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Role of *Vachellia karroo* as a nurse plant in old fields targeted for passive restoration

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Background: In degraded environments such as old fields, nurse plants can facilitate the growth of targeted restoration plant species by ameliorating extreme environmental conditions, creating nutrient-rich microclimates and protecting recruiting plants from grazing.

Aim & objectives: This study examined the role of *Vachellia karroo* (Hayne) Banfi & Galasso as a nurse plant on soil physical and chemical properties and vegetation diversity in old fields targeted for passive restoration at the Tanglewood research farm in the Eastern Cape, South Africa.

Methods: Soils were quantified for physical and chemical properties in 48 plots measuring 25 m^2 (5 × 5 m) that were located under and outside 24 *V. karroo* nurse plants in old fields. In addition, detailed vegetation surveys were conducted in the above-mentioned plots.

Results: Our results show that soil total nitrogen (N) and carbon (C) concentrations were higher under than outside *V. karroo* nurse plants. Soil penetration resistance and water-repellency levels were lower under than outside *V. karroo* nurse plants, however, monthly variations were also observed. Species richness and Shannon-Wiener diversity were higher under than outside *V. karroo* nurse plants, with species such as *Searsia crenata, Azima tetracantha, Asparagus africanus* and *Opuntia* sp. frequently occurring under *V. karroo* nurse plants.

Conclusion: The study concludes that *V. karroo* nurse plants have a positive effect on some soil physical and chemical properties and vegetation diversity. It is recommended that *V. karroo* needs to be included in future old field restoration strategies if passive restoration at Tanglewood research farm is to be successful.

Keywords: nurse plant syndrome, ecological restoration, plant-to-plant facilitation, pioneer plants, soil nutrients.

Introduction

The establishment of native woody plants in abandoned agricultural fields (hereafter old fields) targeted for passive restoration is constrained by several factors that include soil legacy effects linked to past cultivation, lack of native plant soil seedbanks, grazing, fire and harsh environmental conditions that suppress plant establishment (Badano et al. 2016; Uselman et al. 2018). Nevertheless, some woody plants can overcome the above-mentioned constraints and establish in old fields as nurse plants that kickstart the restoration process through positive plant-to-plant facilitation (Navarro-Cano et al. 2019). Nurse plants are defined as plant species that positively facilitate the growth and establishment of other plant species beneath their canopy (Ren et al. 2008). Several studies have shown that nurse plants create microhabitats underneath them that are favourable for germination and growth of other plant species (Ren et al. 2008; Navarro-Cano et al. 2019; Ruwanza 2019). They also protect plants underneath from herbivore damage, mostly preventing grazing and trampling (Ren et al. 2008). For example, Navarro-Cano et al. (2019) showed that the nurse plant species *Pinus halepensis*, *Osyris lanceolata* and *Atriplex halimus*, promote positive plant–microbial interactions that benefit other recruiting plants, thus facilitating their growth. Ruwanza (2019) reported that soils underneath the nurse plants *Vachellia nilotica*, *Peltophorum africanum* and *Senegalia nigrescens* had improved soil properties such as moisture and soil penetration resistance compared to soils outside nurse plants. The above-mentioned examples show that nurse plants play an important role in facilitating the establishment of other plants (Ren et al. 2008; Navarro-Cano et al. 2019).

Few studies have examined the role of nurse plants in old fields targeted for passive restoration (Padilla et al. 2004; Padilla & Pugnaire 2006; Ruwanza 2019), especially in South Africa were old fields are on the increase due to several economic (declining farming profits), social (urban migration) and environmental (climate change) factors (Blair et al. 2018). Elsewhere, studies on the role of nurse plants in old fields have shown that nurse plants such as *Retama sphaerocarpa* enhance the germination and seedling survival of other plants like *Olea europaea* in semi-arid old fields of Almeria, Spain (Padilla et al. 2004). In another study, Padilla and Pugnaire (2006) concluded that targeted restoration species tend to survive and grow better underneath nurse plants in old fields, thus the need to include nurse plants in old field restoration guidelines. In South Africa, Ruwanza (2019) showed that the diversity of native plants was higher underneath nurse plants in 35-year-old Lapalala Wilderness old fields, an indication that nurse plants need to be protected from grazing so that they act as restoration foci.

The above-mentioned studies seem to suggest that several mechanisms explain the positive role of nurse plants in old field restoration (Ren et al. 2008; Navarro-Cano et al. 2019; Ruwanza 2019). These mechanisms include improved microclimatic conditions underneath nurse plants, increased soil moisture and nutrient availability underneath nurse plants, and protection of native plants against environmental and external stresses like heat and herbivory (Padilla & Pugnaire 2006; Ruwanza 2019). Ren et al. (2008) and Lopez et al. (2007) used the term nurse plant syndrome to explain the positive effects of nurse plants on native species underneath. Within old fields, such positive effects of 'nurse plant syndrome' could include abiotic stress amelioration, e.g., shade provided by nurse plants can improve soil moisture content underneath the plant, resulting in enhanced seedling establishment and growth. A recent study by Ruwanza (2022) showed that the presence of nurse plants in old field ridges creates nutrient-rich islands underneath the plants, which could facilitate plant growth underneath.

Although there is consensus among restoration ecologists that nurse plants could potentially play a key role in facilitating passive old field restoration (Padilla & Pugnaire 2006), few studies have been conducted in South Africa (Ruwanza 2019), where land abandonment is on the increase (Blair et al. 2018). Besides, for South Africa to meet its ecological restoration targets aimed at achieving land degradation neutrality by 2030 (Von Maltitz et al. 2019), more research is needed to unpack the restoration dynamics in old fields, particularly the role of nurse plants in facilitating passive restoration. Apart from that, old field restoration trajectories might differ due to several factors like soil legacy effects and cultivation history, therefore there is a need to assess passive restoration dynamics in old fields across different environments to develop adaptive interventions.

