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Soil seed banks after *Acacia dealbata* Link invasion and removal: implications for restoration

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Abstract

Background *Acacia dealbata* Link is a problematic invasive alien tree in South Africa, with severe environment effects such as native plant displacement and soil nutrient manipulation (nitrogen fixation). Most studies on *A. dealbata* invasion are on aboveground vegetation effects, with a few studies on belowground soil seed bank impacts associated with both invasion and removal for restoration purposes. This study assessed the impact of *A. dealbata* invasion and removal on soil seed banks in grasslands targeted for ecological restoration in the upper Tsitsana communal area of Eastern Cape Province, South Africa. Soils were collected from *A. dealbata* invaded, cleared, and uninvaded treatments and germinated in an ambient greenhouse over 11 months. We measured species diversity, density, frequency of occupancy, and identified all the seedlings that germinated in trays measuring 20 cm wide × 20 cm long × 15 cm deep.

Results Species richness and abundance were significantly ($P < 0.001$) lower in the cleared and invaded treatments compared to the uninvaded treatment, with this trend being more pronounced for forbs and graminoids than for trees and shrubs, indicating that soil seed bank impacts are growth-form specific. Species density for all species was significantly ($P < 0.001$) lower in the invaded treatment compared to the cleared and uninvaded treatments. The removal of *A. dealbata* increased species composition in the cleared treatment with woody species such as *Diospyrus* and *Searsia* species occurring in the cleared than invaded treatment.

Conclusions The study concludes that *A. dealbata* invasion reduces soil seed bank community diversity and composition in upper Tsitsana grasslands. However, seed banks in the cleared treatment appear adequate to facilitate grassland recovery following the removal of *A. dealbata*.

Keywords Biological invasion, Seed bank diversity, Ecological restoration, Greenhouse, Plant germination, Plant diversity

Introduction

Invasive alien plants are a problem to both the environment and humans (Rai and Singh 2020). The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) thematic assessment report on invasive alien species and their control suggests that six percent of all alien plant species have established and cause negative effects on biodiversity and human health (IPBES 2023). The invasion process is generally influenced by species-specific traits (e.g., rapid reproduction, allelopathy, and fast growth) and ecosystem-based traits (e.g., ecosystem disturbance and climatic matching). Once introduced, most invasive alien plants must overcome biotic and abiotic barriers for them to colonise and naturalise in the new area before they become invasive (Richardson et al. 2000). Most invasive alien plants

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become invasive (trigger negative socio-economic and ecological impacts) once they start to produce reproductive offspring that can spread and transform the ecosystem (Richardson et al. 2000). Negative effects of invasive alien plants on natural ecosystems include the displacement of native plants through the creation of mono stands and changes in soil properties (Le Maitre et al. 2011). The negative effects on ecosystems caused by invasive alien plants tend to vary depending on the invader, invasion extent, invasion duration, and the invaded landscape. For example, the invasion of South African ecosystems by Australian *Acacias* and *Eucalyptus* has triggered the loss of native endemic species on riparian zones (Le Maitre et al. 2011). In contrast, invasive alien plants have socioeconomic benefits such as timber for furniture, construction poles, shade provisioning, and natural capital in various industries, e.g., wood and bee industry (Ngorima and Shackleton 2018). Nevertheless, the negative effects of invasive alien plants on ecosystems have broader socioeconomic implications such as loss of productive land and agricultural income (Eschen et al. 2021), thus the call of action to manage invasive alien plants. Recent studies by Eschen et al. (2021) estimated that the cost of invasive alien species, particularly plants, in the agricultural sector in Africa alone is approximately USD 65 billion annually. In South Africa, the economic costs associated with invasive alien plants range from USD 45 million per year on rangelands to USD 73 million per year on water resources (De Lange and van Wilgen 2010). These negative socioeconomic impacts are huge, which points to the need to manage invasive alien plants. The South African government spends more than ZAR 2 billion per year (approximately USD 106 million using May 2024 exchange rate) through the Working for Water (WfW) programme to manage invasive alien species (mostly plants) (van Wilgen et al. 2020a). However, successful management of invasive alien plants needs information related to invasion pathways, impacts, and control options. Although several studies have been conducted in South Africa to understand invasion processed and patterns (van Wilgen et al. 2020b), little is known regarding belowground invasion effects, particularly soil seed bank impacts caused by transformer invaders such as *Acacia dealbata* Link.

