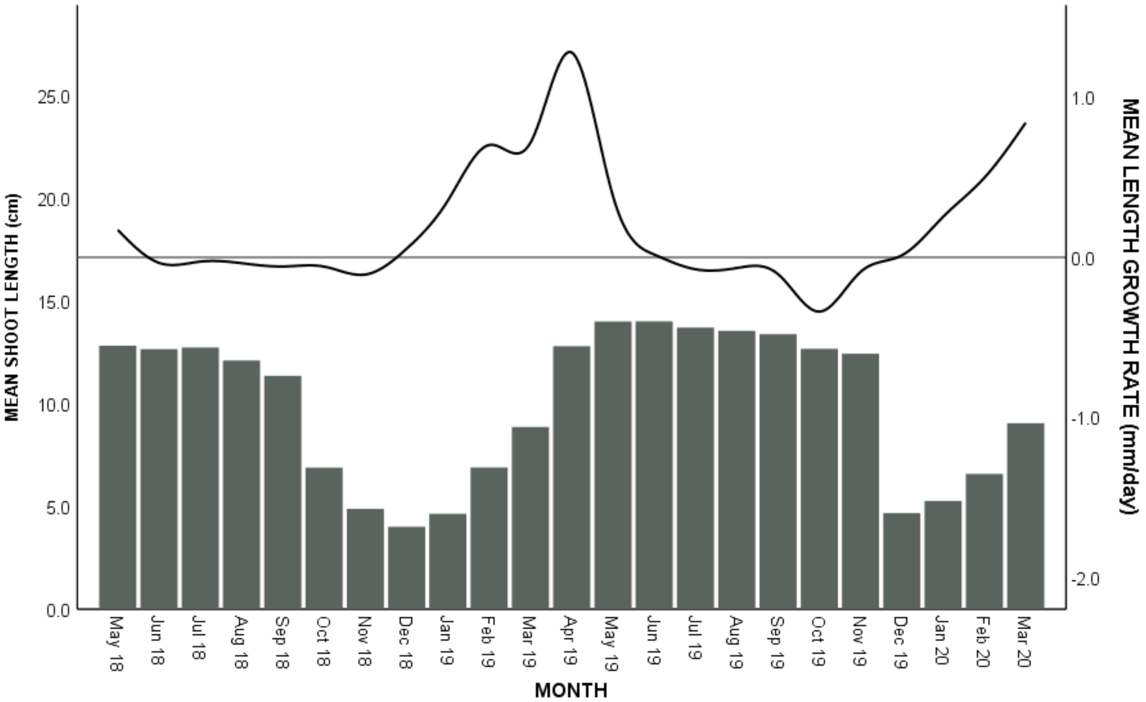

Figure 6.3: *T. camphoratus* mean shoot length (bars) and length growth rate (line) from May 2018 to March 2020

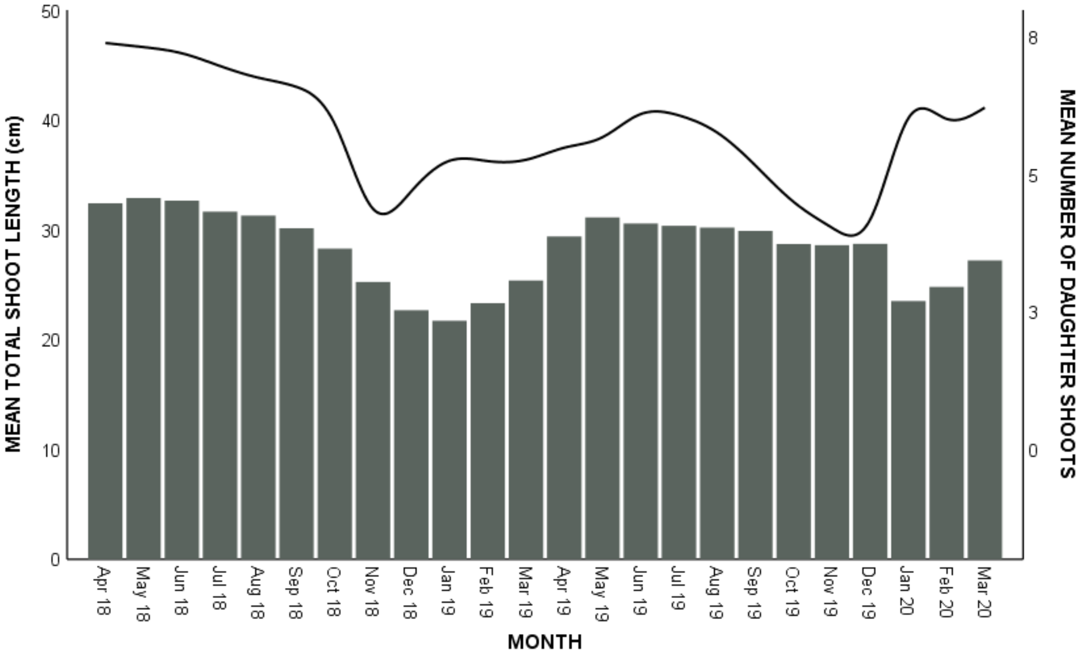

Figure 6.4: Mean total shoot length (bars) and the mean number of daughter shoots on each focal shoot from April 2018 to March 2020

No significant differences ($p > 0.05$) were found between the diameter and length growth rate, as well as the number of shoots cm^{-1} between male and female *T. camphoratus* shrubs. However, female shrubs had significantly more ($F_{1;3643} = 33.786$, $p < 0.001$)

daughter shoots per focal shoot (mean ± SE: 6.06 ± 0.99) compared to male shrubs (5.37 ± 0.79). Overall, soil type had no significant effect on diameter growth rate ($F_{1;3643} = 2.071$, $p = 0.150$) and length growth rate ($F_{1,3643} = 0.072$, $p = 0.789$), but the number of daughter shoots cm^{-1} on the focal shoot was significantly higher ($F_{1;\ 3838} = 45.138$, $p < 0.001$) for shrubs growing in the rocky soil (0.231 ± 0.003) compared to shrubs growing in the sandy soil (0.202 ± 0.003).

The climatic variables of temperature, day length and rainfall were investigated as possible factors causing the variation in growth throughout the year. A moderate positive correlation was established between the sum of the rainfall of four weeks prior to observation with a three-day delay and diameter growth rate ($r = 0.481$, $p <0.001$) and length growth rate ($r = 0.548$, $p < 0.001$). In terms of temperature, minimum temperature and mean minimum temperature variables were the best correlated with shoot growth rate, while maximum temperatures were only poorly correlated with shoot growth. The temperature variable, minimum temperature of four weeks prior to the observation with 14 days' delay was correlated the highest with diameter growth rate ($r = 0.502$, $p < 0.001$) and length growth rate ($r = 0.481$, $p < 0.001$). Day length had a weak correlation with shoot growth. The best correlation between diameter growth rate ($r = 0.324$, $p < 0.001$) and length growth rate ($r = 0.250$, $p < 0.001$) was found with maximum day length of four weeks prior to observation with 14 days' delay.

The number of daughter shoots on the focal shoot had a weak negative correlation with the average maximum temperature of the week prior to observation with a three-day delay ($r = -0.239$, $p < 0.001$). Similarly, minimum day length in the week prior to observation had a weak negative correlation with the number of daughter shoots on the focal shoot ($r = -0.217$, $p < 0.001$). Correlations between rainfall and number of daughter shoots were negligible ($r < 0.2$). Likewise, number of shoots cm^{-1} had negligible correlations ($r < 0.1$) with each of the tested climate variables.

Regression analyses indicated that temperature, rainfall and day length influenced shoot growth significantly ($p < 0.05$), while soil type did not appear to affect growth significantly ($p > 0.05$), controlling for the other factors. Increasing minimum temperatures and cumulative rainfall resulted in faster diameter and length growth rates and decreasing day length resulted in positive shoot growth (Table 6.2 & Table 6.3). Nevertheless, according to the standard linear model, temperature, day length, rainfall and soil type only explained 25.7% ($F_{4;1821} = 158.9$, $p < 0.001$) and 29.1% ($F_{4;1821} = 187.9$, $p < 0.001$) of the variation in diameter and length growth rate, respectively.

Environmental variables temperature, rainfall, day length and soil type explained only very little of the variation in the number of daughter shoots and shoots cm^{-1} (R^2 = 0.05 and R^2 = 0.04, respectively). However, relationships indicate that higher maximum temperatures resulted in decreased total number of daughter shoots as well as the shoots cm^{-1}, while increased rainfall resulted in an increased number of daughter shoots. A positive relationship was found between day length and the number of daughter shoots.

Table 6.2: Random effects of diameter and length growth

Model	Source of variability	Variance	Std. deviation
Diameter growth	Shoot: shrub (intercept)	≈ 0.00	≈ 0.00
	Shrub (Intercept)	1.900×10^{-22}	1.378×10^{-11}
Shoot growth	Shoot: shrub (intercept)	2.408×10^{-4}	0.01552
	Shrub (Intercept)	2.217×10^{-3}	0.04709

Table 6.3: Regression analysis predicting shoot diameter and length growth rate from soil type, temperature, day length and rainfall

Model		ß (SE)	df	t value	ρ
Diameter growth	Intercept	0.0086 (0.00198)	1821	4.334	<0.0001
	Soil type	0.0004 (0.00024)	1821	1.587	0.1127
	Temperature	0.0004 (0.00005)	1821	8.851	<0.0001
	Day length	-0.0184 (0.00388)	1821	-4.766	<0.0001
	Rainfall	0.0002 (0.00006)	1821	3.789	0.0002
Length growth	Intercept	1.342 (0.221)	1761	6.081	< 0.0001
	Soil type	-0.005 (0.034)	18	-0.174	0.8630
	Temperature	0.031 (0.005)	1744	5.609	<0.0001
	Day length	-2.960 (0.430)	1744	-6.887	<0.0001
	Rainfall	0.070 (0.007)	1744	10.072	<0.0001

6.4.2 Coppicing ability

All *T. camphoratus* shrubs coppiced readily after the cutting treatments. However, 30% of the summer treated coppices growing in the sandy soil have completely died off during the study and another 20% died back to less than eight shoots (Figure 6.5).

Soil type significantly (Mann-Whitney U: $z = -11.927$, $p < 0.001$) influenced the shoot density of summer-treated coppice plants. Summer-treated coppice plants growing in the sandy soil had significantly ($p < 0.05$) lower shoot densities from April 2018 to August 2018, in November 2018 and from January 2019 to March 2020, in comparison to coppice plants growing in the rocky soil. Even though soil type did not significantly influence (Mann-Whitney U: $z = -1.888$, $p = 0.059$) the shoot density of winter-treated coppice plants, coppice plants growing in the sandy soil had higher shoot densities from October 2018 to February 2019 than coppice plants growing in the rocky soil. However, from March 2019 to June 2020 coppice plants growing in the rocky soil had slightly higher shoot densities compared to winter-treated coppice plants growing in the sandy soil.

Figure 6.5: Coppice with major shoot die-back (Photo: IJ Stehn)

The shrubs which were cut in late summer (March) all coppiced within one month, regardless of the soil type they grew in, while shrubs which were cut during winter (June) took between two and three months to coppice on the sandy soil and between two and seven months to coppice on the rocky soil (Figure 6.10 and Figure 6.11). The overall season of treatment had a highly significant (Mann-Whitney U: $z = -6.849$, $p < 0.001$) influence on the shoot density of coppices. Significantly ($p < 0.05$) higher shoot densities were recorded for summer-treated coppice plants in the first three and seven months post-treatment on the sandy and rocky soil, respectively. Furthermore, shoot densities differed significantly ($p < 0.05$) 20 – 22 months post-treatment for coppice plants growing in the sandy soil and 11, 12 and 24 months post-treatment for coppice plants growing in the rocky soil. The average shoot density of winter-treated coppice plants growing in the rocky soil was continuously lower compared to summer-treated coppice plants throughout the study Figure 6.6 b. But, the shoot density of winter-treated coppice plants growing in the sandy soil rapidly increased to match shoot densities of the summer-treated coppice plants and, since January 2019, the shoot density of winter-treated coppice plants was higher compared to summer-treated coppice plants (Figure 6.6 a).

The leaf size of *T. camphoratus* coppice plants was notably larger than the leaf size of undamaged shrubs. In addition, coppice plants in both treatments growing in the sandy and the rocky soil had fleshy stems with thick diameters for the first few months post-treatment (Figure 6.7). As the shoots grew older their stems lignified and hardened thus resulting in a negative diameter growth rate and a drop in stem diameters before stem diameters increased again.

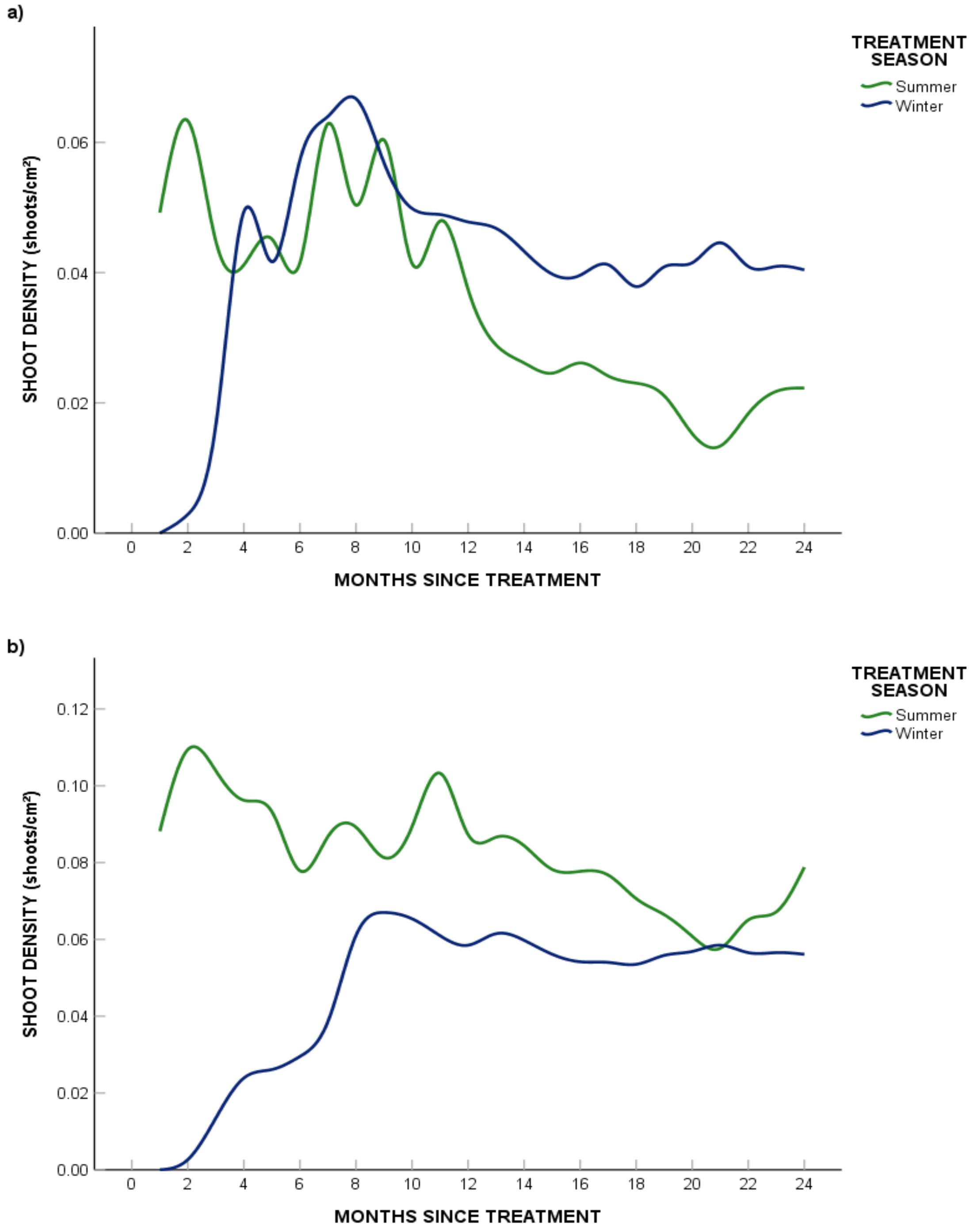

Figure 6.6: The influence of season of treatment on the shoot density (shoots cm^{-2}) of *T. camphoratus* coppice plants growing in the a) sandy and the b) rocky soil.

Figure 6.7: *T. camphoratus* coppice (Photo: IJ Stehn)

Diameter growth rate (Mann-Whitney U: z = -3.301, $p = 0.001$) and shoot diameter (Mann-Whitney U: z = -12.655, $p < 0.001$) were significantly influenced by soil type. The diameter growth rate of summer-treated coppice plants growing in the sandy soil was significantly ($p < 0.05$) higher in April 2018, January and October 2019 and significantly ($p < 0.05$) lower in May and July 2018, as well as February 2019, compared to the summer-treated coppice plants growing in the rocky soil. The diameter growth rates of winter-treated coppice plants growing in the rocky soil were significantly slower in August 2018, January and September 2019 and significantly faster in November and December 2018, February, April, May and September 2019, as well as from March to May 2020, compared to winter-treated coppice plants growing in the sandy soil. In addition, the summer-treated coppice plants growing in sandy soil had significantly ($t_{1,98}= 2.606$, $p = 0.011$) thicker shoots during April 2018 (1 month post-treatment) and significantly thinner ($p < 0.05$) shoots from October 2018 to January 2020 compared to coppice plants growing in the rocky soil. Similarly, winter-treated coppice plants growing in the sandy soil had significantly ($p < 0.05$) thicker shoots from August to November 2018, but significantly thinner ($p < 0.001$) shoots from February 2019 to June 2020 in comparison to winter-treated coppice plants growing on the rocky soil.

The season of treatment significantly influenced overall diameter growth rates (Mann-Whitney U: z = 2.225, $p = 0.026$) and shoot thickness (Mann-Whitney U: z = -4.754, $p < 0.001$). Shoot diameters of winter-treated coppice plants growing in either soil type were significantly ($p < 0.05$) thinner for the first six months post-treatment. Thereafter, shoot diameters of coppice plants growing in the sandy soil were significantly ($p < 0.05$) thicker 7 – 15 and 19 – 24 months post-treatment (Figure 6.8 a). From the eighth month post-treatment onwards, coppice plants growing in the rocky soil treated during winter had significantly thicker shoots compared to summer-treated coppice plants (Figure 6.8 b).

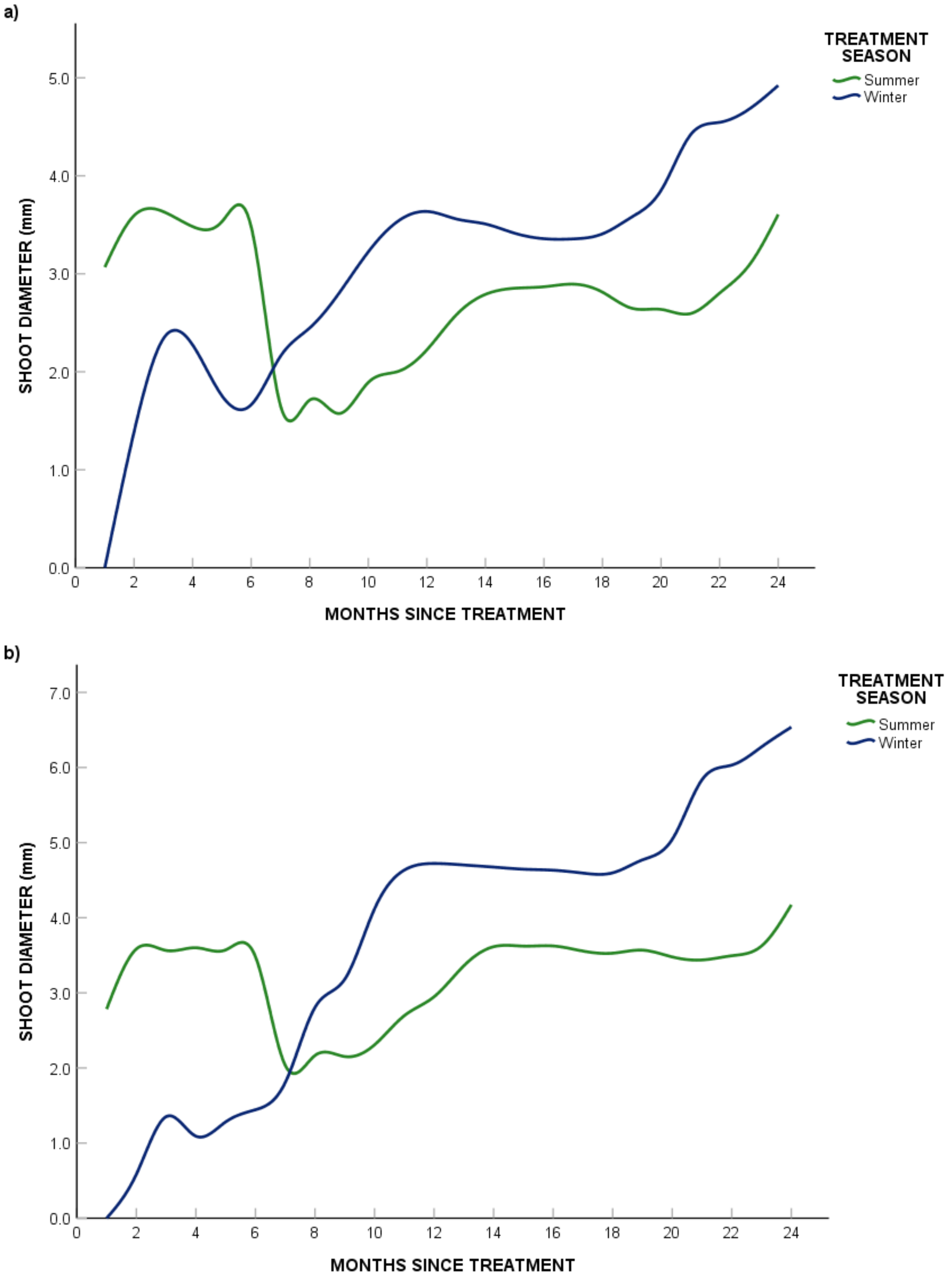

Figure 6.8: The influence of season of treatment on the shoot diameter of *T. camphoratus* coppice plants growing in the a) sandy and the b) rocky soil.

Highly significant differences were found in overall shoot height growth rates (Mann-Whitney U: $z = -3.807$, $p < 0.001$), as well as total shoot height (Mann-Whitney U: $z = -7.739$,

$p < 0.001$) between coppice plants growing in the sandy and the rocky soil. The rate of change in shoot height was significantly ($p < 0.05$) faster for summer-treated coppice plants growing in sandy soil in November and December 2018, August and November 2019, as well as February 2020 and significantly ($p < 0.05$) slower In February and April 2019 in comparison with summer-treated coppice plants growing in the rocky soil. While significantly ($p < 0.05$) slower height growth was recorded in August, September and December 2018, as well as January 2019, significantly ($p < 0.05$) faster height growth was recorded in November 2018, February, April and December 2019, as well as from January to March 2020 for winter-treated coppice plants growing in rocky soil compared to winter-treated coppice plants growing in sandy soil (Figure 6.9 b). Also summer-treated coppice plants growing in the sandy soil had significantly ($p < 0.05$) shorter shoots compared to those growing on the rocky soil in November and December 2018 and from February 2019 to March 2020 (Figure 6.9). While the shoots of winter-treated coppice plants growing in sandy soil were significantly ($p < 0.05$) taller compared to the shoots of winter-treated coppice plants growing in rocky soil from August 2018 to January 2019, they were significantly ($p < 0.01$) shorter from April 2019 until June 2020.