Assessing the positive effects of nurse plants on underneath recruiting plant species requires determining if facilitation is occurring (Navarro-Cano et al. 2019). It is generally assumed that facilitation occurs when ecological benefits underneath the species are displaying positive co-occurrence patterns that are evident at multiple locations (Badano et al. 2016; Uselman et al. 2018). However, it is important to note that nurse plant facilitation could take time depending on several factors like degradation extent, rate of nurse plant establishment, and other external factors like fire, grazing and climate change (Ren et al. 2008). Nonetheless, nurse plant facilitation is not only measured from a plant co-occurrence standpoint, but some studies have looked at it from a species diversity and community dynamics standpoint (Navarro-Cano et al. 2015). Examples are in dry arid regions where nurse plants provide refuge for diverse species that could probably fail to establish outside nurse plants due to harsh environmental conditions (Pérez-Sánchez et al. 2015). However, the role of nurse plant facilitation needs to be examined from both a soil and vegetation standpoint, particularly understanding plant and soil changes since they are essential in understanding ecosystem functioning. Indeed, plant-soil interactions and feedback can significantly influence species recruitment in old fields, thus ultimately playing a key role in regulating vegetation recovery trajectory (Ruwanza 2019).

Few studies have looked at how nurse plants promote changes in soil physical and chemical properties and how this can regulate plant diversity and community structure underneath nurse plants (Navarro-Cano et al. 2015; Ruwanza 2019). Navarro-Cano et al. (2015) showed that nurse plant canopy cover can facilitate changes in litter quantity, which ultimately alters soil nutrients. However, changes in soil physical and chemical properties due to nurse plants could be determined by several factors, such as nurse plant type, age and litter release, as well as other external factors, such as microbial activity underneath the nurse plant (Navarro-Cano et al. 2015, 2019). Indeed, studies on the effects of nurse plants on soil physical and chemical properties are long overdue if the facilitative role of nurse plants in old fields is to be fully understood. Given the high costs of assisted old field restoration (active restoration), research on the role of nurse plants in old fields can provide valuable information to enrich our understanding of the natural succession patterns in old fields. Theoretically, nurse plants can enhance germination and growth of underneath recruiting native plants in old fields; however, positive and negative feedback interactions can occur, thus shifting recruitment dynamics and plant composition structure (Callaway et al. 2002). For example, positive plant-soil interactions can facilitate increased plant diversity underneath nurse plants, yet negative interaction can trigger dominance of one species thus triggering bush encroachment or alien plant invasion. This needs to be tested to assess the facilitative role of nurse plants in germination and growth of native plants that can trigger passive restoration in old fields.

In this study, we assessed the influence of the *V. karroo* nurse plant on soil physical and chemical properties and underneath vegetation diversity in old fields targeted for passive restoration at Tanglewood research farm in the Eastern Cape, South Africa. Based on the nurse plant facilitation theory, the research questions were: (i) does the nurse plant *V. karroo* facilitate changes in soil physical and chemical properties underneath its canopy; and (ii) does the nurse plant *V. karroo* affect vegetation diversity underneath its canopy? We predict that old fields are resource-limited environments, and the *V. karroo* nurse plant will create positive plant–soil feedback that creates suitable conditions for soil and vegetation recovery underneath its canopy compared to areas outside its canopy. Our prediction is centred on existing knowledge related to nurse plant syndrome and associated amelioration effects (Lopez et al. 2007).

Materials and methods

Study area

The study was conducted in old fields located at Tanglewood research farm (33°30′57.57″S, 26°14′59.70″E), which is approximately 45 km from the town Makhanda (previously Grahamstown) in the Eastern Cape, South Africa (Figure 1). The 760-hectare ex-privately owned dairy farm is currently used as a conservation farm with a few wild animals, such as Cape mountain zebra (*Equus zebra zebra*) and giraffe (*Giraffa camelopardalis*). Due to the change of property ownership, it is not clear when crop cultivation and subsequent dairy farming were abandoned; however, personal communication with the current manager (Dylan Blew in 2024) and Google Earth images seem to suggest that cultivation was last done in