The ability of invasive alien plants to produce and deposit large quantities of seeds into the soil can have direct (promote invasiveness) and indirect (displacement of native vegetation) effects on the invaded ecosystem (Le Maitre et al. 2011). For example, most invasive Australian acacias produce large quantities of seeds (e.g., approximately 11,500 seeds/m^2 for *A. longifolia*) that end up being stored in the soil seed banks (Richardson and Kluge 2008). Of the total *Acacia* seeds produced, less than 10% germinate immediately, implying the bulk of the seeds remain in the soil (Richardson and Kluge 2008). Most of the buried *Acacia* seeds are found in the topsoil and can remain dormant for more than 50 years (Milton 1980). Once germination conditions are suitable, these seeds can germinate and promote the spread of *Acacias*, and this is more prevalent in fire-prone ecosystems since the seeds are fire-adapted. Apart from soil seed banks promoting invasiveness, *Acacia* seed banks tend to germinate fast under varied environmental conditions, thus outcompeting seedlings of slow-growing native species and ultimately displacing them (Le Maitre et al. 2011). Studies that have examined the effects of *A. dealbata* invasion on soil seed banks have reported that the plant modifies the seed bank of native species by decreasing species diversity, density, and composition (González-Muñoz et al. 2012). The above-mentioned study reported that soil seed banks of native species were significantly lower underneath *A. dealbata* invaded sites compared to uninvaded sites, although impacts varied based on plant growth form (González-Muñoz et al. 2012). Gioria and Pyšek (2016) suggested that the displacement of native vegetation after alien plant invasion is strongly linked to changes in soil seed banks and the creation of mono stands. Ecologically, as seeds of the invaders are dropped into the soil, they germinate fast resulting in the creation of mono stands, which ultimately affect the germination of native species, thus displacing them. Given that invasive alien plants can affect soil seed banks directly and indirectly, there is a need to understand seed bank dynamics after plant invasion to develop effective management strategies.

Efforts to control invasive alien plants and restore invaded ecosystem in South Africa intensified around 1995 when the WfW programme was established (van Wilgen et al. 2020b). The WfW programme is a government funded initiative that has a dual mandate to conserve the environment (conservation) through using alien plant clearing to create employment (social responsibility) (van Wilgen et al. 2020b). The programme uses a passive restoration approach, based on the assumption that once alien plants are removed, native vegetation will recover spontaneously (Ruwanza et al. 2013). Passive restoration after alien plant removal relies on the availability of soil seed banks to kick-start the restoration process (Ruwanza et al. 2013). Gaertner et al. (2014) and of late Holmes et al. (2020) used the ecological threshold concept to show that passive restoration after alien plant removal is only possible if soil seed banks are not severely depleted, meaning seed banks of native species are still dormant and viable in the soil awaiting appropriate germination conditions. Several studies have confirmed the above-mentioned notion that passive restoration after

alien plant removal is dependent on availability of soil seed banks (Fill et al. 2018; Ruwanza 2024). For example, Fill et al. (2018) observed an increase in native species diversity and cover three years after alien plant clearing and attributed the increase to soil seed bank availability and germination. Recently, Ruwanza (2024) reported increased native plant diversity after *Eucalyptus* removal and concluded that remnant species in the cleared site are creating suitable microclimatic conditions for soil stored seed banks to germinate. However, both studies noted that re-invasion by the invader and secondary invasion by alien grasses and forbs, stimulated by soil seed bank availability, is a deterrent to the passive restoration process (Fill et al. 2018; Ruwanza 2024). Re-invasion and secondary invasion from soil seed banks have been reported in other studies (Blanchard and Holmes 2008; Ndou and Ruwanza 2016; Ruwanza et al. 2018; Nsikani et al. 2019). For example, Blanchard and Holmes (2008) reported that soil seed banks of *Acacia* trigger re-invasion after its removal thus retarding native vegetation recovery since most native species were outcompeted for resources such as water and soil nutrients. Also, Ruwanza et al. (2018) showed that seed banks tend to promote the proliferation of invasive alien grasses and forbs after *Eucalyptus* removal thus slowing down the passive restoration of native species in cleared sites. Therefore, the passive restoration process after alien plant removal depends on soil seed banks, although the recovery trajectory might differ depending on the types of soil seed banks. Given the importance of soil seed banks in shaping our understanding of passive restoration trajectories after alien plant removal, more studies on soil seed banks are needed to inform restoration decisions. For example, Tererai et al. (2015) used soil seed banks study to recommend active restoration after *Eucalyptus camaldulensis* removal along the Berg River after observing that the invader had significantly depleted seed banks of native woody species. Similarly, Vosse et al. (2008) used soil seed bank results to conclude that restoration of native species along four Western Cape rivers is possible given the availability of native species soil seed banks, although the same study noted that not all riparian species were present in the seed banks. Therefore, more soil seed bank studies are needed at various cleared sites to inform site-specific interventions.