Moreover, the season of treatment significantly ($p < 0.001$) affected both rate of change in shoot height and total shoot height throughout the study. While the shoots of summer-treated coppice plants growing in the sandy and rocky soil were significantly ($p < 0.05$) taller compared to the shoots of winter-treated coppice plants for the first four and six months post-treatment, respectively, the shoots of winter-treated coppice plants became significantly ($p < 0.05$) taller from 9 – 24 months on the sandy soil and 8 – 24 months on the rocky soil.

After 24 months, the winter-treated coppice plants produced on average 474.00 ± 36.575 g shrub^{-1} ($n = 20$) leaf DM and 463.65 ± 49.073 g shrub^{-1} ($n =20$) wood DM, while summer-treated coppice plants produced 287.24 ± 43.063 g shrub^{-1} ($n = 17$) leaf DM and 245.18 ± 46.545 g shrub^{-1} ($n = 17$) wood DM. There was no significant difference in proportional leaf DM production of winter-treated coppice plants growing in the sandy and the rocky soil ($p > 0.05$). However, in summer-treated coppice plants, proportional leaf DM production differed significantly ($F_{1;15} = 15.594$, $p = 0.001$) between the soil types. In addition, summer- and winter-treated coppice plants growing in the sandy soil differed significantly in leaf DM production ($F_{1;15} = 4.757$, $p = 0.046$), while no significant differences were recorded between the summer- and winter-treated coppice plants on the rocky soil ($p > 0.05$). Taking into account the growth rate during the two-year study, coppice plants growing in the sandy soil are expected to regrow to their original leaf dry mass within 21.1 ± 9.95 years (mean ± SE), if treated during summer and 5.0 ± 0.53 years, if treated during winter. Coppice plants growing in the rocky soil are expected to regrow to their original leaf DM within 3.8 ± 0.52

years and 4.1 ± 0.56 years if treated during summer and winter, respectively. However, it is expected to take coppice plants growing in the sandy soil 26.6 – 156.1 years, if treated during summer, and 13.4 – 109.1 years, if treated during winter, to regrow to their original wood DM. In the rocky soil, it would take summer-treated coppice plants 10.3 – 92.4 years and winter-treated coppice plants 8.5 – 98.2 years to regrow to their original wood DM.

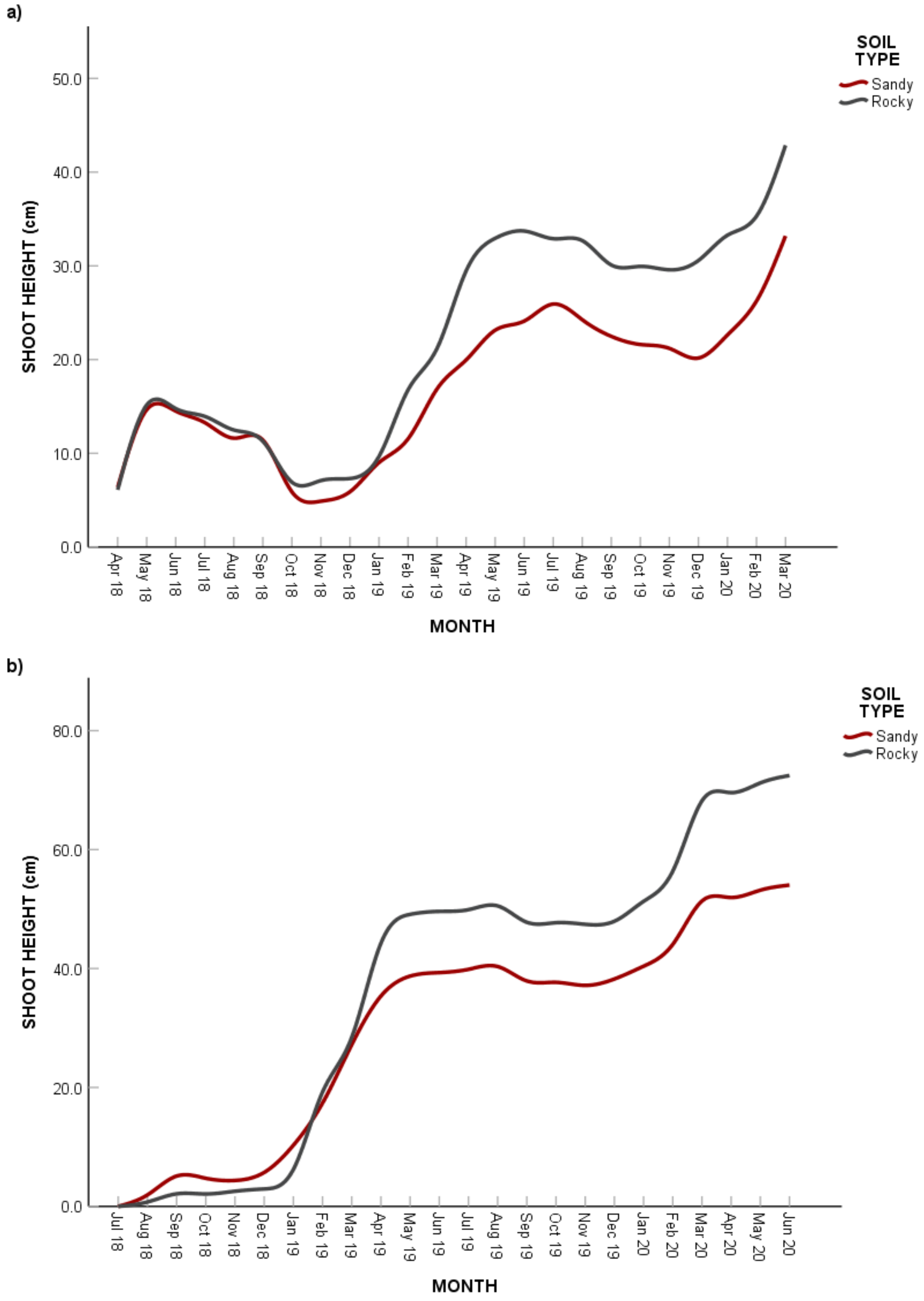

Figure 6.9: The influence of soil type on the *T. camphoratus* shoot length (cm) in a) summer-treated coppice plants and b) winter-treated coppice plants.

Figure 6:10: The development (from top to bottom) of summer-treated coppice plants growing in the sandy (left) and the rocky (right) soil in April 2018, September 2018, April 2019, September 2019 and March 2020 (Photos: IJ Stehn).

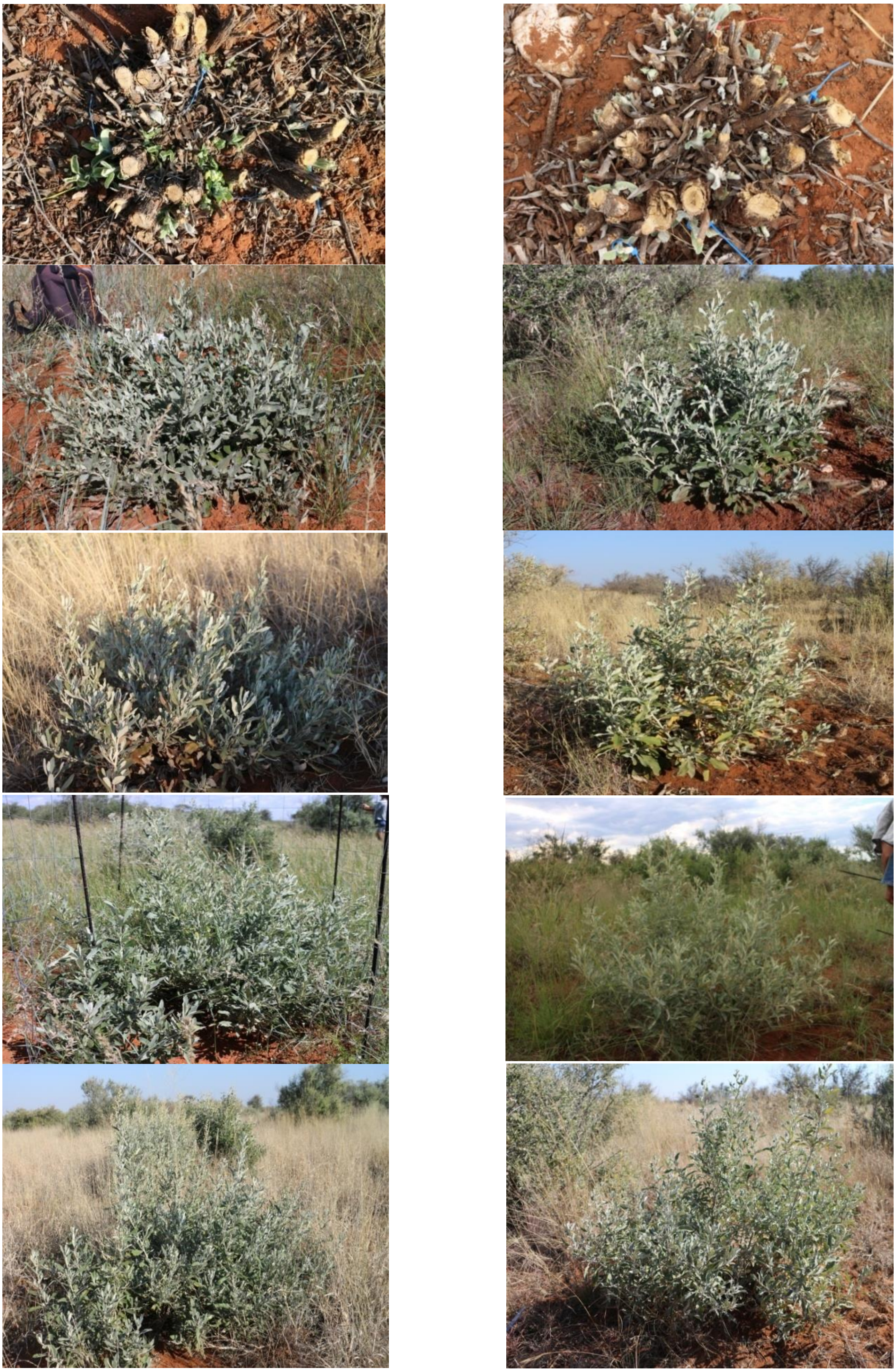

Figure 6.11: The development (from top to bottom) of winter-treated coppice plants growing in the sandy (left) and the rocky (right) soil in September 2018, April 2019, September 2019, March 2020 and June 2020 (Photos: IJ Stehn)

6.5 Discussion

6.5.1 Shoot growth

As illustrated by the growth pattern of *T. camphoratus* shoots, the critical period for vegetative growth was between December and May. This corresponded well to the rainy season at Rooipoort Nature Reserve, usually starting in November, which also supported the use delay periods for climate data, as woody plant growth responds to environmental changes with a time-lag (Ogle & Reynolds 2004; Wu *et al.* 2015). Yet, severe frost events could terminate shoot growth immediately and signs of frost damage become apparent within a few hours after the event (Muller *et al.* 2016).

Contrary to many other savanna species, in which the initiation of growth activity is triggered by photoperiodism and increasing temperatures (Rutherford & Panagos 1982; Milton 1987; Sekhwela & Yates 2007), the initiation of growth in *T. camphoratus* seemed to be triggered by rainfall in combination with minimum temperatures above a certain threshold. Hence, this confirms the prediction of hypothesis A. The notable decline in shoot growth after April coincided with the end of the rainy season, as well as flowering in most *T. camphoratus* shrubs. Very few new leaves were produced on extending shoots during April and May, as the production of reproductive organs was prioritised at this time. Similar results were found for *Baccharis dracunculifolia,* a species also belonging to the family of Asteraceae (Espírito-Santo *et al.* 2003) and it is expected that this is a function of a redirection of resources to support reproductive organs rather than vegetative growth.

Moreover, it was shown that *T. camphoratus* had a comparatively long growing season and growth peaked only towards the end of the growing season. This is different from many other woody species growing in the savanna in which shoot extension was most rapid at the beginning of the growing season (Milton 1987; Chidumayo 2001; Schutz *et al.* 2011). Van Schaik, *et al.* (1993) suggested that the growth activity of some woody plants could be set to fully utilise seasonal nutrient pulses, which result from the decomposition of leaf litter after the commencement of rain. This is of increased significance to plants such as *T. camphoratus,* which grow in nutrient-poor soils.

The increase in shoot growth during the rainy season and the shoot die-back of the following dry season were of similar magnitude, while the mean number of daughter shoots was slightly less in the second season compared to the first season of the study. The unusual cumulative effect of below-average rainfall in the season preceding the study and both seasons during the study, as well as the abnormally long absence of spring rains between September 2019 and February 2020 (see Figure 2.3) probably hampered growth. However, this indicates that adult *T. camphoratus* shrubs are relatively resistant to extended periods of drought.

Opposing hypothesis B, sex did not result in differential growth between male and female shrubs, even though it was expected that female shrubs would invest more resources into fruit maturation and therefore less in vegetative growth (Thomas 2011). However, more sensitive measurements including shoot mass would be necessary to investigate whether there are differential trade-offs between vegetative and reproductive resource allocation in male and female shrubs. Soil type also had no effect on shoot growth, thus contradicting hypothesis C, which predicted that higher shoot growth rates were expected for shrubs growing in the sandy soil. Interestingly, more daughter shoots where present on focal shoots of shrubs growing in the rocky soil compared to those on the sandy soil.

Relatively low coefficients of determination for the tested regressions indicate that the included variables (weather and soil type) play a significant but small role in the growth variability of *T. camphoratus.* There are many more endo- and exogenous determinants, which were not considered in this study that may play an important role in determining the timing, duration and rate of growth in woody plants. Further research is recommended.

6.5.2 Coppicing ability

The above results indicate that soil type, as well as the season in which the cutting treatment was applied, influenced the coppicing vigour of *T. camphoratus.* Unfortunately, large scale damage caused by frost, severe and prolonged drought (see Figure 2.3) and browsing herbivores, including mammals and insects, such as the armoured ground cricket (*Acanthoplus discoidealis*), various grasshopper and ant species, had resulted in variation of coppice growth that cannot be accounted for. Shackleton (2001) reported from a study conducted in the lowveld savanna of South Africa that the growth of browsed *Ocotea bullata* shoots was slowed by 66% relative to undamaged shoots. Browsing of *T. camphoratus* coppices was most severe during the dry season (September to December), probably resulting from a shortage of available browse in the area, caused by a lack of palatable evergreen woody plants and deciduous woody plants with low leaf-carriage scores (see section 5.4.2). In addition, green coppices could be relatively nutritious. High browsing pressure on *T. camphoratus* coppices has also been reported by Kiruki and Njung'e (2006).

Furthermore, it was evident that young shoots of summer-treated coppice plants were very susceptible to low minimum temperatures during the first winter post-treatment. Even though minimum temperatures during the second winter post-treatment were approximately similar to the minimum temperatures of the first winter, coppice plants suffered less damage during the second winter. This indicated that shoots become more resistant to low temperatures as they grow older. Exceptionally hot and dry conditions experienced in early summer (October to December/January) also cause young shoots to shed leaves and die back partly or entirely.

In contrast to Kaschula *et al.* (2005) who reported that shoot production increased with stem size in *D. cinerea, C. collimum* and *A. harveyi, T. camphoratus* shoot production could not be linked to its stem area. Initially, shoot density increased rapidly up to a maximum. Even though new shoots were continuously produced throughout the study period for plants of both treatments growing in the sandy and the rocky soil, shoot density declined and stabilized with time. This may be as a result of self-thinning or inter-shoot competition with older and stronger shoots suppressing younger shoots (Young & Francombe 1991). It is interesting to note that, while shoot die-back, in order to reduce transpiration losses from high leaf volumes, was expected to occur during the hot dry season when water is most limited, this phenomenon continued throughout the rainy season (February to April). This indicates that factors other than environmental conditions such as apical dominance and resource allocation to encourage height gain (Shackleton 2000), drive self-thinning in *T. camphoratus* shrubs. Similar results were found in coppicing *T. sericea* by Moyo *et al.* (2015).

Contrary to hypothesis D, summer-treated *T. camphoratus* shrubs did not coppice more vigorous than winter-treated *T. camphoratus* shrubs, but will depend on the temperature and rainfall of the season. Coppicing occurs at the expense of stored carbohydrate reserves (Schutz *et al.* 2011). Similar to the findings of Milton (1988) and Strohbach (1998), summer-treated shrubs coppiced more rapidly after treatment and initially produced larger numbers of shoots per unit stem area but showed weaker growth towards the end of the study compared to winter-treated coppice plants. Phenology and the seasonal cycle of carbohydrate reserve depletion during spring and summer and replenishment during autumn and winter (Schutz *et al.* 2009) may have attributed towards the differential growth vigour of summer- and winter-treated coppice plants. At the time of cutting, summer-treated coppices were in their active growth period, where carbohydrates reserves were utilised for leaf-flushing and rapid growth (Milton 1988) and large energy inputs were required by shrubs to initiate the reproductive growth phase starting in March (see section 5.4.2). Resprouts of summer-treated coppices were further subjected to stress factors, such as low minimum temperatures during winter followed by a hot and dry early summer and occasional browsing which significantly reduced their shoot height and density. Repeated defoliation without allowing sufficient time for the replenishment of depleted carbohydrate reserves (Schutz *et al.* 2011) possibly resulted in the weaker growth and higher mortality of summer-treated coppice plants compared to winter-treated coppice plants. However, it is questionable whether summer-treated coppice plants would still coppice less vigorous than winter-treated coppice plants if the study was repeated during normal and above-average rainfall years. Reduced intensity of the hot and dry early summer before the rain start, as well as reduced browsing pressure may result in increased growth and higher survival of shoots in summer-treated coppice plants.

On the other hand, winter-treated *T. camphoratus* shrubs had probably replenished most carbohydrate reserves by the time the cutting treatment was applied, as they had fewer budding leaves and more yellowing and dry leaves with, depending on the sex, either dry flowers or unripe fruits. Furthermore, winter-treated coppice plants delayed coppicing until growing conditions became more favourable and they produced shoots at a slower rate compared to summer-treated coppice plants. Therefore, winter-treated coppice plants utilised less carbohydrate reserves for shoot production and were subjected to their first winter and dry season only after shoots grew strong and more resistant to stress factors, resulting in vigorously growing coppice plants. Shackleton (2000) found that, due to reduced inter-shoot competition, coppice plants with a lower shoot density grew faster. This may explain the slower growth of summer-treated coppice plants compared to the winter-treated coppice plants growing in the rocky soil. However, winter-treated coppice plants growing in the sandy soil grew more vigorously than summer-treated coppice plants, despite their higher shoot density.

Contrary to hypothesis E, coppice plants in both treatments grew less vigorously and produced less leaf dry mass in the sandy soil compared to the rocky soil, but the reasons are unclear. On the sandy soil, lower woody plant density may cause increased exposure to weather elements such as cold and heat, whereas coppice plants growing in the rocky soil, with a higher woody plant density, are sheltered by surrounding shrubs. Furthermore, the significantly lower soil calcium, total nitrogen and organic matter content of the sandy soil compared to the rocky soil (see section 4.4) may also cause coppice plants growing in the sandy soil to grow less vigorous compared to coppice plants growing in the rocky soil. Warmer soil temperatures (Onwuka & Mang 2018), as well as large, widespread root systems of *T. camphoratus* with less competition for resources (especially water) in the sandy soil, are possibly the cause for faster resprouting (within two months post-treatment) of winter-treated coppice plants growing in the sandy soil compared to those growing in the rocky soil.

Similar to findings by Smit (2003), coppice plants prioritise the investment of resources into the replacement of the lost leaf biomass, taking much less time to regrow to the original leaf biomass compared to the approximate time to regrow to the original wood biomass. These approximate time spans will be affected by rainfall, browsing intensity and increasing time since the cutting treatment. *T. camphoratus* continued coppicing despite the below-average rainfall. It is therefore expected, with increased rainfall, (1) coppice plants could support more shoots (reduced self-thinning), and (2) browsing pressure would be reduced, thus reducing the effective time until the shrub is back to its original leaf and wood biomass. However, the opposite is also true and the effects intensified because it is expected that

T. camphoratus will not coppice or coppice plants die off more frequently if soil water availability drops below a minimum threshold.

6.6 Conclusion

This study has shown a moderate to strong positive correlation between cumulative rainfall, as well as minimum temperature, and *T. camphoratus* shoot growth. Soil type and sex of the plant did not influence shoot growth significantly. The critical time for *T. camphoratus* shoot thickening and elongation was between December and May. Furthermore, soil type as well as season of cutting influenced the coppicing vigour of *T. camphoratus,* with shrubs cut during the winter in this study growing significantly faster than shrubs cut during the active growth period during summer. The exceptionally hot and dry conditions experienced in early summer of the study period undoubtedly influenced shoot growth. Shrubs cut during summer on the sandy soil were especially vulnerable and coppiced relatively poorly.

The management objective as well as economic considerations will determine which treatment should be applied for shrubs growing on the different soil types. If the objective is to manage bush-thickening it is advised that the remaining stems of cut *T. camphoratus* stems are treated with an arboricide to prevent coppicing. If this is not done, *T. camphoratus* is guaranteed to coppice and follow-up treatment will be necessary within a short time. Nevertheless, partial success can still be achieved if plants are cut during their active growth period (January to April) and coppice is repeatedly removed, either by mechanical means (cutting) or by introducing browsers, in order to deplete carbohydrate reserves.

If the objective is sustainable use of *T. camphoratus* to produce fodder from browse, also known as “boskos”, shrubs should be cut during winter, allowing for shorter return times (within four to five years) and higher leaf biomass. No matter which treatment is applied, *T. camphoratus* in this area is probably unsuitable for sustainable charcoal or wood production, as returning periods are too long (> 25 years).

CHAPTER 7

Reproductive ecology of *Tarchonanthus camphoratus*

7.1 Introduction

The increase in woody cover across savanna ecosystems worldwide is a function of increased vegetative growth of existing woody plants as well as increased woody plant abundance resulting from increased reproductive success (Smit *et al.* 1996). The effective management of potential bush-thickening species therefore necessitates a good understanding of the factors contributing to the success of those woody species. Therefore, understanding the reproductive processes, including the timing of reproductive events, seed production, dispersal, predation, seed bank persistence, germination and seedling survival, as well as their interaction with environmental conditions, site characteristics and various disturbance regimes, is crucial. This further aids in predicting the response of the thickening woody vegetation to various management approaches and their timing.

While the reproductive ecology of the co-dominant bush-thickening species, *S. mellifera,* has been well-studied in the literature (for example, Hagos 2001; Kraaij & Ward 2006; Joubert *et al.* 2008; Joubert *et al.* 2013), little is known about *T. camphoratus.* It is known that *T. camphoratus* is a dioecious shrub, which propagates by sexual reproduction with seeds (Herman 2002) or asexual reproduction with root suckers (Pratt 1966; Beentje 1999). However, *T. camphoratus* seed production and seed longevity, as well as seedling recruitment, are poorly understood, but are of utmost importance for management decisions and restoration of cleared or thinned sites.

Therefore, the main objectives of this study were to:

a) quantify the seed production of female *T. camphoratus* plants and
b) examine the existence of a *T. camphoratus* seed bank in the soil

Furthermore, the following hypotheses were tested:

a) the expected sex ratio of male and female *T. camphoratus* shrubs is 1:1,
b) There is a relatively strong positive correlation between leaf dry mass and seed production,
c) Soil type does not influence seed production.
d) Soil originating from the canopied subhabitats contains more viable seeds compared to soil from the uncanopied subhabitat.