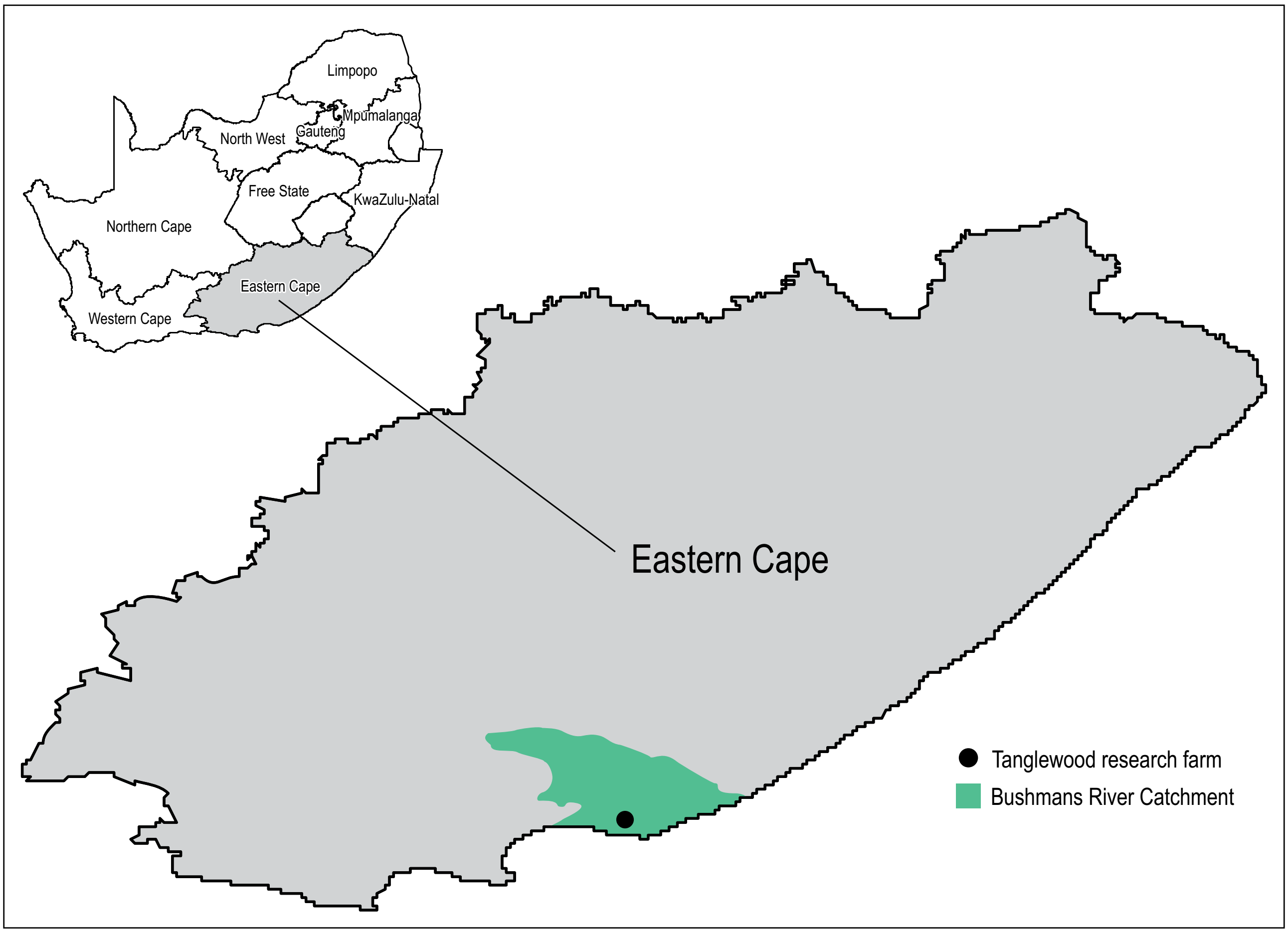


Figure 1. Map showing the location of the study area in the Eastern Cape, South Africa.

2008. Tanglewood research farm is earmarked for upscaling Albany Thicket restoration. As a result, a restoration trial to introduce a mixture of Albany Thicket species, including the ecosystem engineer *Portulacaria afra* (Van der Vyver et al. 2013), is being implemented in the old fields. The vegetation type in the study area falls within the Albany Thicket biome and is known as Kowie Thicket (Hoare et al. 2006). Although the geology in this region is complex, soils in the study area is predominantly clay and sand of the Weltevrede and Darlington formations. Vegetation is dominated by succulent euphorbias, aloes and understorey shrubs such as *Capparis*, *Secamone* and *Rhoicissus* species (Hoare et al. 2006). Although rainfall is nonseasonal, most rain falls in austral summer, with optima in March and October/November (Hoare et al. 2006). The mean annual precipitation is 650 mm and temperatures range from an average of 35°C in summer to 6°C in winter (Hoare et al. 2006).

Nurse plant

Vachellia karroo (formerly *Acacia karroo* and commonly known as sweet thorn), is the dominant tree in the old fields study site. It is indigenous to southern Africa and belongs to the Fabaceae family (Beukes et al. 2019). The tree is widely distributed in southern Africa and grows in different soil types, biomes, climatic and edaphic conditions (Taylor & Barker 2012; Dingaan & Du Preez 2018; Beukes et al. 2019). The tree can resist salinity, fire, drought and frost, which contribute towards its dominance and expansion in degraded ecosystems such as old fields, thus being regarded as an expansive bush encroacher, or pioneer species (Dingaan & Du Preez 2018). Like most legumes, *V. karroo* fixes nitrogen into the soil by forming mutualistic symbioses with *Rhizobium* soil bacteria (Beukes et al. 2019). *Rhizobium* bacteria converts atmospheric nitrogen to nitrogen compounds that can be used to enhance *V. karoo* growth (Dingaan & Du Preez 2018). Apart from that, *V. karroo* can uptake water and nutrients from deep underground soils, which can be used to increase its growth (Dingaan & Du Preez 2018).

The plant grows to a height of 5 to 12 m in disturbed areas and to more than 20 m in undisturbed areas like riparian zones where growth conditions are favourable (Dingaan & Du Preez 2018). *Vachellia karroo* is usually single stemmed, branching low on the trunk and has a rounded crown (Dingaan & Du Preez 2018). Leaves are generally dense and dark green in colour. Flowers are yellow and the pods are flat and sickle-shaped (Dingaan & Du Preez 2018). The tree has many uses that include: (i) medicinal properties in the leaves and bark for diarrhoea treatment; (ii) pods and fruits for livestock fodder; (iii) flowers for honey production; and (iv) seeds that can be roasted and used as a coffee substitute (Van Wyk 2011; Cock & Van Vuuren 2015; Dingaan & Du Preez 2018). Its nurse plant properties have resulted in the plant being used as an indicator for surface and groundwater availability, as well as for good grazing sweetveld (Dingaan & Du Preez 2018; Beukes et al. 2019).