Soil seed banks are viable reserves of seeds found in the soil or on the soil surface (Roberts 1981; Gioria et al. 2014). These seed could have been produced recently or over several years and they help in shaping plant communities and functions particularly in plant succession and restoration (Gioria et al. 2014). The persistence of soil seed banks relates to the survival of seeds in the soil once they reach maturity (Long et al. 2015). Seed banks that remain viable in the soil for short periods (days to 1 year) are normally called transient soil seed banks, whereas those that last for more than a year in the soil are called persistent soil seed banks (Bicalho 2024). Several factors can affect soil seed bank persistence, e.g., seed type, seed shape, seed burial depth, biotic factors such as herbivory, and environmental factors such as temperature and soil moisture (Bicalho 2024). The ability of seeds to persist in the soil for a long time is important because it has implications for restoration after the degrader (in this case invasive alien plant) is removed. Two methods are commonly used to assess seed banks, namely, the seed extraction method and the seedling emergency method. The seed extraction method is based on the technique of separating seeds from soil particles using either a sieve or floating the seeds in a salt solution, whilst the seedling emergency method consists of placing soils under suitable germination conditions (e.g., growth chambers or greenhouse) (Gonzalez and Chermandi 2012). Both methods have advantages and disadvantages, but in cases where a germinable fraction of the seed needs to be determined, the seedling emergency method is regarded as appropriate (Gonzalez and Chermandi 2012). de Villiers et al. (1994) observed that the seedling emergency method can detect both small and large seeded species, thus the method is appropriate to estimate seed banks species composition and density.

This study used the seedling emergency method with particular focus on soil seed banks after *A. dealbata* invasion and removal for restoration purposes in South Africa. *Acacia dealbata* (commonly known as silver wattle) is a notorious invasive alien tree that invaded South Africa around the mid-nineteenth century from Australia (Hirsch et al. 2021). The tree has been introduced to many countries such as Madagascar, New Zealand, Chile, and Portugal for various purposes such as forestry, horticulture, fuelwood, shade, and shelter (Kull et al. 2008; Lorenzo et al. 2010; Richardson and Rejmánek 2011). *Acacia dealbata* grows to a height of 2–15 m but can attain 30 m under favourable conditions such as along riparian areas. The tree reaches reproductive maturity within 4 to 5 years and tends to dominate disturbed areas such as old fields, riparian zones, road-river intersections, and road verges (Hirsch et al. 2018). *Acacia dealbata* has hairy bipinnate leaves, yellow flowers, and oblong shaped seed pods. Invasion by *A. dealbata* is aided by its ability to create mono stands, mature early, flower throughout the year, allelopathy, and the ability to change soil properties through nitrogen fixation from the atmosphere (Lorenzo et al. 2010). Although negative impacts of *A. dealbata* invasion are well documented, the plant has several benefits such as erosion control, shade provisioning, fuelwood, and income from the sale of

poles (Ngorima and Shackleton 2018; Hirsch et al. 2021). Considering the above context, this study used the seedling emergency method to shed more light on the effects of *A. dealbata* invasion and clearing on soil seed banks in South Africa. Specifically, the study investigated the germination potential, density, diversity, and composition of soil seed banks on *A. dealbata* invaded, cleared, and uninvaded treatments. The study's results generate knowledge that can be used to understand belowground effects of *A. dealbata* invasion and benefit ongoing initiatives to develop effective species and site-specific management options for the plant.