7.2 Literature review

7.2.1 Seed production

The quantity and quality of seeds produced by woody plants is dependent on the species, size, density, and availability of resources, as well as environmental conditions from flower initiation through to seed maturation. For most woody plants, age / size is positively correlated to seed production within limits, such as pre-reproductive age and old age (Thomas 2011). Hagos (2001) and O'Connor *et al.* (2010) respectively reported that larger *S. mellifera* and *V. karroo* plants, produced more pods than smaller plants. Witkowski and Garner (2008) reported that *Solanum mauritianum* seed production increased linearly with increased plant height but only occurred on plants taller than 1.5 m. While similar results were reported for *V. robusta*, no correlation between seed production and tree height was established for *V. tortilis* in the Serengeti National Park in Tanzania (Rugemalila *et al.* 2017). Furthermore, *C. mopane* and *V. karroo* were found to produce more seeds per plant in low-density plots relative to high-density plots; however, the total number of seeds produced per hectare was not density-dependent (Smit & Rethman 1998; O'Connor *et al.* 2010).

Mixed evidence exists on the influence of rainfall and soil nutrients on seed production. Joubert *et al.* (2013) reported that there was a strong positive correlation between *S. mellifera* seed production and annual rainfall. Seghieri *et al.* (1995) conducted a study in the savanna of Cameroon and found that low soil water reserves strongly reduced the abundance of woody plants that flower as well as their intensity of flowering and seed production. Smit and Rethman (1998), and O'Connor *et al.* (2010) on the other hand, found that rainfall played a less important role in the quantity of seed produced by *C. mopane* and *V. karroo.* Similarly, rainfall did not influence seed production of *V. robusta* and *V. tortilis* (Rugemalila *et al.* 2017). A study conducted in a mixed-oak forest in southern Spain showed that variability in soil nutrients and soil pH explained much of the variation in seed production between individuals of *Quercus canariensis* but not *Q. suber*. Higher seed yields were measured for *Q. camariensis* growing on nutrient-rich, less acidic soil compared to trees growing in nutrient-poor, more acidic soils (Pérez-Ramos *et al.* 2014).

The timing of flowering and subsequent fruiting is critical for optimal seed production (Cleland *et al.* 2007), as these are strongly influenced by changes in environmental conditions. Depending on the species, frost occurrences in late spring, extremely hot temperatures, a delayed onset of the rainy season and heavy rains during pollination have been reported to result in flower drop (Van Rooyen *et al.* 1986; Bonner *et al.* 2008), which significantly reduced seed yield. Decreased frost occurrences and increasing minimum temperature coupled to climate change may also result in reduced flowering intensity and decreased seed production, especially in woody plant species such as *Carya illinoensis* and *Olea europaea,* which have a certain cold requirement (Bonner *et al.* 2008).

7.2.2 Seed predation

The fate of the produced seed crop depends on many endo- and exogenous factors varying between years, habitats and species. Seed predation and infestation by pests, insects and mammals, for example, can significantly reduce the viable seed crop (Rugemalila *et al.* 2017). Confirming the results of Hagos (2001), Joubert *et al.* (2013) found that bruchid beetle infestation on *S. mellifera* seeds was very low (0 - 6.9%) in most years but can be as high as 28.7%. However, bruchid beetles infested up to 52% of *V. erioloba* seeds (Barnes 2001), 41.5% of *V. robusta* and 68% of *V. tortilis* seeds (Miller 1996).

In addition, many seeds serve as a valuable fodder source for animals, which is detrimental for some plant species seeds but is an important dispersal strategy for others. Barnes (2001) reported from a study conducted in northern Botswana that significant amounts of *V. erioloba* seeds were lost to chacma baboons and vervet monkeys feeding on the unripe pods. In west Africa, 46 – 87% and 2 – 74% of the woody plant seeds which were fed to cattle and sheep, respectively, were still viable after recovery from the dung (Razanamandranto *et al.* 2004). The seeds' survival after ingestion thus depends on its maturity, hardness and shape as well as the animal's body mass (Barnes 2001; Razanamandranto *et al.* 2004; Anderson *et al.* 2014). Miller (1994) and Walters *et al.* (2005) reported that the recruitment of woody plants in the savanna was significantly limited by rodents foraging on approximately 2 – 4% and 9 – 25% of the annual seed production of *V. tortilis* and *V. karroo,* respectively.

7.2.3 Soil seed bank

Studies of the soil seed bank in savannas function to predict the resilience and restoration potential of degraded areas and plan future management (Mndela *et al*. 2019). The chances for re-encroachment after clearance of woody plants and the establishment of a stable perennial herbaceous layer can be predicted (Mndela *et al.* 2019; Witkowski & Garner 2008) and therefore post-clearance management actions such as follow-up treatment and seeding can be budgeted and planned. The capacity of seeds to remain dormant in the soil is a species-specific trait (Ordonez-Salanueva *et al.* 2017) associated with seed physiology (dormancy mechanism, starch reserves, seed coat characteristics and germination requirements), pathogen presence, soil characteristics and environmental conditions (Garner & Witkowski 1997; Dos Santos *et al.* 2018). In many cases the burial of seeds is crucial to persistence, because this reduces predation risks and exposure to fire, temperature extremes and fluctuations (Thompson *et al.* 1993; Garner & Witkowski 1997; O'Connor *et al.* 2010).

Thompson *et al.* (1993) defined three classes of soil seed bank persistence, namely, (1) transient, seeds persist less than one year in the soil, (2) short-term persistence, seeds survive less than five years in the soil, and (3) long-term persistence, seeds survive more than five years in the soil. Relatively large, flattened or elongated seeds tended to persist for shorter periods in the soil compared to seeds which were relatively small, compact and spherical and therefore easier buried (Thompson *et al.* 1993; Garner & Witkowski 1997). For example, it was found that the relatively large *S. mellifera* seeds did not persist in the soil for longer than one year (Hagos 2001; Joubert *et al.* 2013). O'Connor *et al.* (2010) found that 24% of *V. karroo* seeds lying on shaded soil surface persisted for two years, while seeds which were buried or exposed on the surface did not persist longer than one year.

Seed bank density and richness vary by season, canopy cover, above-ground species composition, soil moisture, soil nutrient status and soil depth (Leckie *et al.* 2000; Arroyo & Giner 2017; Mndela *et al.* 2019). Seasonal and annual variation in soil seed bank dynamics are ascribed to variations in the reproductive phenology of different species, seasonal and annual variation in rainfall (Kellerman & Van Rooyen 2007; Dos Santos *et al.* 2016; Mndela *et al.* 2019) and variation in management (timing of grazing or clearance).

Knowledge of seed bank dynamics therefore partly provides clarification about seedling establishment, which has implications for bush control programmes.

7.2.4 Seedling establishment

For successful establishment of woody plants, successful germination and survival of the seedlings have to be ensured. The seeds of some woody plant species are known to have seasonal dormancy to ensure that germination only takes place during favourable environmental and seed internal conditions (Smit *et al.* 1996). Natural ways by which this dormancy is overcome include, expired seed rest periods and embryo maturity of quiescent seeds, animal gut activity, fire or sufficient water (Bareke 2018). Once dormancy is broken and the specific temperature, water, light and substrate requirements are met, the seed will germinate. Occasionally the presences of allelochemicals or too deep burial prevent germinated seeds from emerging (Walters *et al.* 2005; Singh *et al.* 2014, Arroyo & Giner 2017).

The temporal distribution of rainfall (Barnes 2001; Joubert *et al.* 2013), as well as competition, play a critical role in the survival rate of emerged seedlings. Joubert *et al.* (2013) found that, even though three times more *S. mellifera* emerged under the tree canopy compared to the uncanopied area, the survival rate of seedlings in the uncanopied area was five times greater than under the canopy. Competition for water, rather than shade intolerance was found to be the responsible mechanism. In contrast, *V. karroo* seedlings under the tree canopy had higher survival rates compared to those in an uncanopied area, which was attributed to the influence of shade on soil moisture availability and the species' shade tolerance (O'Connor 1995). Smit and Rethman (1998) ascribed the absence of a pattern in *C. mopane* seedling establishment across a tree density gradient to competition from the herbaceous layer at a low tree-density and competition from woody plants at a high tree-density. In addition, Stevens *et al.* (2014) predicted from laboratory experiments with *C. mopane* and *S. nigrescens* that increasing temperatures associated with climate change would improve seedling establishment but an increased prevalence of drought will decrease the frequency of germination events and decrease survival rates.

Moreover, woody plant species which have strong coppicing abilities or reproduce asexually are less dependent on recruitment from seeds. Bond and Midgley (2012) reported that woody plants which regenerate vigorously generally produce fewer viable seeds, have lower seed bank densities, poorer germination and lower seedling survival rates compared to non-coppicing woody plants. However, Clarke and Knox (2009) reported that seedlings of woody plant species with strong coppicing ability had higher seedling survival rates post-fire or drought events and withstood competition from grasses better compared to non-coppicing species. This was attributed to the increased resource allocation to roots relative to above-ground parts in coppicing species.

7.3 Procedure

7.3.1 Sex ratio and seed production

In July 2018, six 100 m x 30 m (3 000 m^2) belt transects were demarcated approximately parallel to each other across the rocky and the sandy site each. In each transect, the number of rooted female and male *T. camphoratus* shrubs were counted. Individual plants were considered those with stems growing more than 0.5 m apart (Coetzee *et al.* 2007). Shrubs with both male and female reproductive parts were recorded as 'mixed' and shrubs without any reproductive parts were recorded as 'unidentified'.

In order to determine the seed production of *T. camphoratus* shrubs, at least 50 fruit-bearing shoots from female *T. camphoratus* shrubs of all represented plant sizes and all canopy parts were sampled on each soil type (rocky and sandy), in mid-August 2018. The number of seeds per fruiting head was counted for 500 randomly selected fruiting heads from each site. In order to test the accuracy of the planned procedure, the spatial canopy volume of four female *T. camphoratus* shrubs (two on each soil type) was determined by following the procedures of the BECVOL 3 – model (see chapter 9). A plastic right angle fastened to a short piece of blue twine (for better visibility) was thrown over the shoulder onto the shrub to determine the unbiased position where the 0.25 x 0.2 m quadrate was placed. To determine the volume occupied by the fruit-bearing shoots – which are only positioned on the outer parts of the canopy at the terminal end of actively growing shoots – the maximum depth of fruit-bearing shoots was measured at 90° to the quadrate. All fruiting heads within the quadrate were harvested and placed into a marked paper bag to be counted. This method was repeated for five quadrates. Thereafter, all the remaining fruit-bearing shoots on the shrub were also harvested to obtain the true number of fruiting heads on each shrub. After this method proved to be accurate to ± 5%, the spatial canopy volume of a further eight shrubs on each soil type was measured and five quadrates per shrub were cut following the same procedures.

The total number of harvested fruiting heads was counted for each shrub and from this the total seed production per shrub was estimated as y = 0.5 x total canopy volume / total sampled volume x quantity of sampled fruiting heads x average number of seeds per fruiting head. Sampling was done at the end of August 2018, just before seeds started to drop.

7.3.2. Soil seed bank and survival

On each site, five large female *T. camphoratus* shrubs (a total of ten shrubs) were chosen at random at the end of August 2018. This specific time was chosen because this was just before the first female shrubs in the area started shedding the current season's dry seeds and to be able to test whether *T. camphoratus* seeds can persist in the soil longer than one year. This assessment had to be done just before fresh seeds were dispersed.

At each of the ten selected shrubs, three subhabitats were identified, namely, (1) at the stem (< 25 cm from the stem), (2) under the canopy away from the stem, and (3) in the uncanopied zone between shrubs. A 0.25 x 0.20 m (0.05 m^2) quadrate was placed at four random locations 90° to each other within each subhabitat and used to excavate soil to a depth of 10 cm from the soil surface. The excavated soil was sieved through a 4 mm sieve to remove all larger stones and branches and the rest retained to ensure no seeds were removed from the sample. The soil excavated from the four locations in each subhabitat of each sampled plant was bulked and thoroughly mixed. Thereafter, a subsample of each of the 30 bulked soil samples was taken and placed into two 23 cm x 37 cm plastic seed trays to a depth of 2 cm. In this way, a total of 60 trays were filled with soil (10 shrubs x 3 subhabitats x 2 trays). The seed trays were placed in a random order under controlled conditions in a greenhouse at the University of the Free State where the temperature was kept constant at about 25°C. The soil was watered and kept moist from 28 September 2018. Seedlings of all germinated plant species were carefully removed from the tray once they were identified, keeping track of the number of plants which emerged in each tray. On 22 January 2019, the experiment was terminated. By this date, no new seedlings emerged from the soil and the last seedlings were identified and counted. Also, *T. camphoratus* seeds planted at the same time in adjacent pots (see chapter 8) had all germinated by this date and, based on this observation, it was decided that all viable *T. camphoratus* seeds that may have been present in the soil had sufficient time for germination. Seed bank density (all plant species combined) in each subhabitat was determined by recording the seedling emergence in each tray and extrapolating to 1 m^2. Species abundance was calculated as a percentage of the proportional frequency of each species in each treatment (3 subhabitats x 2 soil types).

7.3.3 Statistical analyses

Normal data distribution was tested by using the Shapiro-Wilk test ($p > 0.05$) (Shapiro & Wilk 1965) and visual inspection of Q-Q plots and histograms. Seed bank density was square-root transformed. The chi-square goodness of fit test was used to test whether the sex ratio deviated from the expected 1:1. The independent sample t-test was used to test for difference in sex ratio, seeds per fruiting head and estimated seed production per ETTE between the sandy and rocky soil. Pearson's correlation was used to test for the correlation between estimated seed production and estimated total leaf dry mass. To test for seed density and species richness differences in the three soil subhabitats, as well as differences between soil types, one-way ANOVA in combination with Tukey's *post hoc* honest significant difference (HSD) were used.

7.4 Results

A beetle belonging to the order Coleptera and family Lycidae – illustrated in Figure 7.1 – was frequently observed on flowering *T. camphoratus* shrubs, and may be one of the pollinator species. Illustrations of *T. camphoratus* flowers, as well as the male and female reproductive shoots are represented in Figure 7.2, 7.3 and 7.4, respectively.

Figure 7.1: Beetle belonging to the Lycidae family feeding on the nectar of *T. camphoratus* (Photos: IJ Stehn)

Figure 7.2: *T. camphoratus* flowers (Photos: IJ Stehn)

Figure 7.3: Male reproductive shoots of *T. camphoratus* represented by dry flowers (Photos: IJ Stehn)

Figure 7.4: Female reproductive shoots of *T. camphoratus* with unripe fruits (top left) and ripe fruits (Photos: IJ Stehn)

7.4.1 Sex ratio and seed production

A total of 1774 *T. camphoratus* shrubs were counted across all 12 transects (714 on the sandy soil and 1061 on the rocky soil). Six percent of all shrubs were classed “unidentified” and 0.4% were classed as “mixed”. Soil type had no significant influence on the sex ratio ($t_{1;10} = 0.211$, $p = 0.837$) and the sex ratio of all *T. camphoratus* shrubs combined from both soil types was 1:0.995, which did not differ significantly from the expected 1:1 ratio ($\chi^2 = 0.01$ df = 1, $p = 0.941$).

The average number of seeds per fruiting head was 4.077 ± 0.03 (n = 1000), ranging between two and eight seeds per fruiting head. There was no significant difference ($t_{1;998} = 0.734$, $p = 0.463$) in number of seeds per fruiting head between the sandy and rocky soil. Estimated seed production per shrub was strongly correlated with estimated leaf dry mass ($r = 0.88$, $p < 0.001$) and ranged between 22 023 and 1 023 484 seeds per shrub depending on the shrub size with an average of 40 469 ± 4504 seeds ETTE^{-1} (mean ± SE). Furthermore, it was observed that most shrubs which were cut or burnt down to ground level and allowed to coppice produced flowers and seeds in the second season post-treatment. Estimated seed production per ETTE was significantly higher ($t_{1;18} = 2.864$, $p = 0.011$) for shrubs growing on the sandy soil compared to shrubs growing in the rocky soil.

7.4.2 Soil seed bank

A total of 22 species belonging to ten plant families emerged from the soil seed bank, but no *T. camphoratus* seedlings germinated from any of the seeding trays (Table 7.1). *Eragrostis lehmanniana* and *Schmidtia pappophoroides* were the most dominant species. Seed bank density differed significantly between the subhabitats (Figure 7.5) on the sandy ($F_{2;27}$ = 17.118, $p < 0.001$) as well as the rocky soil ($F_{2;27}$ = 8.170, $p = 0.002$). On the sandy soil, seed bank density was significantly lower ($p = 0.001$) in the uncanopied subhabitat compared to the two canopied subhabitats. On the rocky soil, seed bank density was significantly higher ($p < 0.05$) in the subhabitat closest to the stem compared to the canopy middle and uncanopied subhabitats (Figure 7.6). Soil type had no significant influence ($p > 0.05$) on the soil seed density in the two canopied subhabitats but significantly higher ($F_{1;18}$ = 9.347, $p = 0.007$) seed density was observed in the uncanopied subhabitat of the rocky soil compared to the same subhabitat of the sandy soil.

Species richness differed significantly ($F_{2;27}$ = 11.719, $p < 0.001$) between the subhabitats on the sandy soil. There were significantly more ($p < 0.001$) different species in the two canopied subhabitats compared to the uncanopied subhabitat (Table 7.1). Species richness on the rocky soil did not differ significantly ($F_{2;27}$ = 1.578, $p = 0.225$) between the three subhabitats.

Figure 7.5: Seedling density in the soil collected in the open, canopy middle, and stem subhabitat (from left to right) of *T. camphoratus* (Photo: GN Smit)

Soil type significantly influenced ($F_{2;27}$ = 8.647, $p = 0.009$) the species richness in the uncanopied subhabitat only, with significantly more different species present in the soil seed bank of the rocky soil (2 ± 0.422) compared to the sandy soil (0.6 ± 0.221). However, overall species richness was slightly higher in the sandy soil compared to the rocky soil.

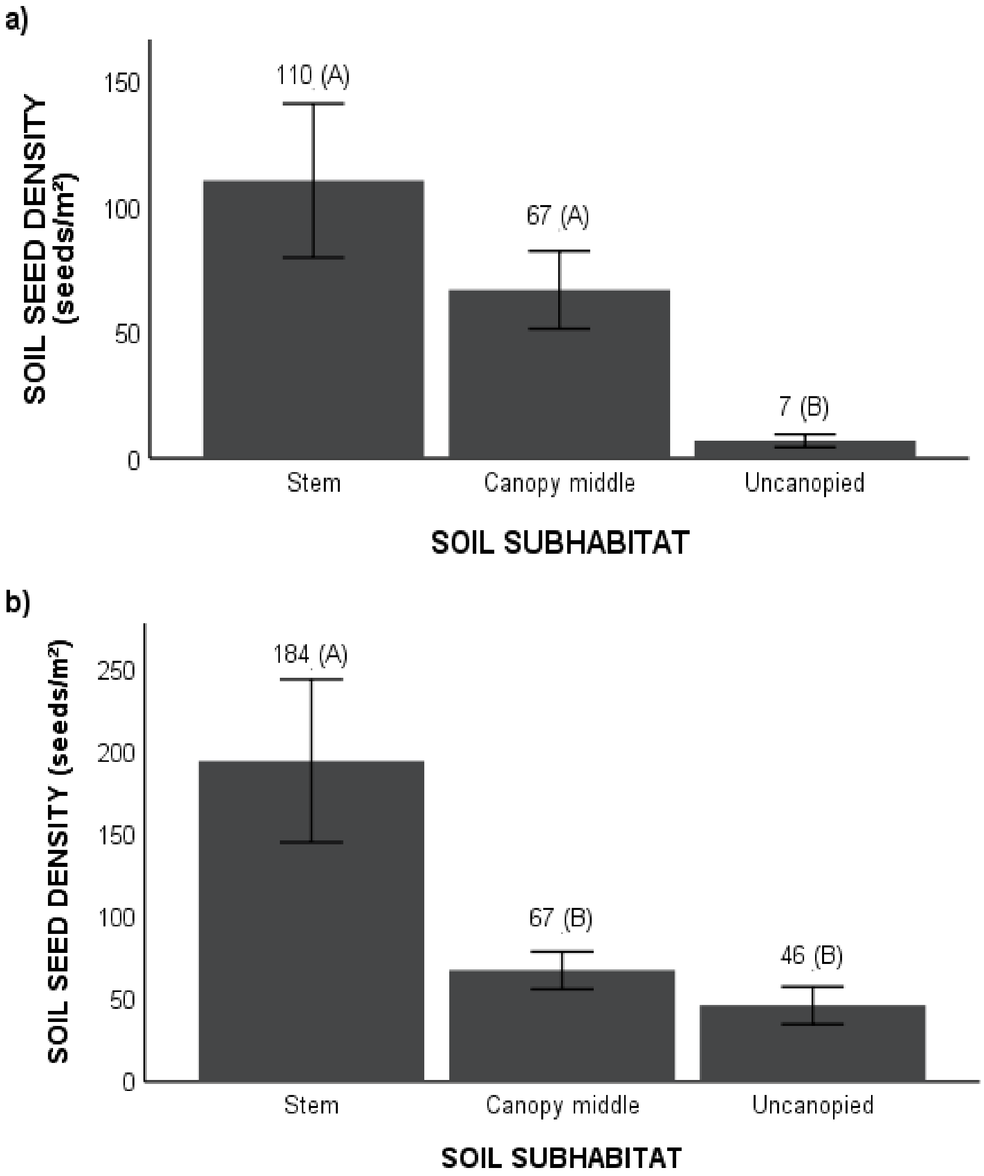

Figure 7.6 The seed density (seeds m^{-2}) in three soil subhabitats of the a) sandy soil and, b) rocky soil

Table 7.1: Abundance (%) and richness of the soil seed bank on the sandy and rocky soil in three soil subhabitats.