Experimental design

Three old fields of varied sizes ranging from 125 000 m^2 to 969 000 m^2 were purposively selected in April 2022. Purposive sampling was done to allow old fields dominated by *V. karroo* to be selected. The selected old fields were approximately 1 km apart and dominated by *V. karoo* and low grass cover, mainly *Cynodon dactylon, Aristida junciformis* and *Paspalum distichum* in open patches. In each of the above-mentioned old fields, eight *V. karroo* nurse plants were purposively selected for soil and vegetation measurements. The eight selected plants per old field were approximately 50 m apart to minimize sampling plants that are close to each other. Nurse plants were purposively selected based on the following minimum requirements: (i) height of 4.5 m; (ii) diameter at breast height of 70 cm; and (iii) tree crown of 7.5 m. Tree height was measured using a sectional measuring pole, whereas diameter at breast was measured using a digital vernier calliper. Tree crown, a measure of canopy area of influence on the ground was measured using a tape measure. We acknowledge that purposive selection of nurse plants is prone to sampling bias that could have implications on generalisation of results, however it was used to give us insights on the role of nurse plants on soil and vegetation recovery. Using the selected tree as the centre of the plot, a 25 m^2 (5 × 5 m) plot was set up underneath the canopy of each selected nurse plant tree (the plots were referred to as under nurse plants with 100% *V. karoo* canopy cover). To assess if changes in both soil and vegetation underneath the nurse plants were a result of the selected plants, plots with similar above-mentioned dimensions were set up 5 m away from the nurse plant plot boundary (the plots were referred to as outside nurse plants – with less than 75% grass and forb cover). For consistency, all outside nurse plant plots were placed on the east side of the under-nurse plant plot. In total, 48 plots were surveyed [8 replicated trees ×2 locations (under and outside) ×3 old fields].

Soil measurements

Topsoil cores measuring 10 cm in diameter and 10 cm in depth were collected as close to the centre of all the plots, after the removal of overlying debris. After soil collection, soils were transported immediately to Rhodes University laboratory for gravimetric soil moisture and soil water repellency measurements, which were conducted over a three-month period from May to July 2022. A subset of the collected soil samples were sent to a commercial laboratory, namely Bemlab (Pty) Limited, for macro element (N, C and P), pH and exchangeable cation (K, Ca, Mg, Na) measurements.

Soil penetration resistance levels and soil water infiltration measurements were conducted in all plots over the above-mentioned three-month period.

Prior to laboratory measurements, soils were sieved using a 2 mm sieve to remove stones and plant debris. Gravimetric soil moisture content was measured by weighing soil samples wet, oven drying them for 72 hours at 105°C, and re-weighing them to obtain moisture content, which was then converted to a percentage (Black 1965). Soil water repellency was measured using the Water Droplet Penetration Time (WDPT) method as described by Bisdom et al. (1993) and Doerr and Thomas (2000). Sieved soils were placed in Petri dishes and air-dried for seven days under laboratory conditions. After drying, the WDPT test was conducted by placing four drops of distilled water onto the soil surface and recording the time taken by each drop to penetrate the soil. The drops were placed using a syringe, and the average time (in seconds) for the four drops was taken to represent the WDPT per sample. The WDPT classes used in the study were adopted from Bisdom et al. (1993) as wettable (below 5 s), slightly water repellent (5–60 s), strongly water repellent (60–600 s), severely water repellent (600–3 600 s) and extremely water repellent (above 3 600 s).

Soil pH was analysed in 1:5 soil-KCl extract as described by Rhoades (1982). Soil phosphorus (P) was analysed using a Bray-II extract method as described by Bray and Krutz (1945). Soil total nitrogen (N) was determined by complete combustion using a Eurovector Euro EA Elemental Analyser, whilst soil total carbon was determined using a modified Walkley-Black method as described by Chan et al. (2001). Exchangeable cations, namely potassium (K^+), calcium (Ca^+), magnesium (Mg^+), sodium (Na^+), were extracted in a 1:10 ammonium acetate solution using the centrifuge procedure (Thomas 1982). The samples were then filtered, and analysed by atomic absorption spectrometry (SP428, LECO Corporation, USA). Soil penetration resistance levels were measured using a pocket penetrometer (SOILTEST, Inc.), as described by Leung and Meyer (2003). Soil infiltration was measured using a mini disc infiltrometer (Decagon Devices 2014). The infiltrometer was filled with water in both the upper and lower chambers and placed on the soil surface after hand removal of litter and debris. After every 30 seconds for 5 minutes, the level of water infiltrating into the soil was measured from the drop of water level in the lower chamber of the infiltrometer in ml. The level of infiltration rate was determined from the measured cumulative infiltration rates over time as described by Zhang (1997).

Vegetation measurements

Within each plot, a detailed vegetation survey was conducted in June 2022. Grasses and annual forbs were excluded during vegetation surveys since they were dry and tended to die back in winter. The richness and abundance of perennial trees, shrubs and forbs were determined through counting the total number of individual plant species present in the entire plot. Plant samples were collected and visually identified in conjunction with local plant books (Manning 2007, Manning & Goldblatt 2012) and the PlantzAfrica online directory (South African National Biodiversity Institute 2017). Those that could not be positively identified were sent to Selmar Schonland Herbarium in Makhanda.

Data analysis

Prior to selecting an appropriate statistical test to test for differences between under and outside nurse plants, all quantitative datasets were tested for normality using the Kolmogorov-Smirnov test and homogeneity of variance using Levene's test, and data was normally distributed. Comparisons between under and outside nurse plants for measured soil properties of N, C, P, pH, K, Ca, Mg and Na were done using a t-test since the data was collected once. Gravimetric soil moisture, soil penetration resistance levels, and infiltration rates were analysed using repeated measures ANOVA since data was collected monthly over a three-month period. Comparisons between under and outside nurse plants for WDPT were done using Chi-squared goodness of fit test since the WDPT data were categorical. Species abundance, richness, Shannon-Wiener diversity, Simpson's index of diversity, and Evenness index were calculated per plot and analysed between under and outside nurse plants using a t-test since data was collected once. All statistical analyses were done using TIBCO STATISTICA version 13.0 software (TIBCO Software Inc 2019).