Methods

Study area and soil collection sites

Soil samples for the seed banks were collected in February 2021 on four conveniently selected sites that are in the upper Tsitsana communal area (site 1 = − 30.830391, 28.306261; site 2 = − 30.835210, 28.302580; site 3 = − 30.865666, 28.352227; site 4 = − 30.873167, 28.341335) in the Eastern Cape Province of South Africa (Fig. 1). The distance between the sites was approximately 5 km to allow for site independence as suggested by Galatowitsch and Richardson (2005). The study area is approximately 60 km from the nearest town of Nqanqarhu (previously called Maclear) and it is in Joe Gqabi district municipality. The study area is rural with most villagers dependent on livestock grazing and government social welfare grants (Coka et al. 2024). Vegetation in the area is classified as grasslands, specifically East Griqualand grassland (Mucina and Rutherford 2006), which are characterised by veld degradation and severe soil erosion, mainly due to overgrazing. Apart from the invasive alien plant *A. dealbata*, the grasslands are dominated by grasses such as *Cynodon dactylon*, *Sporobolus indicus*, and *Aristida stricta*. Soils in the study area are predominately sandy and loamy from the Tarkastad Subgroup, the Molteno, and Elliot formations of the Karoo Supergroup (Mucina and Rutherford 2006). The area receives summer rainfall (October to April), between 600 to 800 mm a year. Temperatures are hot in summer (averaging 20 °C) and cold in winter (averaging 0 °C) (Mucina and Rutherford 2006).

At each of the above-mentioned conveniently selected sites in the study area, soils for the soil seed banks were collected on three treatments: invaded, cleared, and

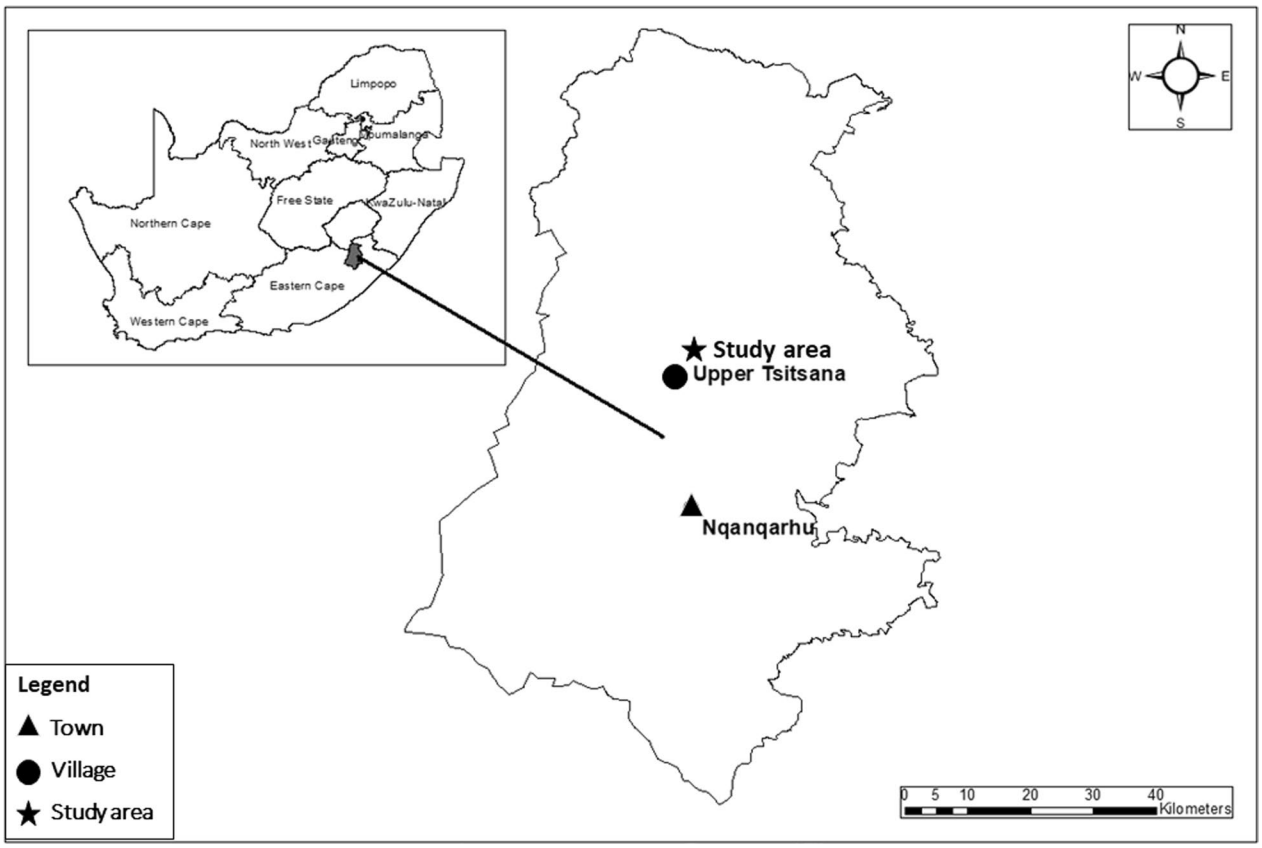


Fig. 1 Map showing location of study are in upper Tsitsana communal area where soils for seed banks were collected