Species	Family			Sandy soil			Rocky soil		
		Functional group	Perenniality*	Stem	Canopy middle	Uncanopied	Stem	Canopy middle	Uncanopied
Aristida adscensionis	Poaceae	Grass	A	1.1	-	-	1.2	-	2.6
Aristida congesta subsp. *congesta*	Poaceae	Grass	A	-	-	-	0.6	1.8	2.6
Aristida stipitata	Poaceae	Grass	A	-	1.8	-	0.6	-	2.6
Barleria macrostegia	Acanthaceae	Forb	A	1.1	-	-	0.6	-	-
Brachiaria nigropedata	Poaceae	Grass	P	31.9	19.3	-	-	-	-
Chenopodium album	Amaranthaceae	Forb	A	4.3	3.5	-	0.6	1.8	-
Chenopodium carinatum	Amaranthaceae	Forb	A	1.1	-	-	1.2	1.8	-
Cleome mbella	Cleomaceae	Forb	A	1.1	1.8	-	-	1.8	2.6
Enneapogon cenchroides	Poaceae	Grass	A	-	-	16.7	29.1	19.3	7.7
Eragrostis lehmanniana	Poaceae	Grass	P	40.4	33.3	-	42.4	54.4	41.0
Gisekia africana	Aizoaceae	Forb	A	-	1.8	-	4.2	1.8	-
Hermannia modesta	Malvaceae	Forb	A	1.1	1.8	-	-	-	-
Heteropogon contortus	Poaceae	Grass	P	2.1	-	16.7	-	-	-
Leucas capensis	Lamiaceae	Forb	A	-	1.8	-	1.2	-	2.6
Limeum aethiopicm	Mollugiinaceae	Forb	A	-	3.5	-	1.8	-	-
Limeum viscosum	Mollugiinaceae	Forb	A	3.2	3.5	-	-	-	-
Pogonarthria squarrosa	Poaceae	Grass	P	2.1	10.5	-	-	-	-
Schmidtia pappophoroides	Poaceae	Grass	P	8.5	12.3	50.0	0.6	1.8	-
Setaria verticillata	Poaceae	Grass	A	-	-	-	5.5	-	-
Talinum caffrum	Talinaceae	Forb	A	1.1	1.8	-	0.6	-	-
Tragus racemosa	Poaceae	Grass	A	1.1	1.8	16.7	0.6	-	35.9
Tribulus terrestris	Zygophuyllaceae	Forb	A	-	1.8	-	9.1	15.8	2.6
Species richness per soil subhabitat				14	15	4	16	9	9
Species richness per soil type				20			17		

*A = Annual and P = Perennial

7.5 Discussion

The *T. camphoratus* population in this study showed a balanced sex ratio, confirming hypothesis A. Dioecious plants always tend towards an even sex ratio. According to López and Domínguez (2003), plants sense a disequilibrium between sexes by mechanisms such as pollination intensity and respond by allocating reproductive advantage towards the lesser represented sex. Furthermore, male and female plants each have distinctive resource allocation patterns, thus resulting in different resource requirements, which may be strongly influenced by environmental conditions and plant density (Teitel *et al.* 2016; Tonnabel *et al.* 2017). Dioecy is viewed as a reproductive strategy decreasing inbreeding and optimising resource allocation between sexes (Amorim *et al.* 2011). This characteristic could therefore become increasingly important for the success of *T. camphoratus* in its semi-arid environment and could give a reproductive advantage over other species in the same environment.

Similar to the observations of Smit (2003) on *Salvadora australis* in the Mopane savanna, it has been observed that *T. camphoratus* shrubs occurred in groups arranged in a circle throughout the study area, but especially on the sandy soils. Each association consisted of either only male or only female shrubs and is probably caused by vegetative reproduction. Beentje (1999) reported a similar phenomenon of *T. camphoratus* in Kenya. Root studies would be necessary to confirm this. This spatial aggregation of same-sex shrubs caused the biased sex ratio in some transects.

Accepting hypothesis B, the total number of seeds produced by female *T. camphoratus* was strongly related to the shrub's leaf production and size, with even smaller, coppicing plants (± 0.5 m maximum height) producing flowers and seeds. Although the study was conducted during below-average rainfall years, *T. camphoratus* seed production remained relatively high. In contrast, *S. mellifera,* whose seed production is known to be highly correlated with rainfall (Joubert *et al.* 2013), produced only a few or no pods during the study period (2018 - 2020). This suggests that *T. camphoratus* seed production, similar to that of *V. karroo* (O'Connor *et al.* 2010) is relatively independent of rainfall and results in a relatively constant seed supply each year.

Plants growing in the rocky soil produced fewer seeds ETTE^{-1}, thus rejecting hypothesis C. However, because the number of seeds per fruiting head was not affected by soil type, the lower seed production is ascribed to factors other than soil type, such as the negative influence of shrub density on seed production (Smit & Rethman 1998), as well as the generally smaller sized shrubs on that soil type. It is therefore questionable whether seed production ha^{-1} would be significantly influenced. In addition, *T. camphoratus* seeds are wind-dispersed (Schleicher *et al.* 2011) but losses of the seed crop to predation pre- and post-dispersal and the fate after dispersal are still unknown and require further research.

The findings of this study also suggest that *T. camphoratus* seeds are transient and thus do not persist in the soil for longer than one year (Thompson *et al.* 1993). This is in line with reports which suggest that smaller elongated seeds are generally short-lived (Thompson & Grime 1979; Thompson *et al.* 1993; Garner & Witkowski 1997). This further indicates that there is large seasonal variation in the soil seed bank, directly influenced by the timing of seed dispersal and germination or seed decay. The response and restoration potential of an area is amongst other factors determined by the timing of the control operations as well as the state of the soil seed bank at that time.

However, not only the temporal but also the spatial variation of the soil seed bank influences management decisions. Similar to the reports of Arroyo and Giner (2017), and Tessema *et al.* (2017), seed density was highest under the canopy and decreased with distance from the stem, which also confirms hypotheses D. While species richness followed a similar trend on the sandy soil, it did not differ between the soil subhabitats on the rocky soil. Higher seed density under the canopy compared to the uncanopied subhabitat can be ascribed to a few factors. It is expected that the canopy of *T. camphoratus* causes a drop in wind speed and thus windblown seeds are deposited and trapped underneath the shrub. This is in line with similar studies conducted in arid and semi-arid ecosystems which reported that vegetation patches trap seeds and lead to increased seed density and richness beneath them (Liu *et al.* 2012; Giladi *et al.* 2013). Furthermore, living *T. camphoratus* shrubs could possibly exhibit allelopathic effects on the soil, inhibiting seed germination underneath their canopy and therefore resulting in an accumulation of seeds over time. Differences in physical soil properties such as compaction, bulk density, crust formation, soil moisture and temperature between subhabitats (Belsky *et al.* 1993; Holdo & Mack 2014), influencing the ease of burial of seeds, as well as seed persistence in the soil (Garner & Witkowski 1997; Leckie *et al.* 2000), are suggested as other potential factors resulting in higher seed densities under the shrub canopy. Ward *et al.* (2018) suggested that the seed availability underneath the canopy of *T. camphoratus* could be limited, thus causing the low grass and forb cover underneath the canopy. However, this study showed that seed availability was not limiting, thus other factors such as tree-grass competition and resource availability resulted in the reduced plant production under the canopy compared to the uncanopied subhabitat.

Higher woody plant density, high abundance of surface rocks and less crust formation on the rocky soil may have resulted in significantly more seeds trapped in the uncanopied subhabitat of the rocky soil compared to uncanopied subhabitat of the sandy soil.

7.6 Conclusion

This study has shown that *T. camphoratus* male and female plants existed in dynamic equilibrium in the study area. Even though the soil seed bank study revealed that *T. camphoratus* seeds were short-lived and did not persist in the soil for longer than one year, female shrubs produce large quantities of seeds even during below-average rainfall years, ensuring that there are always fresh viable seeds available for germination and establishment when conditions become favourable. This gives *T. camphoratus* a competitive advantage over co-occurring *S. mellifera,* which requires at least two successive above-average rainfall seasons for adequate seed production and for successful seedling establishment (Joubert *et al.* 2013).

Moreover, the findings of this study have important implications for the management of *T. camphoratus*. In order to increase the success rate of the bush control programme, it is advised that the clearance of *T. camphoratus* should be performed before seed maturation occurs (i.e. before July in the study area). The removal of adult plants after seed maturation would increase the quantity of available seed in the environment and patches where adult shrubs grew create an ideal environment for seedlings to establish, thus significantly reducing the time span between follow-up treatments. Whereas, if *T. camphoratus* shrubs are removed prior to seed maturation at the end of the rainy season, chances for seedling recruitment from the soil seed bank are lowered considerably and follow-up treatments can be directed to the control of coppices instead.

Lastly, increased seed bank density and species richness under the shrub canopy highlights the importance of selective thinning approaches, keeping some large woody plants. In this way, species diversity, ecological stability and the restoration potential can be maintained. Owing to the high soil seed bank density of other plant species, notably grasses, and the high soil-nutrient status under the shrubs, a sharp increase in herbaceous layer production is expected in due time after bush clearance.

CHAPTER 8

Effect of soil and subhabitat differentiation on the growth of *Tarchonanthus camphoratus* seedlings

8.1 Introduction

The success of bush-clearing or thinning operations is often measured on the basis of the recovery, productivity and stability of the herbaceous layer, as well as the prevention of the mass re-establishment of woody plants (re-thickening). Many studies have shown a positive response of the herbaceous layer to the partial or complete removal of woody plants (Mapuma 2000; Richter *et al*. 2001; Pienaar 2006; Ndhlovu *et al.* 2011; Harmse *et al.* 2016). Richter *et al.* (2001) found that grass density in the Molopo Thornveld increased by 185% with decreased bush density, while Harmse *et al.* (2016) reported a grazing capacity increase of up to 280% after total bush clearing in the semi-arid Molopo Bushveld. However, the re-establishment of woody plants after thinning or clearing — either by resprouting or by seedling establishment from seed — remains a serious threat and this phenomenon has been widely reported in southern African savannas (Pienaar 2006; Pretorius *et al.* 2008; Witkowski & Garner 2008; Harmse *et al.* 2016).

The specific response of the vegetation to woody plant removal is amongst other factors driven by rainfall and soil properties, such as texture and soil-nutrient status (Dye & Spear 1982; Wiegand *et al.* 2005; Archer *et al.* 2017), especially in water- and nutrient-limited environments, such as the semi-arid savanna of southern Africa. The degree to which woody plants influence the soil nutrient status is species, soil type (see section 4.4) and age dependent (Wiegand *et al.* 2005; Ward *et al.* 2018). In chapter 4, it was reported that potassium and magnesium ion concentration under the canopy of *T. camphoratus* are significantly higher than under *S. mellifera,* and essential cations (potassium and calcium), as well as soil nitrogen and organic carbon, are significantly higher under the canopied than the uncanopied area. Soil enrichment under woody plants is a rather slow process (Smit 2004), developing over time, but also decreases slowly after woody plant removal and tree death (Ludwig *et al.* 2004). According to Facelli and Brock (2000), soil organic matter content can remain at elevated levels for as long as fifty years after tree death.

Even though decreased competition as a result of woody plant removal and increased soil-nutrient status allow for increased herbaceous biomass, it is known that some plants release allelochemicals into the soil. These metabolic secretions, including long chain fatty acids, phenolic acids, terpenoides, organic cyanides and others (Gniazdowska & Bogatek 2005), may have favourable or unfavourable effects in the environment, depending on which plants species it affects. Plant allelochemicals are known to affect seed germination (Ghebrehiwot *et al.* 2014; Arroyo & Giner 2017; Wang *et al.* 2018), seedling emergence (Fernandez *et al.* 2013), seedling mortality (Arroyo & Giner 2017) and seedling growth (Fernandez *et al.* 2013; Ghebrehiwot *et al.* 2014; Harunet *et al.* 2015; Wang *et al.* 2018). In organic crop production, these characteristics are already exploited as natural pesticides to control weeds and insects (Cheng & Cheng 2015), also because allelochemicals are species- and concentration-specific (Fernandez *et al.* 2013; Ghebrehiwot *et al.* 2014).

Matasyoh *et al.* (2007) reported that 80.9% of the essential oil extracted from *T. camphoratus* leaves consisted of monoterpenses, which have the potential to modify mitochondrial respiration (Gniazdowska & Bogatek 2005) and thus be detrimental to seedling establishment and growth. Therefore, after partial or total clearing, allelopathy can potentially play an important role in the rate of re-establishment of a bush-thickening species, such as *T. camphoratus*. In addition, inhibitors may be present in freshly produced seed that may cause dormancy and delay germination (Bareke 2018).

In order to have a better understanding of the pre-productive ecology of *T. camphoratus*, the following hypotheses were tested:

a) fresh *T. camphoratus* seeds exhibit dormancy that prevent or delay their germination,
b) *T. camphoratus* causes allelopathic effects on the soil,
c) soils originating from different subhabitats will have an effect on seedling establishment and growth, and
d) soils with different soil potential (soil type) will have an effect on the vegetative growth of established seedlings.

8.2 Procedure

8.2.1 Soil sampling

Topsoil (0 – 20 cm) was excavated from three identified subhabitats, namely, (1) < 25 cm from the stem, (2) halfway between the shrub's stem and the canopy edge (canopy middle), and (3) in the uncanopied area between adjacent shrubs (see section 4.3.1; Figure 4.1). Due to the relatively high density of *T. camphoratus* shrubs in the area and their extensive root system, it is expected that the topsoil from the uncanopied zone still originates from within the root zone of the shrubs. This was repeated for two sites with differing soil potential (i.e. deep sandy soil and shallow rocky soil) (see section 2.2.2).

8.2.2 Seed collection

T. camphoratus seeds were collected from randomly selected female *T. camphoratus* shrubs on both soil types (the sandy and the rocky site) on Rooipoort Nature Reserve. Seed harvesting took place at the beginning of September 2018, when shrubs started shedding their seeds. Harvested seeds were placed in paper bags and kept at room temperature until planting.

8.2.3 Seedling establishment and harvesting

Seedling establishment and growth of *T. camphoratus* were studied under controlled conditions in a greenhouse at the University of the Free State, Bloemfontein. The soil collected from the same subhabitats and study site (see section 8.2.1) was bulked and thoroughly mixed before large pots (18 703.5 cm^3) were filled with equal volumes of soil and labelled (Figure 8.1). This amounted to 3 subhabitats x 2 sites x 10 replications = 60 pots. The pots were arranged according to a predetermined randomisation design with five blocks and two columns (Appendix A) to avoid variability due to placement in the greenhouse. *T. camphoratus* seeds were planted at different depths (from on the soil surface to 1 cm deep) in all pots on 28 September 2018. The soil was kept moist at all times in such a way to avoid water stress, but also to prevent nutrient-leaching from the soil as a result of over-watering. Specific optimum germination temperature standards for *T. camphoratus* are not known, but based on general recommendations of the International Seed Testing Association (2009), the temperature in the glasshouse was regulated at 20 - 30°C for the full duration of the study. The first seedlings emerged only at the end of November 2018 (two months after planting) and seed-germination rates were observed until middle of January 2019. On 23 January 2019, seedlings were thinned from pots where multiple seedlings occurred to ensure that there was only one healthy seedling of similar age in each pot. In the case of a small number of pots where seedlings did not establish, seedlings were transplanted from pots of the same treatment where multiple seedlings occurred. Any additional seedlings that emerged after 23 January were removed in order to eliminate any possible competition.

Seedling height was measured weekly and commenced on 30 January 2019 (Figure 8.1). Eighteen weeks later all plants were harvested. The roots were carefully separated from the above-ground parts (Hagos 2001) and carefully washed from the soil with medium pressure water, removing as much soil and organic matter as possible without causing too much damage (Figure 8.2). The tap root was uncurled to determine its length and thereafter all roots were oven-dried at 70°C to constant mass and weighed.

For the above-ground parts, the number of leaves per seedling, number of daughter shoots per seedling, stem diameter at the base and seedling height were recorded. The stems and leaves were separated. All aboveground parts were oven-dried at 70°C to constant mass and weighed.

Figure 8.1: Photographs showing the process of seedling establishment from planting to seedlings at harvest (130 days)

Figure 8.2 *T. camphoratus* seedling roots in washing process

8.2.4 Statistical analyses

The Shapiro-Wilk test ($p > 0.05$) (Shapiro & Wilk 1965) 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 growth parameters (seedling height, stem diameter, number of leaves and stems, dry masses of leaves, stems and roots, and total dry mass). Tukey´s (HSD) *post hoc* test was performed to detect significant differences ($p < 0.05$). Because the number of leaves in the stem subhabitat on the sandy site was non-normally distributed and could not be transformed, Mann-Whitney U test was used to test for significant ($p < 0.05$) differences of all possible combinations. All analyses were conducted by using IBM SPSS for Windows, version 25 (IBM Corp., Armonk 2017) and are represented as mean ± 1 SE.

8.3 Results

By the end of November 2018 the first two seeds had germinated, followed by 27 more by the middle of December 2018. 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 growing in the soil originating from the sandy site differed significantly in height between the subhabitats ($F_{2;23} = 7.742$, $p = 0.03$). Seedlings growing in the soil from the two canopied subhabitats grew significantly ($p < 0.05$) higher than the seedlings growing in the soil from the uncanopied subhabitat (Figure 8.4 a). In the case of the soil originating from the rocky site, only seedlings growing in the soil from the stem subhabitat grew significantly higher ($F_{2;23} = 3.994$, $p = 0.032$) than those from the uncanopied subhabitat. Seedling height in soil from the canopy middle was statistically non-significant ($p > 0.05$) to the stem as well as the uncanopied subhabitat (Figure 8.3 & Figure 8.4 b).

Figure 8.3: Photograph illustrating seedling height at 130 days on sandy soil (left) and rocky soil (right) each in three subhabitats: stem, canopy middle and uncanopied (left to right)

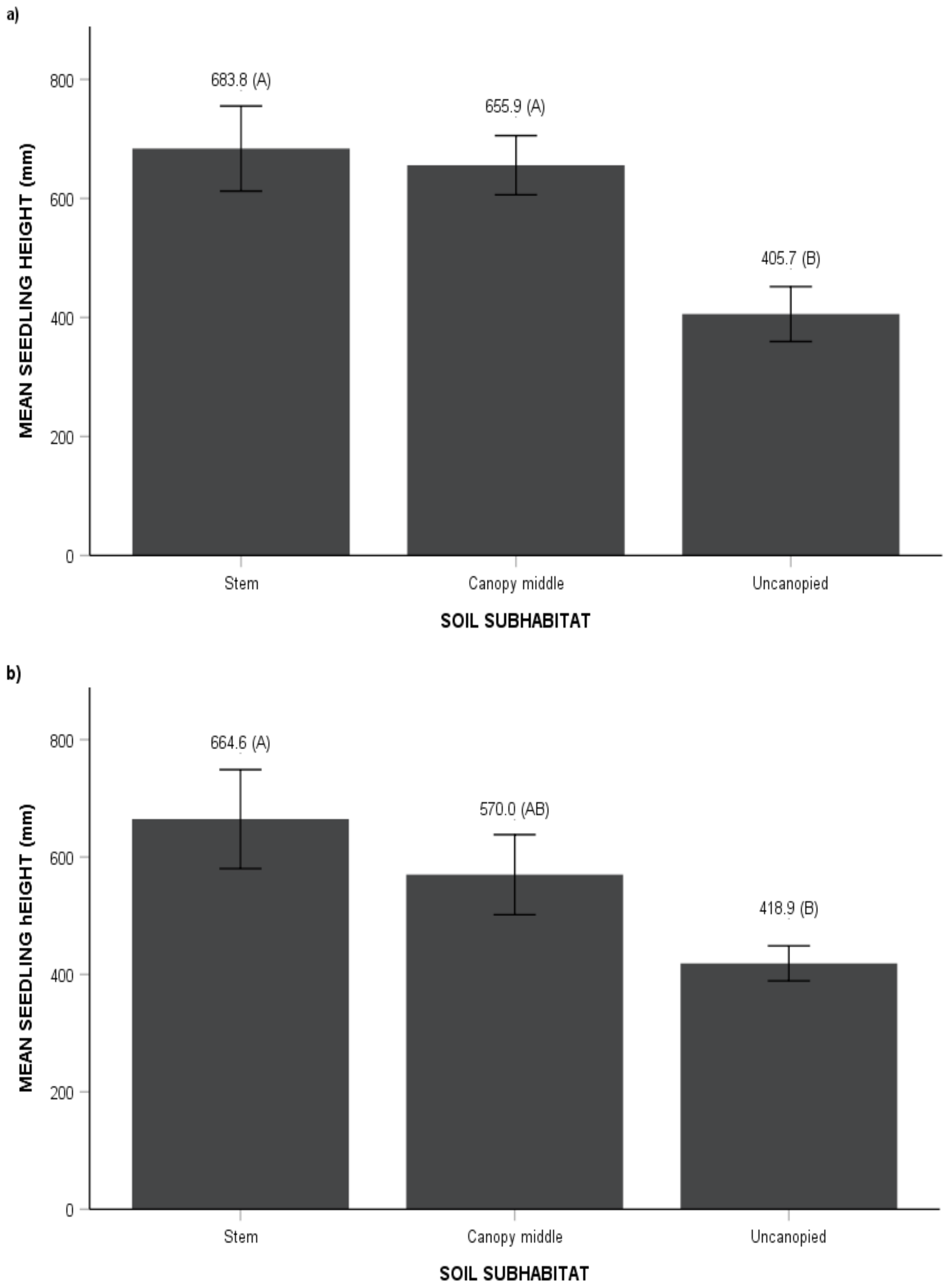

Figure 8.4: Mean (± SE) seedling height of *T. camphoratus* seedlings ($n = 10$) at 130 days of age growing in soil from three soil subhabitats and two soil types: (a) sandy and (b) rocky soil. Different letters indicate statistical significance ($p < 0.05$).

Seedlings growing in the soil from the two canopied subhabitats of both the sandy and the rocky site grew significantly thicker (stem base diameter) compared to those growing in soil from the uncanopied subhabitat ($F_{2;23} = 16.716$, $p < 0.001$ and $F_{2;23} = 8.000$, $p = 0.02$ respectively) (Figure 8.5). However, the stem diameters of plants growing in soil of the canopied subhabitats of both soil types did not differ significantly ($p > 0.05$).

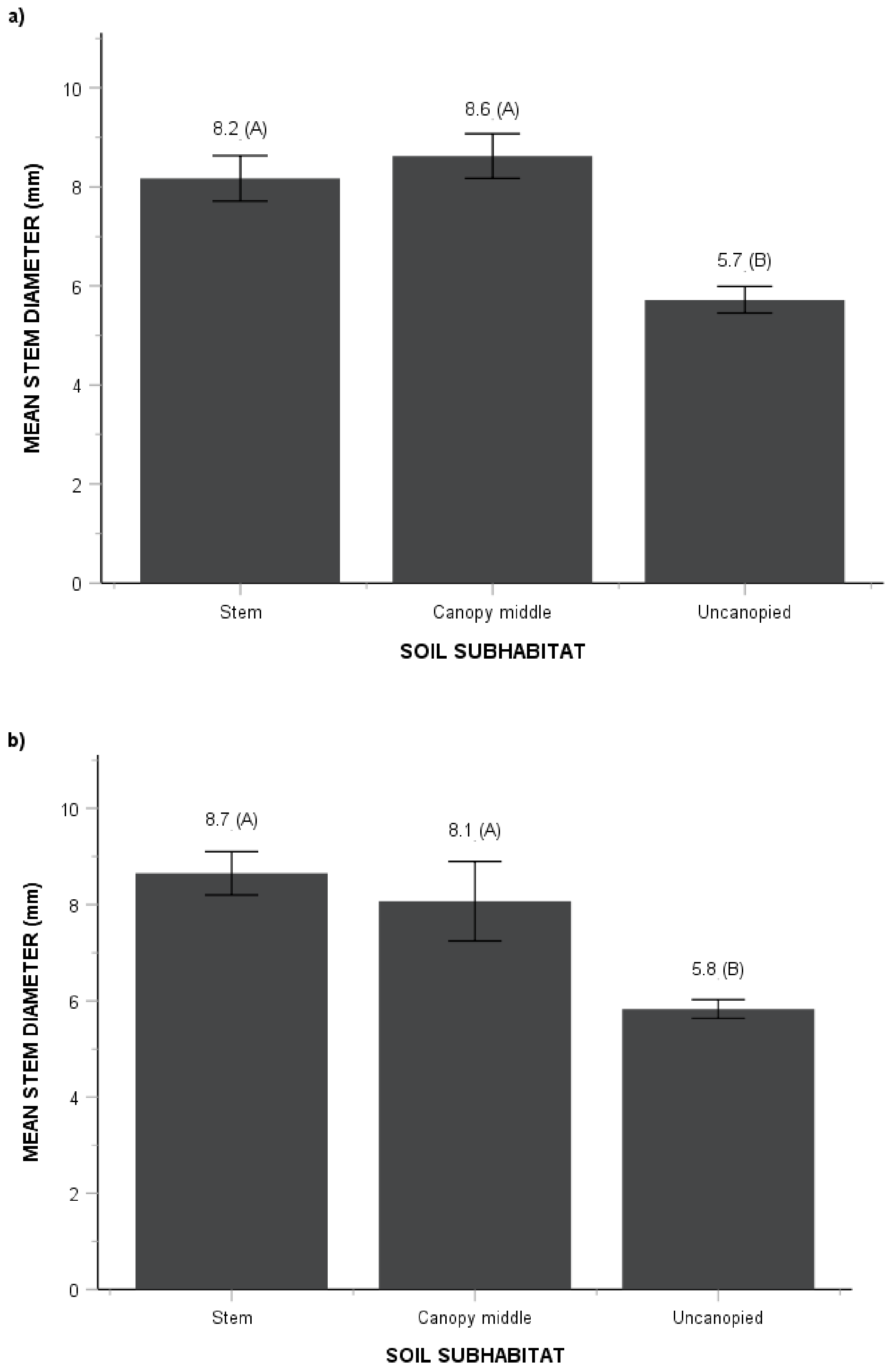

Figure 8.5: Mean (± SE) stem base diameter of *T. camphoratus* seedlings (n = 10) at 130 days of age growing in soil from three soil subhabitats and two soil types: (a) sandy and (b) rocky soil. Different letters indicate statistical significance ($p < 0.05$).