Results

Effect of nurse plant *Vachellia karroo* on soil properties

Soil from under and outside the sampled nurse plants were made up of sand (87%) and loam (13%) soils. Soil in the study area were strongly acidic and pH was significantly ($p < 0.05$) higher outside than under nurse plants (Table 1). In contrast, soil P showed no significant ($p > 0.05$) differences between under and outside nurse plants (Table 1). Measured soil total C and N were significantly ($p < 0.01$) higher under than outside nurse plants (Table 1). Soil N was twice as high under as compared to outside nurse plants. Of the measured micronutrients, only Ca and Mg were significantly ($p < 0.05$) higher under than outside nurse plants (Table 1). Soil K and Na did not show any significant ($p > 0.05$) differences between under and outside nurse plants (Table 1).

Table 1. Comparison of measured soil chemical properties under and outside nurse plants. Data are means ± SE and t-test results are shown

Soil property	Under nurse plants (n = 24)	Outside nurse plants (n = 24)	t-value	p-value
pH	5.48 ± 0.14	5.95 ± 0.16	2.15	0.041
P Bray II (mg/kg)	37.73 ± 5.70	42.15 ± 7.81	0.46	0.651
N (%)	0.18 ± 0.02	0.09 ± 0.01	3.62	0.001
C (%)	1.35 ± 0.14	0.84 ± 0.04	3.39	0.002
K (mg/kg)	232.27 ± 20.07	288.74 ± 29.05	1.60	0.121
Ca (mg/kg)	5.10 ± 0.74	3.11 ± 0.37	2.40	0.023
Mg (mg/kg)	1.56 ± 0.18	1.12 ± 0.12	2.06	0.049
Na (mg/kg)	0.22 ± 0.02	0.35 ± 0.09	1.40	0.172

Comparisons between under and outside nurse plants showed no significant ($p > 0.05$) differences in gravimetric soil moisture content for all three months (Figure 2A). However, monthly comparisons in gravimetric soil moisture content varied, with significantly ($p < 0.001$) higher soil moisture content being reported in May and July as compared to June (Figure 2A). Interactions between nurse plant location and months for soil moisture content showed no significant ($p > 0.05$) differences (Figure 2A). Soil penetration resistance was significantly ($p < 0.001$) higher outside than under the nurse plants for all three months (Figure 2B). However, the above-mentioned differences were more visible in May, where soil penetration resistance levels were twice as high outside than under nurse plants. Monthly comparisons on soil penetration resistance showed significant ($p < 0.01$) differences for all three months, with higher soil penetration resistance levels being recorded

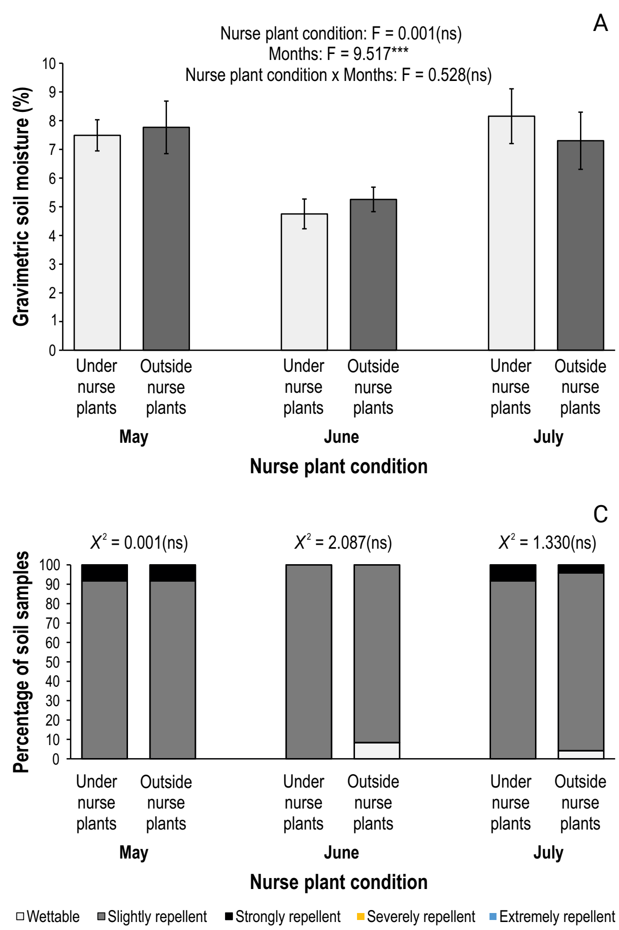


Figure 2. Results of A, gravimetric soil moisture content; B, soil penetration resistance levels; and C, water-repellency classes (based on the Water Droplet Penetration Time method) from soils measured under and outside nurse plants. For soil moisture and penetration resistance bars represent the mean ± SE and repeated-measures ANOVA results are shown. For water-repellency measurements Chi-squared test results are shown. ns = not significantly different with p > 0.05.

in June and July than in May (Figure 2B). Interactions between nurse plant location and months for soil penetration resistance showed no significant (p > 0.05) differences (Figure 2B).