uninvaded. Convenient sampling ensured that all three treatments were represented per site. At each site, the three above-mentioned treatments were separated by rural gravel roads and were of similar soil type and slope angle. The invaded treatment was heavily invaded by mono stands of *A. dealbata* with canopy cover of more than 65%. It is not known when *A. dealbata* was introduced in the area; however, Google Earth images show that the plant was present in the study area several years ago (before 2000). The cleared treatment received WfW alien plant removal which started in late 2017 and ended in 2018. Clearing involved *A. dealbata* cutting at base height and herbicide application to prevent resprouting. Felled trees were piled and stack burn on site after selective harvesting of purposeful cut stumps by villagers for use such as firewood and fencing poles. All burnt patches were omitted during soil collection since highly intensive fire burning of stack piles kills seed banks (Ruwanza 2024). Information regarding the mandatory WfW follow-up treatment to remove recruiting saplings was not provided by WfW. The uninvaded treatment, which acted as the control, had no *A. dealbata* invasion or clearing and were dominated by grasslands. The uninvaded grasslands are open to livestock grazing, with evidence of sheet and gully erosion.

Soil seed bank sampling and assessment

On each of the above-mentioned three treatments per site, six 1 m^2 quadrats were set up along a 40 m transect that cut across the center of the treatment. The six quadrats were 5 m apart with the start quadrat positioned 10 m from the edge of the treatment. The transect stretched from east to west and within each quadrat, and five topsoil cores were collected using a soil core measuring 10 cm in diameter and 10 cm deep. The above-mentioned soil depth assumed that topsoil in the study area is 5–8 cm deep as observed during the reconnaissance field trip that was conducted before the commencement of the study. The five soil cores were collected from all four quadrat corners and at the center and were bulked together to form a single sample per quadrat. A total of 72 soil cores were collected for the soil seed banks study (6 soil cores per treatment × 3 treatments (invaded, cleared, and uninvaded) × 4 sites). The collected soil cores were immediately transported to Rhodes University in Makhanda in seed germination trays measuring 20 cm wide × 20 cm long × 15 cm deep. Upon arrival, the soil cores were sieved using a 2 mm sieve to remove stones and plant debris. After sieving the soils were placed in a passively ventilated ambient greenhouse where the air temperature is close to the one outside. A thin hessian fabric material was placed at the bottom of each tray to prevent soil from getting out but allowed water to pass through. Soil cores were arranged in the greenhouse based on treatments with a 10 m spacing in-between treatment rows. The trays were watered once every two days by hand from February to December 2021 and were rotated monthly to account for air temperature and sunlight penetration variations in the greenhouse. After every two months, seedlings that germinated from the soil seed banks were counted and identified to the species level where possible. Emerging species were identified at the Selmar Schonland Herbarium at the Albany Museum in Makhanda. Seedlings were assigned to four growth forms (trees, shrubs, forbs, and graminoids) based on morphology (Goldblatt and Manning 2000). All seedlings that were counted and identified were removed from the tray to avoid double counting.

Statistical analysis

Seedling counts were used to calculate density, species richness, Shannon–Wiener, and evenness indices per each treatment and these were used to measure seed bank characteristics. The total number of seedlings that germinated per tray were converted to density (seedlings per square meter) and compared across the different treatments. To test for significant differences in these indices of diversity across treatments, a one-way analysis of variance (ANOVA) was conducted using TIBCO STATISTICA version 14.0 software (TIBCO Software Inc. 2020). Data were checked for normality and homogeneity of variances using the Kolmogorov–Smirnov test and Levene's test, respectively. Effect sizes for one-way ANOVAs were reported as Eta Squared (η). Species occupancy frequency (expressed as a percentage) was calculated as the number of times a plant species is present in the different trays. Using the seedling emergency presence and absence data, Principal Component Analysis (PCA) was done to investigate changes in species composition across the treatments. Principal component analysis was performed using Canoco for Windows version 5. The limitation of this study lies in the fact that the soil seed banks study was conducted based on a comparative approach by examining invaded, cleared, and uninvaded areas. Compared to robust approaches like before and after invasion assessment of soil seed bank, the comparative approach fails to identify the direct impacts of *A. dealbata* invasion on soil seed banks. However, robust approaches have been unavailable due to time factors since the invasion. Thus, the comparative approach used in this study can only identify potential effects of *A. dealbata* invasion on soil seed banks, not direct effects. Nevertheless, such knowledge is essential as it provides valuable insights into *A. dealbata* invasion impacts and feeds into the formulation of effective management options.