Furthermore, the number of daughter shoots growing from the main shoot, were significantly less in plants growing in the soil from the uncanopied subhabitat compared to those growing in soil from the canopied subhabitats in both soil types (sandy: $F_{2;23} = 11.092$, $p < 0.001$ and rocky: $F_{2;23} = 8.926$, $p = 0.001$) (Figure 8.6 a & b).

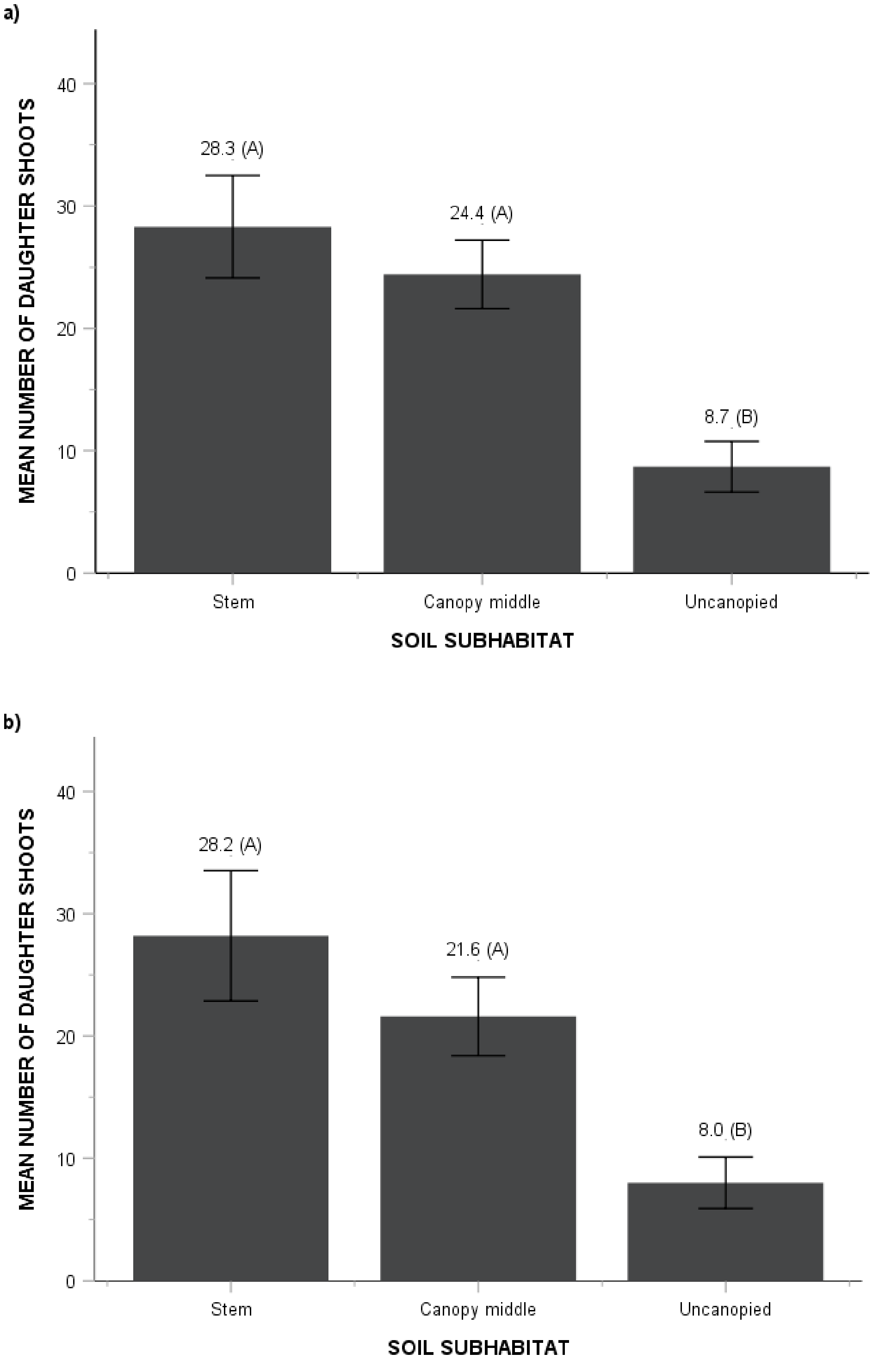

Figure 8.6: Mean (± SE) number of daughter shoots per *T. camphoratus* seedling (n = 10) at 130 days of age growing in soil from three soil subhabitats and two soil types: (a) sandy and (b) rocky soil. Different letters indicate statistical significance ($p < 0.05$).

The number of leaves per seedling were 138% and 88% higher for plants growing in the soil originating from the stem and canopy middle subhabitats, respectively, compared to plants growing in soil from the uncanopied subhabitat of the sandy site (Mann-Whitney U: $p < 0.001$) (Figure 8.7 a). Similarly, plants growing in the soil from the stem and canopy middle subhabitat had 114% and 106% more seedling leaves, respectively, than plants growing in soil from the uncanopied subhabitat of the rocky site (Figure 8.7 b).

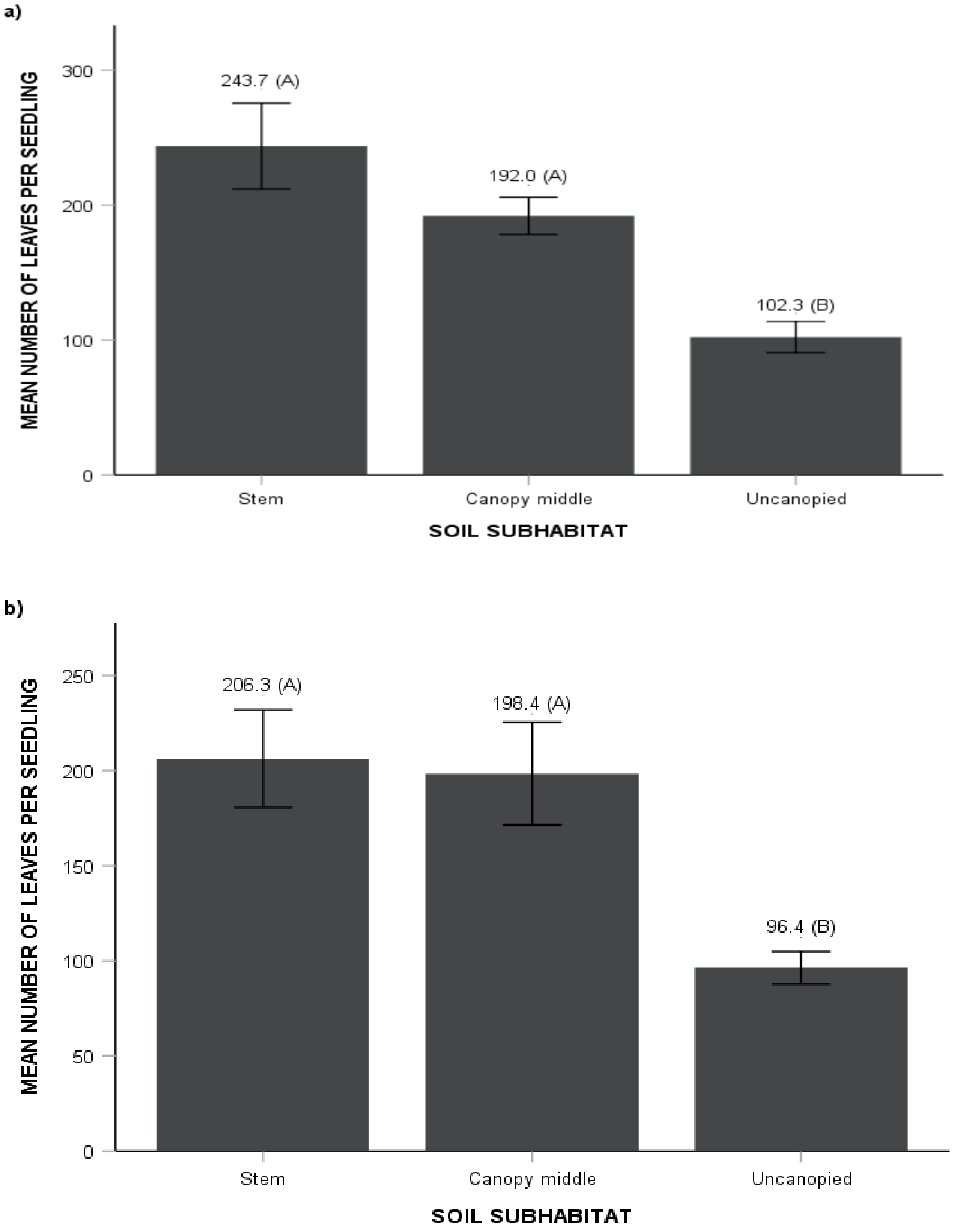

Figure 8.7: Mean (± SE) number of leaves per *T. camphoratus* seedling (n = 10) at 130 days of age growing in soil from three soil subhabitats and two soil types on (a) sandy and (b) rocky soil. Different letters indicate statistical significance ($p < 0.05$).

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 heavier leaf dry mass (sandy: $F_{2;23} = 13.760$, $p < 0.001$ and rocky: $F_{2;23} = 9.363$, $p = 0.001$), shoot dry mass (sandy: $F_{2;23} = 9.255$, $p = 0.01$ and rocky: $F_{2;23} = 8.071$, $p = 0.02$) and total dry mass (sandy: $F_{2;23} = 7.959$, $p = 0.002$ and rocky: $F_{2;23} = 7.812$, $p = 0.003$) was recorded in plants growing in the soil from the canopied subhabitats compared to plants growing in the soil from the uncanopied subhabitat. The plants growing in the soil of the two canopied subhabitats were statistically non-significant ($p > 0.05$) in leaf (Figure 8.8), shoot (Figure 8.9) and total dry mass (Figure 8.10) in both soils.

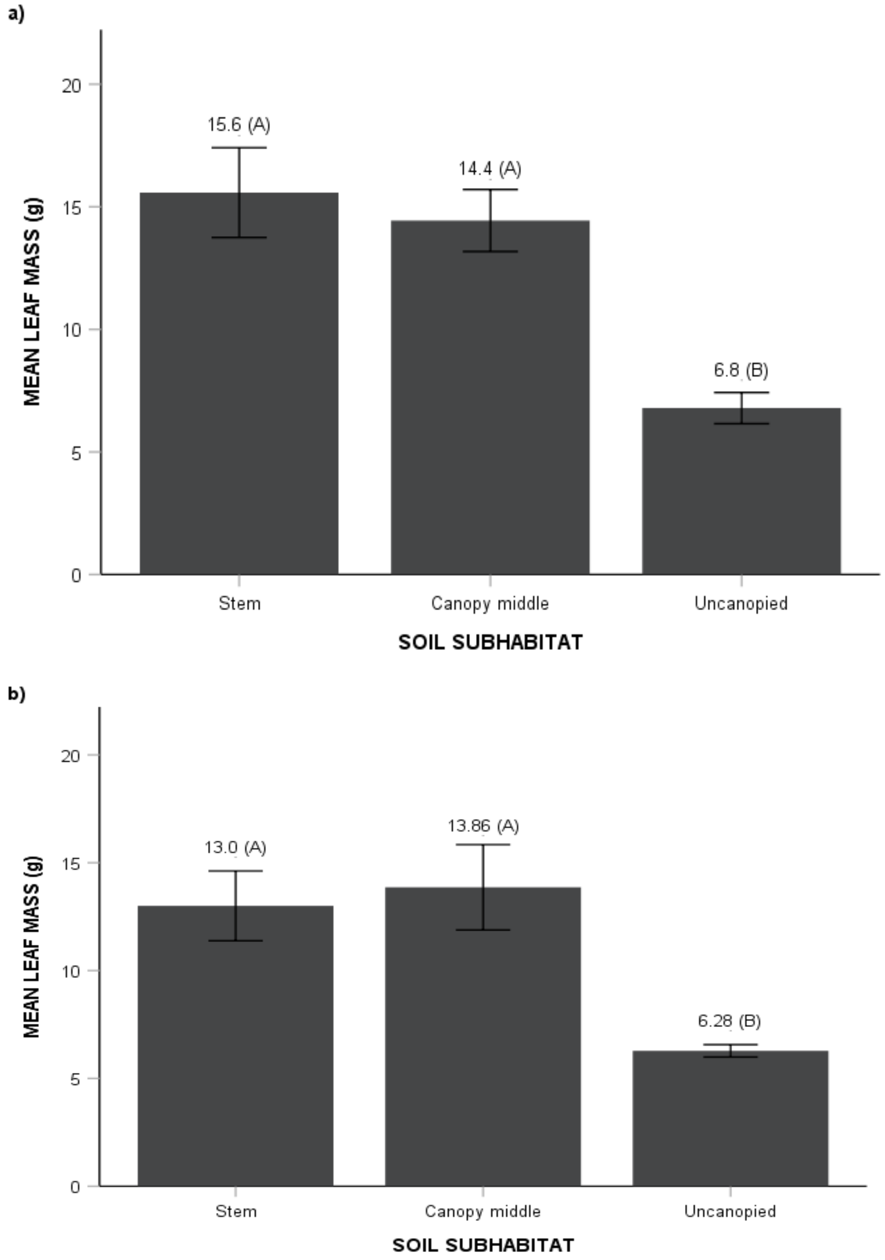

Figure 8.8: Mean (± SE) leaf dry mass of *T. camphoratus* seedlings (n = 10) at 130 days of age growing in soil from three soil subhabitats and two soil types: (a) sandy and (b) rocky soil. Different letters indicate statistical significance ($p < 0.05$).

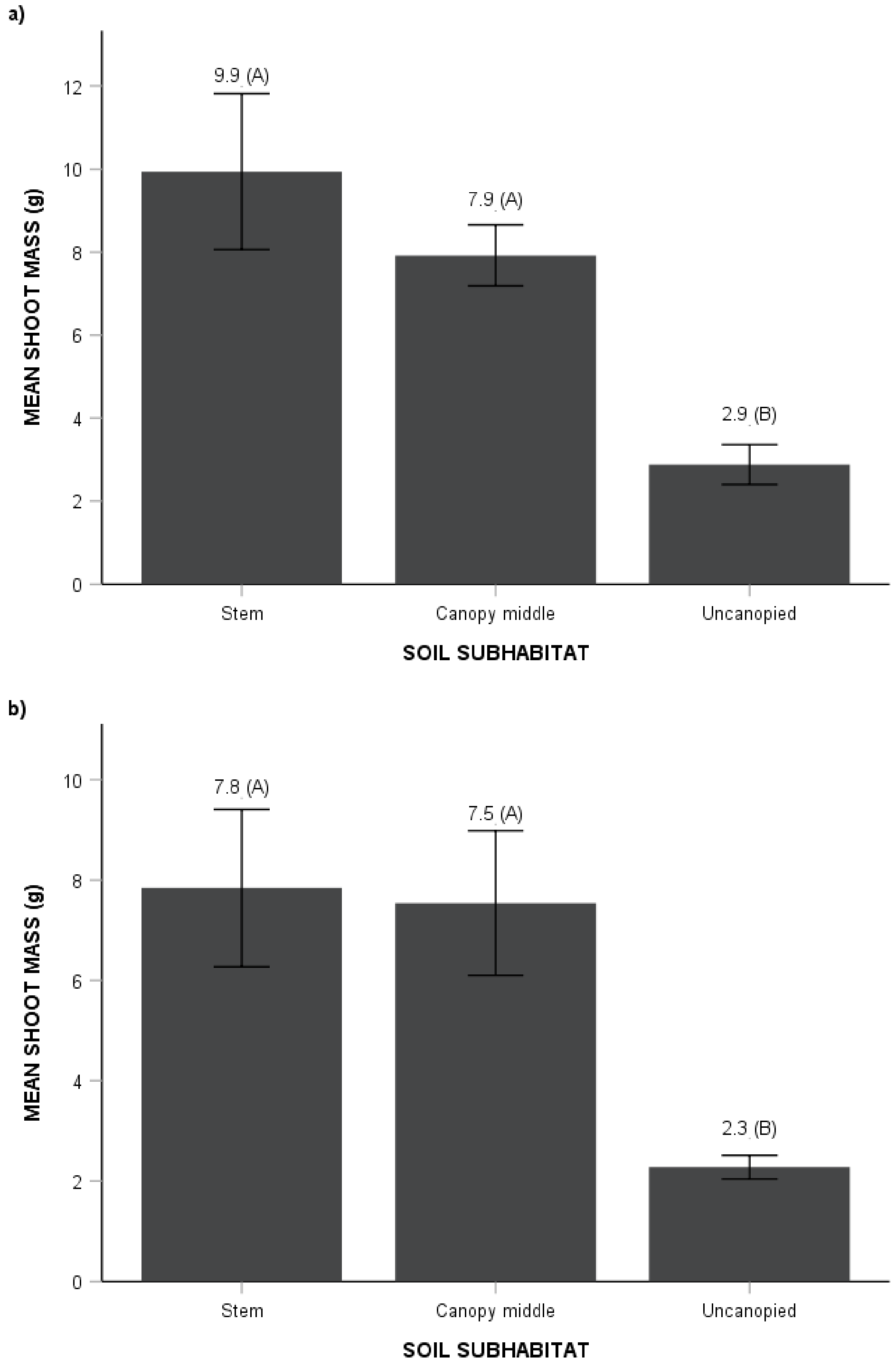

Figure 8.9: Mean (± SE) shoot dry mass of *T. camphoratus* seedlings (n = 10) at 130 days of age growing in soil from three soil subhabitats and two soil types: (a) sandy and (b) rocky soil. Different letters indicate statistical significance ($p < 0.05$).

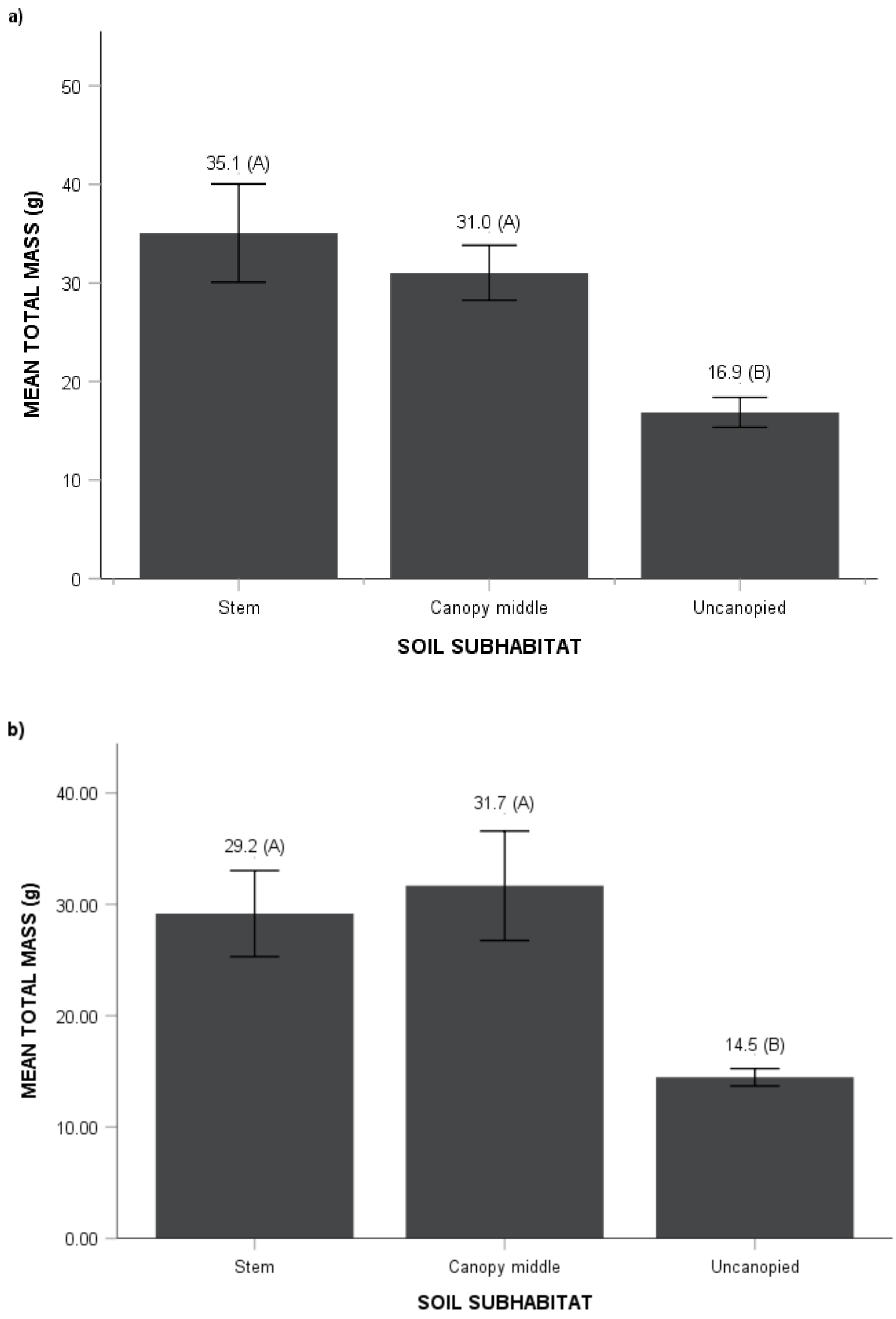

Figure 8.10: Mean (± SE) total dry mass (leaves + shoots + roots) of *Tarchonanthus camphoratus* seedlings (n = 10) at 130 days of age growing in soil from three soil subhabitats and two soil types: (a) sandy, and (b) rocky soil. Different letters indicate statistical significance ($p < 0.05$).

No significant differences ($p > 0.05$) in root length were established between plants growing in soil from any of the subhabitats on either of the sites (Figures 8.11, 8.12 and 8.13). The only significant difference in root dry mass was found between plants growing in the soil from the canopy middle and uncanopied subhabitat of the rocky site ($F_{2;23} = 3.863$ $p = 0.036$).