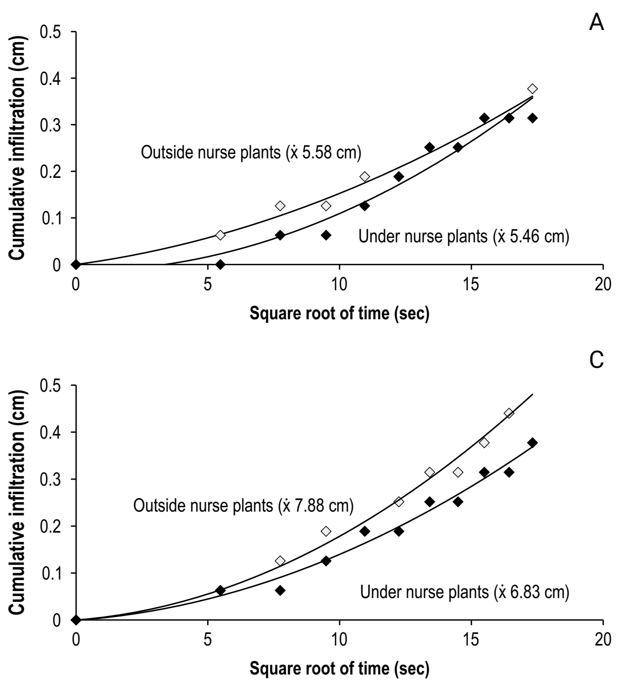
Most soils collected under and outside nurse plants were slightly repellent (more than 92%) for all the three months (Figure 2C). During the month of May, only 8% of the soils were strongly repellent under and outside nurse plants. In July, 8% of the strongly repellent soils were recorded under nurse plants as compared to 4% recorded outside nurse plants. Wettable soils were recorded outside nurse plants in the month of June (8%) and July (4%) only (Figure 2C). The chi-squared test on soil water repellency categories indicated no significant (p > 0.05) differences between under and outside nurse plants for all months (Figure 2C).

Infiltration rates showed no significant (p > 0.05) differences between under and outside nurse plants for all months (Figure 3). The average infiltration rate was 5.46 ± 0.83 cm under nurse plants in May as compared to 5.58 ± 0.79 cm outside nurse plants. In June, the difference in infiltration rates after 5 minutes between under (mean = 5.83 ± 1.85 cm) and outside (mean = 6.00 ± 0.90 cm) nurse plants was 0.17 cm. During July, the average infiltration rate after 5 minutes was 6.38 ± 1.28 cm under nurse plants as compared to 7.89 ± 1.57 cm outside nurse plants (Figure 3C). Although the month of July had the highest average soil infiltration rate (mean = 7.14 cm after 5 minutes) as compared to June (mean = 5.92 cm after 5 minutes) and May (mean = 5.52 cm after 5 minutes), statistical monthly comparisons showed no significant (p > 0.05) differences for all three months. Similarly, interactions between nurse plant location and months for soil infiltration rate showed no significant (p > 0.05) differences (Figure 3).

Effect of nurse plant *Vachellia karroo* on vegetation

Although species abundance was higher under as compared to outside nurse plants, statistical comparisons showed no significant (p > 0.05) differences between the two locations (Table 2). In contrast, species richness was significantly (p < 0.001) higher under than outside nurse plants (Table 2). Shannon-Wiener showed significant (p < 0.001) differences between under and outside nurse plants, being higher under than outside nurse plants (Table 2). Simpson's diversity and species evenness showed no significant (p > 0.05) differences between under and outside nurse plants.

Seven plant species, namely *V. karroo, Searsia crenata, Azima tetracantha, Amaranthus* sp., *Asparagus africanus, Bulbine* sp. and *Opuntia sp.*, had frequency occupancy of more than 50% under nurse plants as compared to only three species, namely *Amaranthus* sp., *Selago* sp. and *Drosanthemum hispidum*, outside nurse plants (Table 3). Four of the above-mentioned



Nurse plant condition: F = 0.35 (ns)
Months: F = 0.85 (ns)
Nurse plant condition x months: F = 0.19 (ns)

Figure 3. Infiltration levels for A, May; B, June; and C, July, from soils measured under and outside nurse plants. The results of the repeated-measures ANOVA (based on the average infiltration rate after 5 min) are shown; ns = not significantly different with p > 0.05.

Table 2. Comparison of measured vegetation diversity indices under and outside nurse plants. Data are means ± SE and t-test results are shown

Vegetation indices	Under nurse plants	Outside nurse plants	t-value	p-value
Species abundance	52.75 ± 5.60	45.96 ± 4.35	0.96	0.343
Species richness	5.75 ± 0.37	3.96 ± 0.34	3.56	0.001
Shannon-Wiener	1.38 ± 0.05	1.08 ± 0.05	3.99	0.001
Simpson's diversity	0.72 ± 0.02	0.66 ± 0.05	1.21	0.234
Species evenness	0.81 ± 0.02	0.84 ± 0.02	1.09	0.281

frequently occurring species, namely *V. karroo, S. crenata, Azima tetracantha* and *Asparagus africanus,* were present under nurse plants but not outside nurse plants. Only *Ammocharis coranica* was not present under nurse plants (Table 3).

Discussion

Our results support our prediction that *V. karoo* nurse plant creates positive plant-soil feedback that creates suitable conditions for soil and vegetation recovery underneath its canopy. We observed improved soil C, N, Ca, Mg, penetration resistance and vegetation diversity (species richness and Shannon-Wiener index) underneath *V. karroo* nurse plants compared to outside. However, some soil properties showed no differences between underneath nurse plants and outside, an indication that results could be varied. The abovementioned soil results seem to suggest that the nurse plant *V. karroo* plays a significant role in improving some soil physical and chemical properties. Previous studies have reported similar results where the effects of nurse plants on soil properties were varied (Mihoč et al. 2016; Navarro-Cano et al. 2018, 2019; Ruwanza 2019). Mihoč et al. (2016) assessed ten nurse plants in the central Chilean Andes and concluded that soil under nurse plants were rich in nutrients as compared to barren soils outside, although this varied with plant type, altitude and soil type. Navarro-Cano et al. (2018) reported that nurse plants increase soil fertility and microbial productivity in degraded ecosystems such as