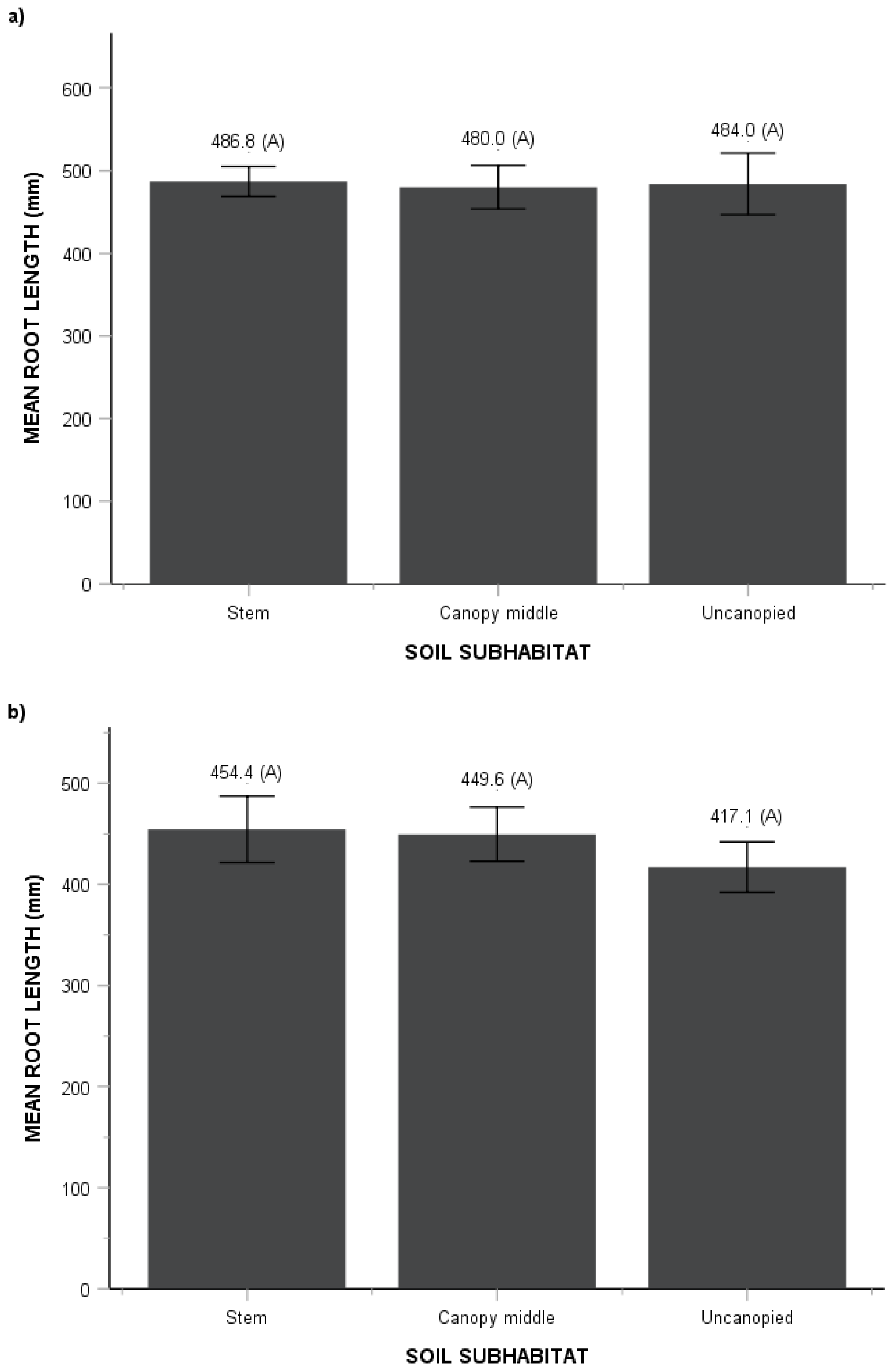

Figure 8.11: Mean (± SE) tap root length of *T. camphoratus* seedlings (n = 10) at 130 days of age growing in soil from three soil subhabitats and two soil types: (a) sandy and (b) rocky soil. Same letters indicate statistical non-significance ($p > 0.05$).

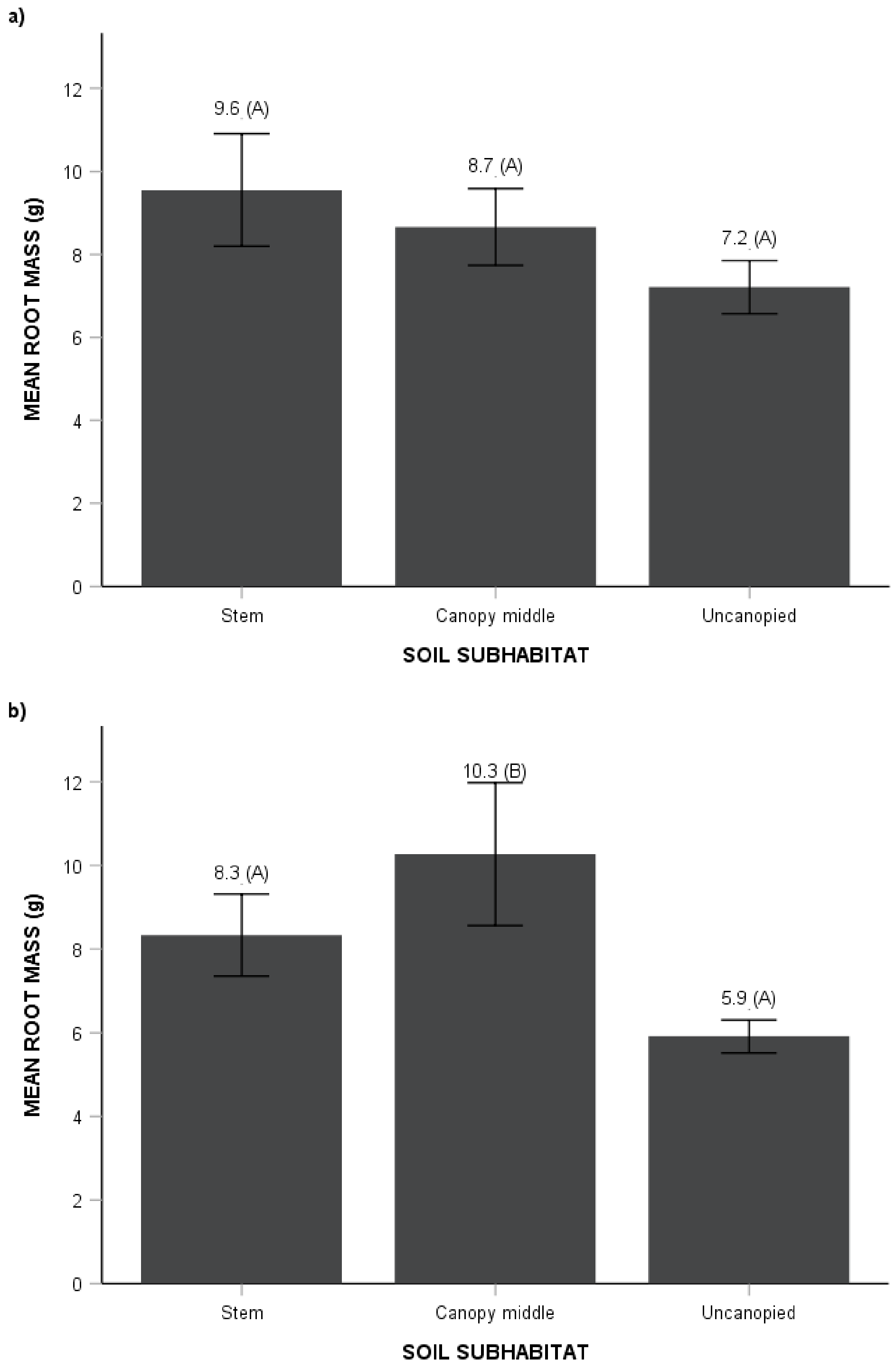

Figure 8.12: Mean (± SE) root dry mass of *T. camphoratus* seedlings (n = 10) at 130 days of age growing in soil from three soil subhabitats and two soil types: (a) sandy and (b) rocky soil. Same letters indicate statistical non-significance ($p > 0.05$).

Figure 8.13: Roots of *T. camphoratus* seedlings growing in soil from stem, canopy middle and uncanopied (from left to right) subhabitat of the rocky site

In addition, the average seedling growth rate (in terms of plant height) per day over the 130 days was statistically higher ($F_{2;23}$ = 7.056 p = 0.004) for plants growing in the soil from the canopied subhabitat compared to those growing in the soil from the uncanopied subhabitats of the sandy site. However, no significant growth rate difference ($p > 0.05$) was established between plants growing in the soil from the canopied subhabitats of the sandy site (Figure 8.14 a). For seedlings growing in soil originating from the rocky site, a significant difference in average growth rate existed between plants growing in soil from the stem and the uncanopied subhabitat ($F_{2;23}$ = 3.362 p = 0.42), but the growth rate of plants on soil from the canopy middle subhabitat did not differ significantly ($p > 0.05$) from the other two subhabitats (Figure 8.14 b).

While the effect of subhabitat differentiation (canopied vs uncanopied) on the various seedling growth parameters on both soil types (sandy vs rocky) was very clear, the soil type did not have a statistically significant ($p < 0.05$) effect on the growth parameters of seedlings in all three subhabitats (Table 8.1 and Table 8.2).

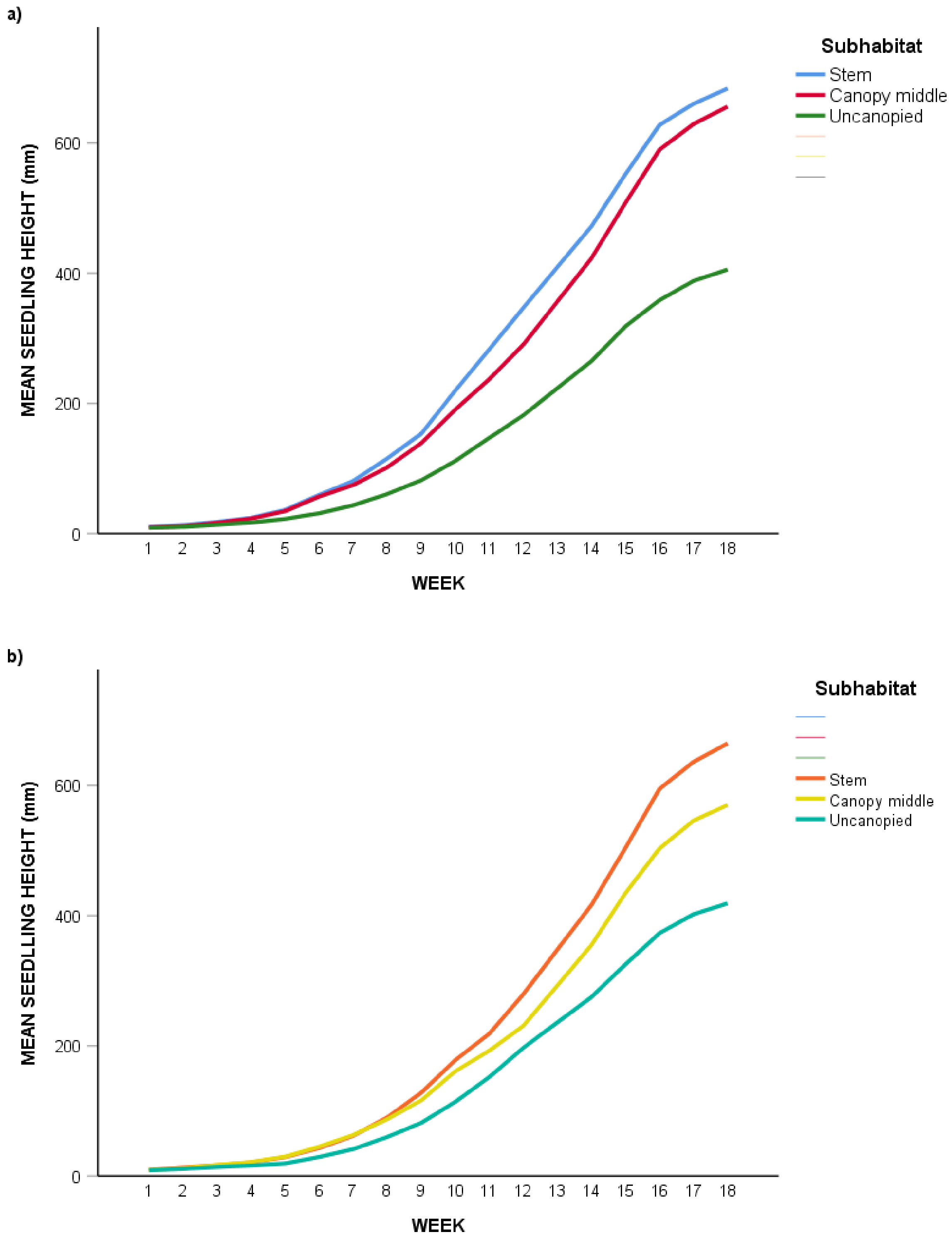

Figure 8.14: Mean *T. camphoratus* seedling height (n = 10) over 18 weeks growing in soil from three subhabitats and two soil types: a) sandy and b) rocky soil.

Table 8.1: Soil effect on seedling height, stem diameter, number of leaves and number of daughter shoots (mean ± 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 ± 71.5^{a}	8.2 ± 0.5^{a}	243.7 ± 31.8^{a}	28.3 ±4.2^{a}
	Rocky	664.6 ± 84.3^{a}	8.7 ± 0.5^{a}	206.3 ± 25.6^{a}	28.2 ± 5.3^{a}
Canopy middle	Sandy	655.9 ± 49.8^{a}	8.6 ± 0.4^{a}	192.0 ± 13.8^{a}	24.4 ± 2.8^{a}
	Rocky	570.0 ± 68.2^{a}	8.1 ±0.8^{a}	198.4 ± 27.0^{a}	21.6 ± 3.2^{a}
Uncanopied	Sandy	405.7 ± 46.1^{a}	5.7 ± 0.3^{a}	102.3 ± 11.5^{a}	8.7 ± 2.0^{a}
	Rocky	418.9 ± 29.8^{a}	5.8 ± 0.2^{a}	96.4 ± 8.6^{a}	8.0 ± 2.1^{a}

Table 8.2: Soil effect on leaf dry mass, shoot dry mass, root length and root dry mass (mean ± 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 ± 1.8^{a}	9.9 ± 1.9^{a}	486.8 ± 18.3^{a}	9.6 ± 1.4^{a}	35.1±5.04^{a}
	Rocky	13.0 ± 1.6^{a}	7.8 ± 1.6^{a}	454.4 ± 32.9^{a}	8.3 ± 1.0^{a}	29.2±3.9^{a}
Canopy middle	Sandy	14.4 ± 1.2^{a}	7.9 ± 0.7^{a}	480.0 ± 26.3^{a}	8.7 ± 0.9^{a}	31.0±2.8^{a}
	Rocky	13.9 ± 2.0^{a}	7.5 ± 1.4^{a}	449.6 ± 26.9^{a}	10.3 ± 1.7^{a}	31.7±4.9^{a}
Uncanopied	Sandy	6.8 ± 0.6^{a}	2.9 ± 0.5^{a}	484.0 ± 37.1^{a}	7.2 ± 0.6^{a}	16.9±1.5^{a}
	Rocky	6.3 ± 0.3^{a}	2.3 ± 0.2^{a}	417.1 ± 25.0^{a}	5.9 ± 0.4^{a}	14.5±0.8^{a}

8.4 Discussion

8.4.1 Seed dormancy

The observed long delay between planting and seed germination (> 2 months), thus accepting hypothesis A, can be ascribed to many factors. Some plant species' seeds are known to be rudimentary at seed fall, meaning that seed maturation only takes place after seed fall, while others contain germination inhibitors. Furthermore, a hard, impermeable seed coat can cause mechanical resistance to radical penetration or prevent water and/or oxygen exchange and therefore delays germination (Smit, Rethman & Moore 1996; Bentsink & Koornneef 2008). Further research on the mechanism of *T. camphoratus* seed dormancy and conditions which eventually trigger seed germination would be necessary to be able to gain a better understanding of its seedling establishment. Regardless of the exact mechanism triggering seed dormancy of fresh *T. camphoratus* seeds, the existence of such dormancy is an important observation with potential practical implications for the management of the species.

8.4.2 Allelopathic effect on the soil

Alllelopathy can play a key role in determining plant community structure and composition (Ghebrehiwot *et al.* 2014; Singh *et al.* 2014; Arroyo & Giner 2017). Allelochemicals enter the environment as root exudates, decomposition residues, volatiles and/or leachates (Gniazdowska & Bogatek 2005), which are then known to alter, amongst others, the soil environment (Ruwanza & Shackleton 2016). In this study, seedlings germinated abundantly in all the pots (rejecting hypothesis B), thus confirming that *T. camphoratus* does not release allelochemicals into the soil that inhibit its own seeds' germination, at least not after the mature plant has been removed, as would be the case in bush-clearing operations. This implies that the high leaf litter which can be found under the *T. camphoratus* canopy (Ward *et al.* 2018) or the roots do not release sufficient concentrations of allelochemicals to inhibit germination or *T. camphoratus* seeds remain unaffected by terpenoids. Furthermore, Inderjit *et al.* (2008), suggested that soil microorganisms can mineralise allelochemicals to below phytotoxic levels, therefore leaving germinating seeds uninfluenced. It has also been found that many plants do not produce allelochemicals throughout their lifetime, but that allelochemical synthesis is growth-stage and age dependent, as well as seasonal (Alford *et al.* 2007; Huang *et al.* 2003), thus indicating that allelopathy is a very dynamic process that may also occur in pulses (Weidenhamer 2005; Perry *et al.* 2007).

8.4.3 Effect of soil and subhabitat differentiation on seedling growth

For all measured growth parameters, except root length and root dry mass, significantly better and faster plant growth was observed in the soils collected in the two canopied subhabitats compared to the uncanopied subhabitat and was similar for both soil types. This corresponds with the findings of Hagos (2001) who, in a similar experiment, also found increased growth of *S. mellifera* seedlings grown in soil collected near the stem of *S. mellifera* compared to those grown in soil from the uncanopied subhabitat. The higher nutrient content of the soil underneath the canopies of *T. camphoratus* shrubs compared to the uncanopied zone (see section 4.4) is considered to be responsible for better growth. Ludwig *et al.* (2004) found that biomass production in the open grassland was limited by nitrogen, while phosphorus limited understory productivity. Vigorous vegetative growth is associated with sufficient nitrogen levels, while phosphorus deficiency leads to stunted growth and poorly developed root systems (Havlin *et al*. 2014). Significantly higher nitrogen levels in the soil around the stem of *T. camphoratus* compared to the open grassland were found in this study (see section 4.4.4), as well as by Ward *et al.* (2018). Leaf development is proportional to nitrogen supply (Havlin *et al*. 2014), thereby explaining the significantly higher leaf numbers and leaf dry mass of seedlings in the canopied subhabitats compared to the uncanopied subhabitats.

Even though statistically non-significant ($p < 0.05$), mean plant-available phosphorus in the soil from the canopy middle subhabitat was notably higher than in the uncanopied subhabitat of the rocky site (see section 4.4.3), which could explain the higher root mass found in plants grown in the soil from the canopy middle of the rocky site. Furthermore, the decreasing trend in plant-available phosphorus from the stem towards the open grassland on the sandy site may partly explain the similar decreasing trend in root mass of *T. camphoratus* seedlings growing in soil from the sandy site. However, this also indicates that phosphorus is not the only factor determining root growth.

No statistically significant differences ($p > 0.05$) in seedling growth could be established between the soils from the sandy and the rocky sites, thus rejecting hypothesis D. Schleicher *et al.*(2011) found that *T. camphoratus* juveniles grew bigger in sandy soil than in rocky soil in a natural environment. Rock fragments may improve growing conditions for plants, by decreasing evaporation and reducing crust formation, thus resulting in increased water availability (Du *et al.* 2017; Mi *et al.* 2016), but may also hinder plant growth by forming physical obstructions to root growth and increase surface run-off on hard soils. Mi *et al.* (2016) found no significant difference in plant height, stem diameter and biomass of korshinsk peashrubs (*Caragana korshinskii*) growing in sandy loam soil (0% rock fragments) and sandy loam soil with up to 30% rock fragments. This is in line with results of this study, because, even though the soil originates from a site with up to 70% surface rocks (see section 2.2.2), large rock fragments were removed during soil excavation. Soil in the greenhouse trial therefore had only very few rock fragments.

8.4.4 Practical implications

T. camphoratus seeds are wind dispersed and, due to the dense canopy structure of the shrubs, as well as their close proximity, many seeds fall below the parent plant or another *T. camphoratus* shrub (Okubo & Levin 1989; Schleicher *et al.* 2011). At the time when *T. camphoratus* sheds the majority of its seeds (September to December 2018 & 2019), its leaf carriage was below 40% (see section 5.4.2) such that the shrub canopy posed very little resistance to seeds to fall through. However, this might be the case for below-average rainfall years only, as leaf carriage may be higher in above-average rainfall years, which could potentially limit seed fall through. Ward *et al.* (2018) also noted that the dense *T. camphoratus* canopy during autumn and early winter could limit seeds of especially herbaceous plants, seeding after the spring and summer rains, to get through the canopy.

Consequently, when removing the mature shrubs a so-called “fertility island”, with high density of *T. camphoratus* seeds, and no competition from a mature shrub and very little competition from the herbaceous layer (Ward *et al.* 2018) is left behind. This gives *T. camphoratus* seedlings excellent chances for recruitment.

8.5 Conclusion

No allelopathic effects that limit seed germination and the survival of *T. camphoratus* were observed in the soil collected from underneath their canopies. This, however, does not totally rule out the possibility that *T. camphoratus* may have allelopathic characteristics, which could negatively influence herbaceous-layer productivity and diversity or seedling recruitment of other woody species in its environment. This specific aspect will need to be investigated in another detailed study.

Statistically significant ($p < 0.05$) differences in above-ground growth of *T. camphoratus* seedlings growing in soil from the canopied (stem and canopy middle) subhabitats, compared to the uncanopied subhabitat, were recorded. 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 ($p > 0.05$). The above-ground seedling growth parameters that were measured included seedling height, stem diameter, leaf and daughter shoot numbers, dry mass of leaves and shoots, total dry mass and average growth rates. In contrast to the above-ground growth parameters, no statistically significant ($p < 0.05$) difference could be established between the root lengths and root dry masses of seedlings grown in the soil of all three subhabitats. Hypothesis C is therefore accepted for the above-ground growth parameters but rejected for the below-ground growth parameters.

Increased nutrient availability under the shrub canopy (see chapter 4) 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.

The absence of allelopathic effects inhibiting *T. camphoratus* seed germination as well as higher nutrient availability are considered to be responsible for the better growth of *T. camphoratus* seedlings in soil from the canopied subhabitats. This has important implications for bush-clearing or thinning operations, as areas where mature *T. camphoratus* shrubs are removed subsequently present hotspots for post-tree clearing/thinning seedling establishment and growth.

CHAPTER 9

Allometric biomass estimations for *Tarchonanthus camphoratus*

9.1 Introduction

The need for an easy, fast, repeatable and cheap procedure for the accurate description and quantification of all above-ground components of the woody plant community on an individual and a landscape basis has been achieved by the development of the BECVOL 3 – model (Biomass Estimates from Canopy Volume). The model has originally been developed by GN Smit in 1989 (Smit 1989a, 1989b) and has since been complimented and expanded into the current version.