Table 3. List of 28 frequently occurring plant species present under and outside nurse plants. '*' species was present and is based on calculated species occupancy frequencies categorised as: * (1–25%), ** (26–50%), *** (51–75%) and **** (76–100%); '-' species not present

Species name	Under trees	Outside trees
Achyropsis leptostachya	**	*
Aizoon glinoides	*	*
Aloe sp.	*	-
Amaranthus sp.	***	***
Ammocharis coranica	-	**
Asparagus africanus	***	-
Asparagus asparagoides	*	*
Asparagus striatus	*	*
Azima tetracantha	***	-
Bulbine sp.	***	**
Crassula expansa	*	*
Delosperma sp.	*	*
Drosanthemum hispidum	**	***
Exomis sp.	*	*

Species name	Under trees	Outside trees
Hermannia althaeoides	*	*
Isoglossa sp.	*	-
Kalanchoe sp.	**	-
Lycium ferocissimum	**	*
Lycium oxycarpum	**	*
Olea europaea subsp. *cuspidata*	*	*
Opuntia sp.	***	*
Searsia crenata	***	-
Selago sp.	*	***
Senecio deltoideus	*	-
Solanum sisymbriifolium	*	-
Teucrium africanum	*	**
Teucrium sp.	*	-
Vachellia karroo	****	-

abandoned mine dumps. Ruwanza (2019) showed that the dominance of three nurse plants, namely *V. nilotica*, *Peltophorum africanum* and *Senegalia nigrescens* in Lapalala Wilderness old fields resulted in positive soil recovery trajectory, with soils under nurse plants canopy showing improved soil moisture and penetration resistance than soils outside. Several factors, such as increased plant litter, role of nurse plant canopy, improved microbial activities, and positive plant-soil feedback have been used to explain why soil underneath nurse plants have improved soil properties (Ren et al. 2008; Mihoč, et al. 2016; Navarro-Cano et al. 2019).

Although not measured in this study, increased litter deposition has been shown to be linked to increased litter biomass, creation of soil fertile microsites beneath nurse plants, and increased microbial productivity (Navarro-Cano et al. 2019). Stuart-Hill et al. (1987) reported that *V. karroo* deposits high litter quantities in soils, which influences soil nutrients and subsequently explains the observed high nutrients underneath *V. karroo* trees. Increased plant litter underneath nurse plants can impact both soil organic matter, bacterial and fungal diversity (Pérez-Valera et al. 2018). Both increased soil organic matter and bacterial diversity affect soil microbial processes such as decomposition and nutrient cycling (Zak et al. 2003), this is likely to explain why soil C and N concentrations were high underneath *V. karroo* nurse plants. Besides the above, *V. karroo* is a known nitrogen-fixing leguminous tree (Dingaan & Du Preez 2018), this is likely to explain the high soil N levels underneath the plant. Leguminous trees form symbiotic relationships with rhizobia (nitrogen-fixing bacteria), which converts nitrogen into ammonia that can be used by the plant. Several studies on leguminous trees such as *V. karroo* and acacias (although invasive alien plants in South Africa) have reported high soil N concentrations underneath these plants and attributed this to the nitrogen-fixing process (Dingaan & Du Preez 2018). Although the actual nitrogen-fixation quantities in soils remain unknown, Dingaan and Du Preez (2018) reported that *V. karroo* fixes nitrogen in the soils, thus enhancing soil fertility underneath it through the creation of nutrient-rich islands. Although our study did not observe soil moisture differences under and outside nurse plants, moist soils underneath nurse plants are known to enhance bacterial and mycorrhizal activity, which have a positive effect on soil nutrient availability (Manzoni et al. 2014; Sierra et al. 2017).

Nurse plants have been shown to create fertile soil islands underneath their canopy (Callaway et al. 2007; Mihoč et al. 2016). These zones of nutrient enrichment underneath nurse plants are a result of a wide range of interacting biotic and abiotic mechanisms (Stock et al. 1999). For example, nitrogen fixation, hydraulic uplift, plant nutrient uptake from surrounding soils, and trapping of windblown and animal transported organic material by plants could explain why some high soil nutrient concentrations were observed underneath nurse plants (Stock et al. 1999). In this study, hydraulic uplift (the process of water movement from wet to dry soil layers through roots) by *V. karroo* roots could explain why some soil properties were high under nurse plants. *Vachellia karroo* has deep long taproots (up to 50 m) that can allow it to extract water from deep underground through hydraulic uplift (Dingaan & Du Preez 2018). This process can benefit soil around the nurse plant in several ways. Firstly, *V. karroo* can increase its daily water uptake because of hydraulic uplift, thus increasing its growth and subsequent litter deposition, which has been shown to benefit soil nutrients (Emerman & Dawson 1996). Secondly, hydraulic uplift can positively affect surrounding plant communities, particularly understorey vegetation, through increased uptake of soil moisture and nutrients being made available through *V. karroo* hydraulic uplift (Ludwig et al. 2003). Improved plant abundance and diversity underneath nurse plants can, in turn, improve soil properties indirectly through increased litter deposition, thus facilitating positive plant–soil feedback. Lastly, hydraulic uplift can increase mineralisation rates, thus maintaining bacterial activities during dry periods, which has a positive effect on soil nutrient concentrations (Ludwig et al. 2003).