With the aid of the BECVOL 3 – model, accurate estimations of the above-ground woody plant biomass (including the leaf and wood components) can be done, which are useful for better understanding and management decisions concerning the savanna structure, productivity, grass-tree-herbivore interactions, different land use practices and their impacts, as well as browser stocking rates (Smit 2014). An added advantage of using the model is its ability to work with either the entire woody plant or only portions (Smit 1989b), which is especially important in terms of determining the browse availability to herbivores with different browsing heights.

The model is based on the relationship between a woody plant's spatial canopy volume and its leaf volume and dry mass, as well as woody dry mass (in three fractions) (Smit 2014). Various savanna species have already been included into the model and two "general" regression models exist for microphyllous species and broad-leaved species which were developed to accommodate estimations of above-ground biomass of species for which unique regression models do not currently exist.

Young and Francombe (1991), and Kiruki *et al.* (2010) have attempted to estimate *T. camphoratus* wood biomass in Kenya. The objective of this study was to further expand the more versatile BECVOL 3 – model by developing additional regression equations from harvested undamaged and coppicing *T. camphoratus* shrubs relating spatial canopy volume to above-ground leaf and wood biomass.

9.2 Procedure

9.2.1 Trial layout and shrub harvesting

The method used was in accordance with Smit (1989a, 1989b, 2014). Twenty healthy shrubs with no signs of damage by browsing herbivores, fire or cutting evident, representing all sizes in the *T. camphoratus* population were selected for harvesting. A further twenty coppicing *T. camphoratus* shrubs which were felled at the beginning of the study in March

2018, or burned by a veld fire in November 2018 and allowed to coppice were also selected for harvesting. Harvesting was done at peak biomass only (February to May) (Figure 9.1). Prior to harvesting the shrub's spatial canopy volume was determined by taking the following measurements: (A) shrub height, (B) height at maximum canopy diameter, (C) height of first leaves or potential leaf-bearing shoots, (D) maximum canopy diameter and (E) base diameter of the foliage at height of first foliage. The average of two measurements perpendicular to each other was taken for the maximum diameter (D) and the base diameter (E), because further calculations of the canopy volume assume a circular canopy. From these measurements (A – E) the spatial canopy volume (cm^3) of each shrub was calculated, by using one or a combination of the following shape's volume formulae: an ellipsoid, a right circular cylinder, a right circular cone or a frustum of right circular cone (Smit 1989b).

For undamaged *T. camphoratus* only, the diameter of all stems emerging from the soil was measured at ground level. After the shrub was harvested, the leaves were separated from the woody component by hand and the woody component was further separated into three diameter classes, namely, shoots ≤ 5 mm, stems > 5 - 20 mm and stems > 20 mm. The three categories of the wood component are distinguished on the basis that shoots ≤ 5 mm in diameter are considered browsable; stems > 5 – 20 mm are neither browsable nor suitable as biofuel, but could be used for brush packing in veld restoration and stems > 20 mm is preferred for fuelwood, as well as charcoal production (Smit 2014). Dead woody material, as well as flowers were separated from the other components but not included in the regression analyses. Even though it had been observed that flowers were readily browsed by wildlife and domestic stock, the flowering time is very short such that it is of little value to include flowers in the browsable component representing the whole year.

In order to minimise moisture loss from the leaves, only as much material as could be separated in one day was harvested at a time; work was conducted indoors and leaves were covered with a wet cloth. The leaves were air-dried after the volume was measured by determining the volume of water displaced in a measuring cylinder. Thereafter, all components were oven dried at 70°C to constant mass and weighed.

9.2.2 Statistical analyses

Separate regression models were developed for undamaged and coppicing *T. camphoratus* shrubs. Regression analyses were applied relating the calculated spatial canopy volume (cm^3) as the independent variable and the leaf volume (cm^3), as well as each of the dried shrub fractions (g) (leaves, shoots ≤ 5 mm, stems > 5 - 20 mm and stems > 20 mm) as dependent variables. Three regression models were tested: linear ($y = a + bx$), exponential ($\ln y = a + bx$) and multiplicative ($y = ax^b$), where y = the estimated leaf volume (cm^3) / dry mass fraction (g), x = the spatial canopy volume (cm^3), a = the intercept and b = the slope. The spatial canopy volume was transformed to its natural logarithmic value (ln) for use in exponential and multiplicative regression models, as this partial transformation only changed the relationship from convex to concave and therefore fitted the model better. The analyses were performed using Statgraphics software (STSC, Inc., Rockville, MD, USA, 1999).

Figure 9.1: Undamaged (top left) and coppicing (top right) *T. camphoratus* selected for harvesting, transportation of harvested material to homestead (bottom left) and air-drying of leaves from harvested shrubs (bottom right) (Photos: IJ Stehn)

9.3 Results and Discussion

Separate regression models were developed for undamaged and coppicing *T. camphoratus* shrubs, because coppice plants prioritise leaf production over wood production (see section 6.4.2) and thus have significantly higher leaf dry mass per unit canopy volume ($F_{1;38} = 24.745$, $p < 0.001$) compared to undamaged shrubs. Furthermore, coppices differ structurally to undamaged shrubs, as they usually have higher shoot density compared to undamaged plants (Pratt 1966). No regression models were developed for stems > 20 mm in diameter for coppicing *T. camphoratus*, because harvested coppices were too young and this woody component only develops in larger and older shrubs. The results of the regression analyses of undamaged *T. camphoratus* are presented in Table 9.1 and those of coppicing *T. camphoratus* shrubs are presented in Table 9.2.

From the results, it was clear that, no matter which regression model was used, all yielded highly significant results. However, in most cases the exponential model yielded the highest coefficient of determination. The trend towards higher coefficients of determination for curvilinear (exponential and multiplicative) regression models compared to the linear model was also noted by Smit (2014) and can be attributed to leaves and leaf-bearing shoots < 5 mm in diameter being concentrated in the outer layer of the canopy and less in the darker canopy middle (Figure 9.2 and Figure 9.3). Therefore, with increasing shrub size, there were fewer leaves and shoots per unit canopy volume and larger stems (Ø > 20 mm) occupy more space in the canopy centre, giving the woody plant its characteristic structure (Van der Meulen & Werger 1984; Bartelink 1997; Ansley *et al.* 2012). The choice of which regression model is selected depends on the required accuracy, preference, convenience and simplicity of use.

A shrub's estimated leaf volume is used to calculate evapotranspiration tree equivalents (ETTE) defined as the leaf volume equivalent of a 1.5 m single-stemmed tree, which according to Smit (1989a) is approximately 500 cm^3 (rounded off median value determined from harvested 1.5 m *Vachellia karroo*). Not only can the developed regression equations now be used to calculate the dry mass of leaves and wood components for a whole *T. camphoratus* shrub but, by applying partial volumes as described in Smit (1989b), the browsable components (leaves and shoots ≤ 5 mm in diameter) can be determined for different browsing heights. The browsing heights used in the BECVOL 3 – model are specified as 1.5 m (average maximum browsing height of the domestic goat and impala, *Aepyceros melampus*), 2.0 m (average browsing height of kudu, *Tragelaphus strepciseros*) and 5.0 m (average maximum browsing heights of giraffe (*Giraffa camelopardalis*) (Smit 2014)..

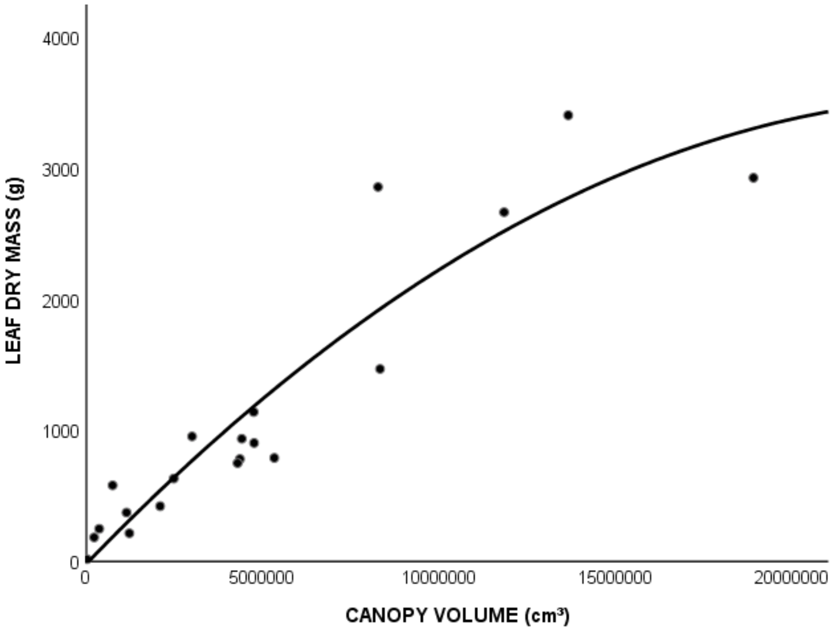

Figure 9.2: The relationship between leaf dry mass (g) of undamaged *T. camphoratus* and spatial canopy volume (cm^3)

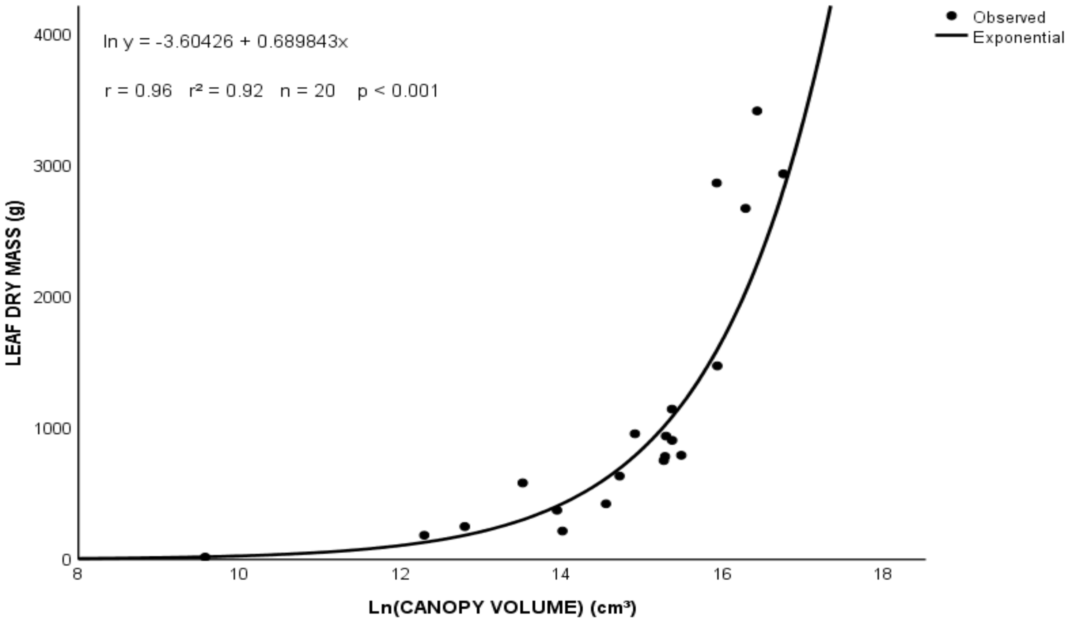

Figure 9.3: Regression analysis of the relationship between leaf dry mass (g) (dependent variable) and the natural logarithm of canopy volume (cm^3) (independent variable) of undamaged *T. camphoratus*. Best fit regression model: Exponential (ln y = a + bx), where y = leaf dry mass (g) and x = natural logarithm of spatial canopy volume.

Generally all rooted woody plants within in a predetermined area (transects) are measured such that with the aid of the developed regression equations further calculations describing the woody plant component on individual, species and landscape level can be performed easily. The BECVOL 3 – model therefore allows users to accurately estimate the following:

- woody plant density (plants ha^{-1})
- evapotranspiration tree equivalents (ETTE ha^{-1})
- total leaf dry mass (kg ha^{-1})
- leaf dry mass below a browsing height of 1.5 m, 2.0 m and 5.0 m (kg ha^{-1})
- shoot dry mass: shoots ≤ 5 mm below a browsing height of 1.5 m, 2.0 m and 5 m (kg ha^{-1})
- stem dry mass: stems > 5 – 20 cm in diameter (kg ha^{-1})
- stem dry mass: stems > 20 cm in diameter (kg ha^{-1})
- total wood dry mass (all fractions) (kg ha^{-1})
- total tree dry mass: leaves and wood combined (kg ha^{-1})
- total browse below 1.5 m, 2.0 m and 5 m respectively: leaves and shoots < 5 mm in diameter (kg ha^{-1})
- canopy subhabitat index

In addition, with the inclusion of further values, such as phenology scores, utilization factors and daily fodder dry matter requirement per browser, the browsing capacity (ha BU^{-1}) for each month of the year can be calculated by the BECVOL 3 - model (Smit 2017). A browser unit (BU) is defined as the metabolic equivalent a kudu (100% browser) with a mean body mass of 140 kg (Dekker 1997).

Table 9.1: Regression equations relating calculated spatial canopy volume (independent variable) of harvested undamaged *Tarchonanthus camphoratus* shrubs (range: 0.4 m – 2.9 m in height) to the different measured plant fractions (dependant variables): linear ($y = a + bx$), exponential ($\ln y = a + bx$) and multiplicative ($y = ax^b$), where y = estimated leaf volume (cm^3) / dry mass fraction (g), x = spatial canopy volume (cm^3).

Dependent variable	**Regression model**	**n**	**r**	**r^2**	**P**	**a (intercept)**		**b (slope)**	
						Value	**SE**	**Value**	**SE**
Leaf volume (cm^3)	Linear	20	0.86	0.74	<0.001	285.178	605.962	0.0006274	0.0000009
	Exponential		0.93	0.87	<0.001	-2.19032	0.895005	0.665115	0.060557
	Multiplicative		0.92	0.84	<0.001	-15.4132*	2.36966	8.57961	0.883281
Leaf dry mass (g)	Linear	20	0.92	0.85	<0.001	172.542	130.817	0.000188	0.0000187
	Exponential		0.96	0.92	<0.001	-3.60426	0.716109	0.689843	0.0484531
	Multiplicative		0.95	0.91	<0.001	-17.6018*	1.81721	9.00423	0.766358
Shoot dry mass (g) (shoots ≤ 5 mm in diameter)	Linear	20	0.89	0.80	<0.001	503.447	114.44	0.0001372	0.0000163
	Exponential		0.98	0.96	<0.001	-3.73549	0.527523	0.709324	0.0356931
	Multiplicative		0.98	0.96	<0.001	-18.3998*	1.11271	9.35982	0.41476
Stem dry mass (g) (stems > 5 - 20 mm in diameter)	Linear	20	0.95	0.90	<0.001	149.164	265.394	0.0004964	0.0000379
	Exponential		0.97	0.95	<0.001	-10.5021	0.992106	1.19043	0.0671275
	Multiplicative		0.98	0.96	<0.001	-35.248*	1.099763	15.7587	0.744609
Stem dry mass (g) (stems > 20 mm in diameter)	Linear	20	0.95	0.91	<0.001	-1168.85	306.305	0.000607	0.0000438
	Exponential		0.77	0.59	<0.001	-20.3321	4.86962	1.69245	0.329486
	Multiplicative		0.73	0.53	<0.001	-51.8171*	12.4673	21.0249	4.64712
Total wood dry mass (g) (all fractions)	Linear	20	0.98	0.97	<0.001	-515.563	366.943	0.001240	0.0000524
	Exponential		0.98	0.97	<0.001	-6.85615	0.664964	0.999177	0.0449925
	Multiplicative		0.97	0.95	<0.001	-27.0612*	1.89657	13.016	0.70694

*a = log a (for multiplicative regression model only), spatial canopy volume transformed to its natural logarithmic value, except for linear model

Table 9.2: Regression equations relating the calculated spatial canopy volume (independent variable) of harvested *Tarchonanthus camphoratus* coppices (range: 0.2 m 1.4 m in height) to the different measured plant fractions (dependant variables): linear ($y = a + bx$), exponential ($\ln y = a + bx$) and multiplicative ($y = ax^b$), where y = estimated leaf volume (cm^3) / dry mass fraction (g), x = spatial canopy volume (cm^3).

Dependent variable	**Regression model**	**n**	**r**	**r^2**	**p**	**a (intercept)**		**b (slope)**	
						Value	**SE**	**Value**	**SE**
Leaf volume (cm^3)	Linear	20	0.92	0.85	<0.001	389.903	128.185	0.001629	0.0001605
	Exponential		0.94	0.88	<0.001	0.651949	0.553844	0.499884	0.0436025
	Multiplicative		0.94	0.88	<0.001	-8.10408	1.3308	5.95794	0.525694
Leaf dry mass (g)	Linear	20	0.97	0.95	<0.001	39.6644	31.0359	0.000686	0.0000388
	Exponential		0.98	0.96	<0.001	-3.597	0.435793	0.733531	0.0343087
	Multiplicative		0.98	0.95	<0.001	-16.3868	1.13812	8.71944	0.449581
Shoot dry mass (g) (shoots ≤ 5 mm in diameter)	Linear	20	0.91	0.83	<0.001	-5.70299	40.3728	0.000477	0.0000505
	Exponential		0.94	0.89	<0.001	-4.71013	0.830568	0.774643	0.0653882
	Multiplicative		0.94	0.88	<0.001	-18.1898	2.05416	9.19745	0.811435
Stem dry mass (g) (stems > 5 - 20 mm in diameter)	Linear	20	0.90	0.81	<0.001	-64.3028	48.6565	0.000526	0.0000609
	Exponential		0.96	0.92	<0.001	-15.3449	1.39284	1.54012	0.109654
	Multiplicative		0.95	0.90	<0.001	-42.0852	3.54012	18.2626	1.39842
Stem dry mass (g) (stems > 20 mm in diameter)	Linear	20	N/A						
	Exponential		N/A						
	Multiplicative		N/A						
Total wood dry mass (g) (all fractions)	Linear	20	0.92	0.84	<0.001	-70.3583	81.6588	0.001004	0.000102
	Exponential		0.97	0.95	<0.001	-6.59648	0.688641	0.960177	0.0542146
	Multiplicative		0.97	0.94	<0.001	-23.2893*	1.79399	11.3943	0.708665

* a = log a (for multiplicative regression model only), spatial canopy volume transformed to its natural logarithmic value, except for linear model

9.4 Conclusion

This study has shown that there is a highly significant relationship between the spatial canopy volume and leaf volume, leaf dry mass, shoot dry mass for shoot ≤ 5 mm in diameter, stem dry mass for stems > 5 – 20 mm in diameter and stem dry mass for stems > 20 mm in diameter of undamaged and coppicing *T. camphoratus*. Regression equations with high coefficients of determination have been developed for the inclusion into the BECVOL 3 – model. The BECVOL 3 – model proved to be a handy tool for the accurate description of the woody plant component in a savanna ecosystem for research purposes, wildlife management and biofuel production estimates.

CHAPTER 10

The response of Tarchonanthus camphoratus to fire

10.1 Introduction

The co-existence and abundance of grasses and trees giving savannas their unique structure is regulated by a number of dynamic interacting factors, including climate, geomorphology, herbivory and veld fires (Scholes & Archer 1997). In the last century, increased suppression of veld fires by human intervention and increased herbivory resulting in reduced fuel loads (De Klerk 2004) has been regarded as a major aspect driving bush-thickening.

Trollope (1980) suggested the use of strategically planned high-intensity veld fires as a management tool to effectively control bush-thickening and maintain woody plants at a browsable height in arid and mesic savannas. The effect of veld fires on the grass and woody layer of savanna ecosystems has received substantial attention in the literature, focusing especially on mesic savanna systems. Fuel loads are rarely sufficient to support high-intensity fires in arid and semi-arid savannas (Teague & Smit 1992; Kraaij & Ward 2006; O'Connor *et al.* 2014) and therefore fire is considered increasingly less important, below a threshold of ± 650 mm mean annual rainfall (Sankaran *et al.* 2005). However, the importance of veld fires in arid and semi-arid savannas was demonstrated by Joubert *et al.* (2012) who reported that, even though infrequent, veld fires in arid areas coinciding with seedling establishment of woody plants are critical in preventing bush-thickening.

The two co-dominant bush-thickening species in the study area, *T. camphoratus* and *S. mellifera* are known to regenerate vigorously after defoliation (Meyer *et al.* 2005; Kiruki & Njung'e 2006). There are indications that *T. camphoratus* is well adapted to survive veld fires and that fire may provide them with a competitive advantage over other woody species. It has previously been reported that *T. camphoratus* gradually replaced *Juniperus piccera* and *Olea europaea* subsp. *africana* after repeated fires, browsing and drought (Young & Francombe 1991). The objective of this study was, therefore, to investigate whether *T. camphoratus* has the potential to replace *S. mellifera* under a fire regime in areas where they co-exist.

This opportunistic study followed an accidental veld fire in October 2018, when it was predicted that:

a) *T. camphoratus* will coppice more vigorously compared to *S. mellifera,* and

b) where *T. camphoratus* and *S. mellifera* are co-occurring species, fire will eventually result in the replacement of *S. mellifera* by *T. camphoratus.*

10.2 Literature review

Fire is a natural ecological process regulating population dynamics and the structure of savannas and grasslands, influencing seed germination and nutrient cycling (Ravi *et al.* 2010; SANBI 2014). Fire is probably the most drastic form of plant defoliation and has long been used as a management tool of rangeland systems worldwide. Veld is burnt for various reasons, including the removal of moribund, unpalatable grass material, as a technique to control bush-thickening, to initiate out-of-season green-up, especially in communal areas and to destroy pests and insects (Trollope 1980, 2004; SANBI 2014).

Different vegetation types respond differently to fire and fire behaviour. Therefore, various factors should be taken into account before fire is included in a management system. The season and timing of burning, the type, frequency and behaviour of fire (Kennedy & Potgieter 2003; Trollope 2007; Gandiwa 2011; Boakye *et al.* 2013; Smith *et al.* 2013), rangeland condition, veld type, and soil moisture availability, as well as the management before and after the fire (Pratt & Knight 1971; Trollope 1980, 2004; Snyman 2002; Little *et al.* 2015) influence fire intensity and consequently the response of vegetation to fire.

The objective and area determine the required fire intensity and frequency. Where the aim is to remove moribund grass material, a cool fire (< 1000 kJ s^{-1} m^{-1}) after the first 13 mm of rain when grass is still dormant is recommended. In such a way, the risk of run-away fires and damage to the grass sward is lowered significantly. However, if woody plants are to be controlled, high-intensity head fires (> 2000 kJ s^{-1} m^{-1}) before the commencement of the rainy season are required (Trollope *et al.* 2002; Trollope 2007). In order to achieve such high fire intensity, a high grass production (> 2000 kg DM ha^{-1}) is necessary (Trollope 1984 as cited from Joubert *et al.* 2012). As a result, fire can only be used as a preventative measure for bush-thickening, because in cases where bush-thickening has already occurred, these high fuel loads are seldom achieved, even if grazing is completely withdrawn.

Provided the fuel load is sufficient, the use of fire can be a cheap, fast and effective way of controlling woody plant abundance, weeds and invaders. However, follow-up treatment will be necessary and unfortunate consequences should be weighed carefully. Fire is always a risk and careful planning and preparation are necessary (Trollope 2004). Controlled burning of veld was found to be a rather unsustainable practice and disadvantageous to the full functioning of arid and semi-arid ecosystems. The plant cover reduction after fire results in an exposed soil surface which is prone to soil compaction, soil erosion and increased soil temperatures (Badia & Martí 2008; Ravi *et al.* 2010; Strydom 2013; Parlak 2015). This reduced soil water content of the top soil by 31% compared to unburnt veld one year after the burn in the semi-arid grassland of South Africa (Snyman 2002). In addition, the burning of veld reduces soil organic matter content, significantly reducing soil fertility in the long-term

(Snyman 2002; Ravi *et al.* 2010; Strydom 2013; Hosseini 2018). Not only are valuable fire-sensitive species lost from the system but fire also reduces the productivity and vigour of the herbaceous layer significantly (Snyman 2006). It may therefore take 2 – 30 years depending on the rainfall and fire intensity for veld to fully recover from a single fire event (Snyman 2006; Van den Berg & du Toit 2013).

Therefore, burning of arid and semi-arid vegetation should be limited to occasional events coinciding with high seedling establishment of undesirable woody plants and dwarf shrubs. This is mostly the case only after a series of above-average rainfall years (Snyman 2002; Joubert *et al* 2012).

10.3 Procedure

10.3.1 Trial layout

An accidental fire occurred on 26 October 2018 and started on the farm neighbouring the Rooipoort Nature Reserve in the north, from where it spread in a south-easterly direction and burnt down more than 6000 ha of farmland, including parts of the Rooipoort Nature Reserve (Figure 10.1). The study was opportunistic, therefore, the study area was only selected after the fire and had a large abundance of *S. mellifera* and *T. camphoratus* affected by the fire in the form of a complete top-kill.

Figure 10.1: Area affected by the veld fire in October 2018 (Photo: IJ Stehn)

Observation of the unburnt area adjacent to the burnt area indicated that the herbaceous layer of the burnt area was dominated by a relatively homogenous stand of *Schmid*tia *pappophoroides*. It was therefore decided to estimate the fuel load of the burnt plot from measuring the fuel load of the adjacent unburnt area. This was done by taking 200 points using a disc pasture meter, which was first calibrated according to the procedures laid out in Bransby and Tainton (1977). Twenty random samples were taken for the development of the regression equation and calibration. Immediately after sampling, the samples were weighed and then they were oven-dried to a constant mass and weighed. The percentage difference between wet and dry sample mass was used to estimate the moisture content of the fuel load. All these measurements were conducted eight days after the fire had occurred.

According to Dayne Knight (personal communication[2]) the study area was affected by the fire between approximately 18:00 and 20:00. The weather conditions during the fire were thus taken as an average for those three hours, as recorded by the mobile weather station at the Rooipoort homestead, approximately 3 km west of the study area.

A regression model suggested by Trollope *et al.* (2002) for the prediction of the fire intensity in South Africa was used. The model used was $FI = 2729 + 0.8684 (FL) - 530 \sqrt{(FM)} - 0.907 (RH^2) - 596 (1/WS)$, where FI = fire intensity ($kJ\ s^{-1}\ m^{-1}$), FL = fuel load ($kg\ ha^{-1}$), FM = fuel moisture (%), RH = relative humidity (%) and WS = wind speed ($m\ ^{-1}$). This fire intensity was then classified into one of five fire-intensity categories, namely, very cool, cool, moderately hot, hot and extremely hot (Trollope 2007).

Fifteen *T. camphoratus* and 15 *S. mellifera* plants were randomly selected and permanently marked. However, two plants, marked *S. mellifera,* and one marked *T. camphoratus* were wrongly identified and one coppicing *T. camphoratus* was severely browsed early in the study. Thus, only 13 plants of each species were used in the study. From November 2018 to June 2020, the number of coppice shoots for each marked plant was counted once a month. In October 2019 and June 2020, the spatial canopy volume of all coppice plants was determined according to the procedures of the BECVIOL 3 – model (see section 9.2). Leaf dry mass for each focal plant was determined using the newly developed regression models (see section 9.3) for *T. camphoratus* coppice plants and the general regression model for microphyllous plants (Smit 2014) for *S. mellifera* coppice plants.

10.3.2 Statistical analyses

All data were tested for normality using the Shapiro-Wilk test ($p > 0.05$) (Shapiro & Wilk 1965). The number of shoots per coppice plant was square-root transformed. Regression analyses using the disc pasture meter reading as an independent variable and fuel load dry mass as the dependent variable were conducted to calibrate the disc pasture meter. A one-way ANOVA was performed to test for significant differences in the number of shoots, Evapotranspiration Tree Equivalents (ETTE), leaf dry mass and wood dry mass production between the *T. camphoratus* and *S. mellifera* coppice plants. These analyses were performed using IBM SPSS Statistics for Windows, version 25 (IBM Corp., Armonk N.Y, USA 2017).

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10.4 Results

The estimated fuel load was 1784.878 kg ha-1 with an average fuel moisture of 9.24 ± 0.19 (mean ± SE). The average temperature at the time of the fire was 29.8°C with a relative humidity of 10% and 1.2 m s^{-1} north-westerly wind. Therefore, the estimated fire intensity was calculated as 2080.56 kJ s^{-1} m^{-1}, which was classified as a hot fire (2001 – 3000 kJ s^{-1} m^{-1}).

All *T. camphoratus* shrubs coppiced after the fire, while only 78% of *S. mellifera* coppiced. In the first two months post-fire, neither *T. camphoratus* nor *S. mellifera* had started to regrow. The *S. mellifera* that survived the fire started coppicing faster after the fire compared to *T. camphoratus.* While there was no significant difference ($p > 0.05$) in shoot numbers between *S. mellifera* and *T. camphoratus* for February and March 2019, *S. mellifera* had significantly higher shoot numbers per coppice plant in January 2019 compared to *T. camphoratus* ($F_{1.21} = 5.887$, $p = 0.024$). From April 2019 until June 2020, the number of shoots per *T. camphoratus* coppice plant was significantly higher ($p < 0.05$) compared to *S. mellifera* (Figure 10.2).

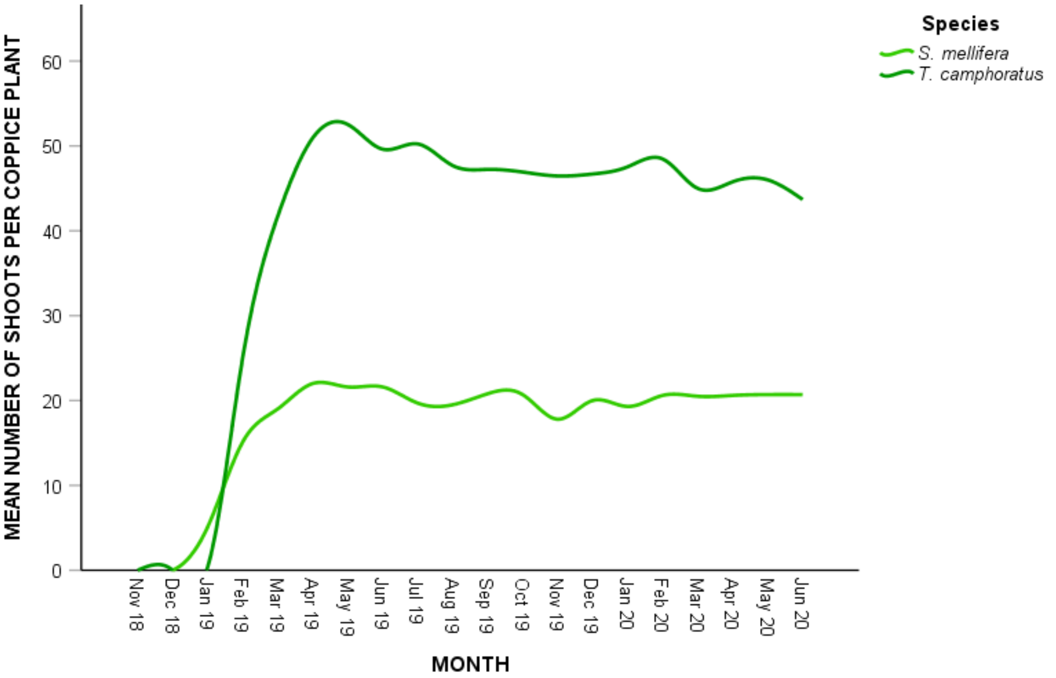

Figure 10.2: The mean number of shoots per coppice plant for *S. mellifera* (n = 10) and *T. camphoratus* (n = 13) for November 2018 to June 2019

The average ETTE per coppice plant differed significantly ($p < 0.05$) between *T. camphoratus* and *S. mellifera* coppice plants for October 2019 and June 2020. The estimated leaf DM production of *T. camphoratus* coppice plants was on average 18 and 20 times higher compared to the leaf DM production of *S. mellifera,* 12 and 20 months after the fire had occurred (Figure 10.3). Similarly, the woody DM of *T. camphoratus* was also significantly higher compared to the wood DM of *S. mellifera* for October 2019 and June 2020 (Table 10.1). No seedling establishment of either species was observed in the 20 months post-fire, probably a result of two below-average rainfall seasons during which the study took place.

Figure 10.3: The development of *S. mellifera* (left) and *T. camphoratus* (right) after the veld fire in November 2018, January 2019, October 2019 and in May 2020 (Photos: IJ Stehn)

Table 10.1: Estimated ETTE, leaf and wood DM (mean ± SE) of *T. camphoratus* and *S. mellifera* coppice plants in October 2019 (12 months after the fire) and June 2020 (20 months after the fire)

	Month	*T. camphoratus*	*S. mellifera*
n		13	10
Average ETTE	October 2019	2.08 ± 0.24	0.07 ± 0.02
	June 2020	2.88 ± 0.30	0.11 ± 0.03
Average leaf DM (g)	October 2019	297.77 ± 44.98	16.20 ± 4.34
	June 2020	475.46 ± 64.27	23.70 ± 5.58
Average wood DM (g)	October 2019	251.15 ± 50.96	26.80 ± 9.71
	June 2020	487.54 ± 86.01	43.40 ± 14.33

10.5 Discussion

Even though fuel loads were relatively low, the low fuel moisture and humidity, as well as high ambient temperatures contributed to the relatively high fire intensity. Furthermore, the fire had occurred in early summer, before the first rains of the season had commenced. From the perspective of managing bush-thickening this accidental fire was ideal, as relatively high intensity fires before the start of the rainy season are preferred for the control of bush-thickening species and to limit damage to the herbaceous layer (Trollope 2007). Farmers have repeatedly reported that *T. camphoratus* is highly flammable even when green; therefore, it mostly burns down entirely, or until only a few thick stems are left behind, while *S. mellifera* is less flammable and often only the leaves and thin shoots are affected by the fire (Figure 10.3). However, it was noted that, after the fire, none of the woody species in the study area greened-up in their crown, but the majority coppiced, which indicates that the fire was effective in top-killing the woody plants.

Although *T. camphoratus* took longer to start coppicing after the fire compared to *S. mellifera, T. camphoratus* coppice plants had more stems and higher above-ground biomass production compared to *S. mellifera.* Hypothesis A, predicting that *T. camphoratus* shrubs will coppice more vigorously post-fire compared to *S. mellifera* is therefore true. Similar to what has been discussed in chapter 6 (see section 6.5.2), phenology of the shrub during which disturbance takes place may play a key role in its coppicing vigour. While *S. mellifera* had probably mobilised and utilised large quantities of stored non-structural carbohydrates for flowering, fruit production (Joubert *et al.* 2013) and leaf-flushing occurring from August to October (see section 5.4.2), *T. camphoratus* was at a relatively dormant stage at the time of the fire. Therefore, carbohydrate reserves of *S. mellifera* were probably very low while those of *T. camphoratus* were fully replenished, which may have contributed to the differential coppicing vigour in the two species.

Schutz *et al.* (2009) found that carbohydrate concentrations in the roots of burnt *V. karroo* matched those of unburnt *V. karroo* within one year after the fire. Consequently, it is expected that the significantly higher ETTE and leaf dry mass of *T. camphoratus,* as well as its semi-deciduous nature, contributed towards much faster replenishment of carbohydrate reserves. *S. mellifera* on the other hand, would take much longer to replenish its lost carbohydrate reserves due to the relatively low leaf volume, as well as its winter deciduous nature reducing the effective time and capacity to restore lost carbohydrate reserves.

In a study conducted in Kenya, Pratt and Knight (1971) reported that repeated burning (three times in five years), with subsequent browsing by goats had led to a high mortality of existing *Vachellia gerrardii, Vachellia hockii, Vachellia nilotica, Senegalia senegal, Vachellia seyal* and *D. cinerea* but no mortality was recorded for *T. camphoratus.* They further found that there was no difference in carbohydrate status in burnt and unburnt *T. camphoratus* plants six months after the fire. However, the number of stems and stem height significantly decreased after the third burn. This together with the preliminary short-term results of this study supports hypothesis B predicting that, where *S. mellifera* and *T. camphoratus* are co-occurring and repeatedly defoliated by fire or browsing, *T. camphoratus* will gradually replace *S. mellifera.*

10.6 Conclusion

T. camphoratus coppiced more vigorously than *S. mellifera* after an accidental fire had top-killed both species. However, in the very unlikely event of fire occurring during the active growth season of *T. camphoratus* or increased browsing pressure, it is expected that *T. camphoratus* will coppice less vigorously than observed in this study (see section 6.5.2). Even though these results are only preliminary and long-term studies would be necessary to confirm this, mortality and weak coppicing of *S. mellifera* after the fire indicated that *T. camphoratus* has the potential to develop into a relatively pure stand, where *S. mellifera* and *T. camphoratus* have previously co-existed, if disturbance by fire, browsing or cutting persists. Nevertheless, because repeated burning in this semi-arid environment is strongly advised against, this phenomenon will probably be limited to areas around settlements where accidental fires are likely to occur more frequently.

EXTENDED ABSTRACT

The increase in woody cover across savanna ecosystems worldwide results from increased vegetative growth of existing woody plants, as well as their increased reproductive success. This form of land degradation has serious consequences for the sustainability and productivity of rangeland ecosystems. Until recently, landowners paid little attention to *Tarchonanthus camphoratus*. However, the observed sharp increase in its abundance during the past decades that resulted in a significant decline in grass production, as well as its low palatability, high fire tolerance and high water requirement, raised concerns about the potential threat this species poses to agricultural sustainability and ecosystem functioning.

The effective management of potential bush-thickening species necessitates a good understanding of the factors contributing to their success. This study therefore represents an attempt to obtain a better understanding of the ecological functioning of *T. camphoratus* by investigating its:

a) effect on the soil nutrient status (soil enrichment),
b) leaf and reproductive phenology,
c) vegetative growth characteristics (shoot growth),
d) coppicing ability in response to mechanical cutting during different seasons,
e) seed production,
f) seed longevity in the soil,
g) seed germination and growth associated with different subhabitats and soil types,
h) browse production, as well as its
i) response to fire.

The study was conducted in the Rooipoort Nature Reserve that forms part of the Kimberley Thornveld vegetation type on deep sandy and shallow rocky soil. It was found that *T. camphoratus* played an important role in soil enrichment, as soil underneath their canopies had a significantly ($p < 0.05$) higher soil-nutrient status compared to the soil from the uncanopied area. Potassium and calcium concentrations, as well as total nitrogen and organic carbon percentages, followed a clear spatial gradient, decreasing with increasing distance from the stem. However, it was also apparent that the influence of woody plants on soil chemistry was specific for each nutrient element, soil type and woody plant species.

Similarly, woody plant phenology and climate variables with which it was the best correlated varied between woody plant species and different phenophases. Woody plants in the study area showed a delayed response to most climate variables. Fourteen days delayed monthly minimum temperature and ten days delayed four-week cumulative rainfall were moderately to strongly correlated with percentage leaf carriage of *G. flava, Z. mucronata* and *S. mellifera.* However, leaf-flushing in these species was triggered by maximum

temperatures and day length, reaching minimum threshold levels, provided that sufficient soil moisture from the previous season's rainfall was present. *T. camphoratus* leaf-carriage percentage on the other hand, was strongly positively correlated with six-month cumulative rainfall, with day length and temperature being only moderately correlated. The commencement of the active growing season in *T. camphoratus* was primarily driven by four weeks' cumulative rainfall with 14 days' delay. Leaf senescence in all species coincided with decreasing temperatures and day length, as well as the end of the rainy season.

Soil type in which the woody species grow, as well as the sex of shrubs (in *T. camphoratus* only), also influenced leaf carriage significantly. Woody plants of all species growing in the deep sandy soil flushed slightly earlier compared to those growing in the shallow rocky soil. Male *T. camphoratus* shrubs retained more leaves during the dry period and produced new leaves faster in the new season compared to female *T. camphoratus* shrubs.

Moreover, *T. camphoratus* shoot growth was positively correlated with monthly minimum temperature, as well as cumulative rainfall of four weeks, but soil type and the sex of the shrub had no significant influence. The critical time for *T. camphoratus* shoot thickening and elongation was between December and May and peaked in April. The exceptionally hot and dry conditions experienced in early summer of the study period had a marked effect on shoot growth of healthy and coppicing *T. camphoratus* plants, resulting in more than usual shoot die-back and a delayed start of the active growing season.

The coppicing vigour of mechanically cut *T. camphoratus* shrubs was significantly influenced by soil type, as well as season of cutting. In this study, shrubs cut during the winter grew more vigorous compared to shrubs cut during the active growth period in summer. Shrubs cut during the active growing season and growing in sandy soil were especially vulnerable and coppiced relatively poorly compared to those cut during winter. It was further found that *T. camphoratus* recovered more rapidly than *S. mellifera* after a hot fire and that, in areas where these two species are co-occurring, frequent fires may eventually result in the replacement of *S. mellifera* by *T. camphoratus.*

This study has further shown that, in the study area, *T. camphoratus* male and female shrubs existed in dynamic equilibrium. While flowering and fruit maturation occurred before the wet season in *S. mellifera* and during the wet season in *G. flava* and *Z. mucronata,* flowering of *T. camphoratus* occurred only at the end of the wet season, and fruit maturation in the early dry season (winter). Female *T. camphoratus* shrubs produced relatively large quantities of seeds (40 469 ± 4504 seeds ETTE^{-1}), even during below-average rainfall years. Since *T. camphoratus* seeds seemed to be very short-lived and did not persist in the soil longer than one year, this ensured that fresh viable seeds are always available for germination and establishment when conditions become favourable. However, large quantities of other plant species' seeds, especially grasses, were found underneath the canopies of *T. camphoratus.* Furthermore, *T. camphoratus* seeds shed during August/September, underwent a three- to four-month dormancy period before they started to germinate, but allelopathic effects inhibiting *T. camphoratus* seed germination were not evident. *T. camphoratus* seedlings growing in the soil originating from underneath the canopy of *T. camphoratus* grew significantly better compared to those growing in soil form the uncanopied area, regardless the soil type. Thus, subhabitat differentiation had more definite effects on seedling growth than differences related to soil type.

Highly significant regression models with very high coefficients of determination relating spatial canopy volume to dry mass fractions of leaves and stems in three diameter classes (< 5 mm, 5 – 20 mm and > 20 mm) were developed for undamaged and coppicing *T. camphoratus* shrubs. This will enable the accurate assessment of the phytomass of *T. camphoratus* for research purposes, wildlife management and biofuel production estimates.

The success of bush clearing or thinning operations is often measured on the basis of the recovery, productivity and stability of the herbaceous layer, as well as the prevention of the mass re-establishment of woody plants. These findings therefore aided in predicting the response of the vegetation to various management approaches, as well as the establishment of objective guidelines. The management objective, as well as economic considerations will determine the treatments applied for shrubs growing on the different soil types.

If the objective is to manage bush-thickening, the remaining stems of cut *T. camphoratus* stems should always be treated with an arboricide to prevent coppicing. Untreated stems are guaranteed to coppice to such an extent that follow-up treatment will be necessary within due time. However, cutting *T. camphoratus* during its active growth season (January to April), when the species is most susceptible to damage, as well as repeatedly removing coppice material, either by mechanical means or by introducing browsers, is expected to deplete carbohydrate reserves and eventually lead to higher plant mortality. If the objective is sustainable browse production, shrubs should be cut during winter, enabling return times of four to five years. Return periods of at least 25 years render *T. camphoratus* in this area unsuitable for sustainable charcoal or wood production.

Additionally, the success rate of a *T. camphoratus* management programme can be increased if clearing/thinning of *T. camphoratus* is performed before seed maturation occurs, preferably towards the end of the rainy season. By following this strategy, the risk of *T. camphoratus* seedling establishment from the soil seed bank in high-nutrient soil where mature *T. camphoratus* were removed is lowered considerably. Follow-up treatments can therefore be directed to the control of coppice plants instead of seedlings.

In the southern African savanna, large areas are often non-selectively cleared of their woody plants in an effort to manage bush-thickening and regain grazing potential without paying attention to the potential positive attributes that especially large woody plants could have. Therefore, in the management of *T. camphoratus,* those positive attributes should not be overlooked. Firstly, the positive influence of *T. camphoratus* on the nutrient status of the nutrient-poor soils, where it typically grows establishes the species as an important biological agent which will ensure a higher soil-nutrient status on a landscape level. Secondly, *T. camphoratus* retained significantly more leaves from May until November compared to deciduous species such as *G. flava, S. mellifera* and *Z. mucronata,* whose new season's leaves only appeared during October/November and, with leaf senescence commencing in April, had very few or no leaves between August and November. Despite being less palatable, *T. camphoratus* therefore acts as an important fodder source for browsers and mixed feeders, especially during the critical period from August to October/November, when browse of more palatable deciduous woody species is most limited. Lastly, the existence of a high seed density and species-rich soil seed bank of especially herbaceous plants under *T. camphoratus* canopies ensures a high restoration potential in terms of herbaceous-layer establishment after bush-thinning.

It is therefore recommended that bush control operations in areas with densities too high to allow sufficient herbaceous production should follow a selective thinning approach, retaining a proportion of the larger *T. camphoratus* shrubs. In this way, the positive attributes of woody plants such as soil enrichment, provision of browse and ecosystem stability are maintained.

It is anticipated that the results of this study will provide valuable information to landowners for the effective and ecologically responsible management of *T. camphoratus* in the semi-arid savanna ecosystem. The study, in combination with existing information, can aid wildlife managers in predicting browse available during different seasons in the year. In addition, this study can give the basis to an approach for further research on this and other woody plant species.

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APPENDIX

APPENDIX A

Table A 1: Randomised placement of 60 pots (6 treatments x 10 replications) in 5 blocks and two columns in the greenhouse.

Obs	Col1	Col2	Block	random number
1	A	F	1	0.18496
2	D	C	1	0.2594
3	E	D	1	0.39982
4	C	B	1	0.9216
5	B	A	1	0.96928
6	F	E	1	0.97009
7	D	F	2	0.04979
8	C	E	2	0.06657
9	A	C	2	0.52387
10	E	A	2	0.53169
11	F	B	2	0.54298
12	B	D	2	0.81932
13	A	D	3	0.06718
14	D	A	3	0.27261
15	E	B	3	0.29719
16	C	F	3	0.68993
17	B	E	3	0.85339
18	F	C	3	0.95702
19	D	B	4	0.22651
20	F	D	4	0.28723
21	B	F	4	0.41276
22	A	E	4	0.55855
23	C	A	4	0.68824
24	E	C	4	0.97676
25	D	E	5	0.37701
26	C	D	5	0.47579
27	E	F	5	0.58258
28	F	A	5	0.59036
29	A	B	5	0.63452
30	B	C	5	0.84499

A – stem subhabitat – sandy soil

B – canopy middle subhabitat – sandy soil

C – uncanopied subhabitat – sandy soil

D – stem subhabitat – rocky soil

E – canopy middle subhabitat – rocky soil

F – uncanopied subhabitat – rocky soil