Our results showed that nurse plants have a positive effect on vegetation diversity, given that we recorded more plants underneath *V. karroo* nurse plants as compared to outside. This observation concurs with results from other studies where the diversity and abundance of other plants were high under nurse plants as compared to outside (Badano et al. 2016; Ruwanza 2019). Badano et al. (2016) reported that most plant species were positively associated with the nurse plant *Larrea tridentata*. The same above-mentioned study also identified high seed density under *L. tridentata,* an indication that the nurse plant traps seeds underneath it. Similarly, Ruwanza (2019) reported increased species diversity underneath three nurse plants in old fields, although diversity varied with growth form, e.g., trees and shrub counts were more underneath nurse plant canopy than outside, yet graminoids showed the opposite trend. A possible explanation for why the diversity of other plant species was high under *V. karroo* nurse plants is the plant–plant facilitation theory that has been reported in previous studies (Navarro-Cano et al. 2019). Several studies have shown that nurse plants have a positive association with surrounding plants, implying that other plants benefit from nurse plants (Brooker et al. 2008; Navarro-Cano et al. 2019). Brooker et al. (2007) reported that plant–plant facilitation can result in enhanced growth, reproduction and survival of species that are benefiting from proximity to other plants. Navarro-Cano et al. (2019) used the term ecosystem engineers to refer to nurse plants that facilitate the establishment of other species. These ecosystem engineer plants also called nurse plants have stress-tolerant traits that allow them to establish easily and support surrounding plants. For example, they provide other plants with canopy shade, moist soils underneath them, and create nutrient-rich microsites that benefit other plants (Graff & Aguiar 2017; Navarro-Cano et al. 2019). Besides creating conducive environments to facilitate the growth of other plant species, nurse plants also reduce abiotic and climatic stress for other plants e.g., temperature reduction through shade provisioning (Callaway 2007).

Besides the dominance of *V. karroo* seedlings underneath the nurse plant, six species, namely *Searsia crenata, Azima tetracantha, Amaranthus* sp., *Asparagus africanus, Bulbine* sp. and *Opuntia* sp., had frequency occupancy of more than 50% under nurse plants. The dominance of these species could be linked to several factors such as competition-related co-occurrence with nurse plants, shade tolerance and invasion traits. Shade-tolerant species need to have specific traits, such as the ability to tolerate limiting factors such as light (Valladares & Niinemets 2008) to survive under nurse plants. It is possible that shrub species such as *S. crenata* have traits that allow it to grow in the shade of other plants, since the plant species can tolerate harsh conditions such as drought and frost. For some plant species, such as *Asparagus africanus*, the ability to propagate both sexually and clonally (vegetatively) could explain its dominance underneath nurse plants. Yang and Kim (2016) suggested that perennial plants tend to favour clonal reproduction under favourable soil nutrients and moisture habitats, conditions that we also observed under *V. karroo* nurse plants. For *Opuntia* species, its invasion traits, such as being adaptable to different environmental conditions and can survive better in degraded conditions, such as old fields (Sipango et al. 2022) could explain its high frequency occupancy underneath *V. karroo* nurse plants. A study by Novoa et al. (2021) reported that *O. stricta* germinated well on soils conditioned by the native plants *V. nilotica* and *Spirostachys africana* than on soils from open patches. The above-mentioned results seem to suggest that nurse plants create conditions for the establishment of other plants, such as the invasive *Opuntia* species. In contrast, the above-mentioned study also reported that *O. stricta* can nurse other plants, implying that *Opuntia* species can co-occur with other plants.

Our observed vegetation and soil results seem to suggest a positive plant–soil feedback that could explain the dominance of other plants underneath nurse plants. Facilitation-driven cascade systems associated with nurse plants have been reported in the past (Navarro-Cano et al. 2019), where surrounding plants benefit from the nurse plant and the benefits impact soil communities through nutrient cycling and microbial decomposition (Navarro-Cano et al. 2019). In turn, below ground nutrient and microbial benefits promote ecosystem feedback that will benefit the nurse plant and the subcanopy plant community, resulting in increased abundance and diversity. Therefore, plant-soil feedback underneath nurse plants can explain the observed diverse and abundant species under compared to outside nurse plants (Clewell et al. 2005; Navarro-Cano et al. 2018).

Conclusion and recommendations

This study highlights the role and importance of *V. karroo* nurse plant in old fields targeted for passive ecological restoration. We reported improved soil properties such as soil C, N, Ca, Mg and penetration resistance, as well as the dominance of native vegetation under the nurse plants. Both the improved soil properties and the presence of diverse vegetation underneath nurse plants are indications that *V. karroo* plays a positive facilitation role that could be crucial to ecosystem recovery in these degraded old fields. These results support our prediction that the nurse plant *V. karroo* facilitates soil and vegetation recovery in old fields targeted for passive restoration. Based on these results, we conclude that *V. karroo* has the potential to act as an ecosystem engineer that could facilitate plant and soil recovery in these old fields. However, *V. karroo* is a well-known bush encroacher that has invasive and expansion traits (Dingaan & Du Preez 2018). Its removal for bush encroachment management purposes should therefore consider: (i) selective removal of *V. karroo* plants that do not provide refugia for underneath vegetation; (ii) removal should be done in a way that protects underneath surrounding vegetation (i.e., remove young rather than older *V. karroo* individuals); and (iii) protect, through fencing, some *V. karroo* plants to reduce the browsing of subcanopy species by mesoherbivores. The successful protection of *V. karroo* as a nurse plant in old fields has the potential to accelerate soil and vegetation recovery during passive restoration in these regions.

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Competing interests

The authors declare that they have no financial or personal relationship(s) that may have inappropriately influenced them in writing this article.

Authors' contributions

S.R. (Rhodes University) was the project leader and V.M. (Rhodes University) was the student. S.R. and V.M. were responsible for experimental and project design. V.M. performed most of the experiments and collected the data. Both S.R. and V.M. made conceptual contributions. V.M. prepared the samples for analysis. S.R. conducted data analysis and wrote the first draft of the manuscript. V.M. reviewed the draft manuscript.

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