Results

Seedling diversity and density

In total 3730 seedlings, representing 30 different species emerged across the three treatments (Table 1). Of the 3730 seedlings, 393 were in the invaded treatment, 1081 in the cleared treatment, and 2256 in the uninvaded treatment. The 30 different species included seven trees and shrubs, 16 forbs, and seven graminoids and sedges (Table 1). Species richness and abundance were significantly ($P < 0.001$) higher in the uninvaded treatment than in the invaded and cleared treatments (Table 2). Species richness was approximately three times higher in the uninvaded than in the invaded treatment, whereas abundance was five times higher in the uninvaded than in the invaded treatment (Table 2). In contrast, species evenness was significantly ($P < 0.001$) higher in the invaded treatment than in the uninvaded treatment (Table 2). Shannon–Wiener index of diversity showed no significant ($P > 0.05$) differences across all the treatments (Table 2). Except for the Shannon–Wiener index of diversity ($\eta = 0.013$), the effect size for the measured diversity of indices revealed large differences among the three treatments (Table 2). Species richness for forbs and graminoids (including sedges)

Table 1 Thirty frequently occurring seed bank species in invaded, cleared, and uninvaded treatments

Plant name	Family	Occupancy frequency (%)			Average density (seedlings/m^2)		
		Invaded	Cleared	Uninvaded	Invaded	Cleared	Uninvaded
Trees and shrubs							
[A]*Acacia dealbata*	Fabaceae	88	88	0	235	218	0
[N]*Diospyrus* sp.	Ebenaceae	0	13	17	0	42	63
[N]*Plumbago auriculata*	Plumbaginaceae	0	0	4	0	0	25
[N]*Leucosidea sericea*	Rosaceae	13	33	8	67	100	50
[N]*Searsia* sp.	Anacardiaceae	0	8	29	0	50	46
[N]*Myrsine* sp.	Primulaceae	0	0	17	0	0	31
[N]*Helicrysum* sp.	Asteraceae	0	0	25	0	0	46
Forbs							
[A]*Pseudognaphalium obtusifolium*	Asteraceae	17	25	50	50	233	131
[A]*Richardia humistrata*	Rubiaceae	4	4	8	25	25	63
[A]*Rumex* sp.	Polygonaceae	0	4	0	0	25	0
[A]*Bidens pilosa*	Asteraceae	0	4	50	0	50	69
[A]*Chenopodium* .	Amaranthaceae	0	17	0	0	31	0
[A]*Cirsium vulgare*	Asteraceae	0	4	4	0	25	25
[A]*Conyza* sp.	Asteraceae	67	67	71	136	345	432
[N]*Cotula* sp.	Asteraceae	0	4	33	0	25	109
[A]*Dichondra* sp.	Convolvulaceae	8	0	21	88	0	160
[A]*Erigeron* sp.	Asteraceae	13	8	0	100	75	0
[A]*Galinsoga paruiflora*	Asteraceae	4	4	0	25	25	0
[N]*Lactuca capensis*	Asteraceae	0	0	13	0	0	25
[N]*Oxalis* sp.	Oxalidaceae	4	46	63	125	366	533
[A]*Sochus oleraceus*	Asteraceae	8	13	13	25	33	125
[A]*Solanum sisymbriifolium*	Solanaceae	0	4	0	0	50	0
[A]*Taraxacum* sp.	Asteraceae	8	4	21	163	25	30
Graminoids and sedges							
[A]*Cynodon dactylon*	Poaceae	58	67	100	59	205	373
[N]*Themeda triandra*	Poaceae	0	29	71	0	161	243
[A]*Aristida stricta*	Poaceae	0	25	58	0	279	361
[A]*Paspalum dilatatum*	Poaceae	0	8	46	0	63	389
[A]*Cyperus rotundus*	Cyperaceae	0	13	46	0	92	350
[N]*Bulbostylis* sp.	Cyperaceae	0	25	42	0	317	388
[A]*Sporobolus indicus*	Poaceae	13	29	88	117	268	238

Values indicate calculated species occupancy frequency (%) and average density per m^2. *N* indicates native species and *A* indicates alien species

Table 2 Analysis of species diversity indices of seed bank communities in invaded, cleared, and uninvaded treatments

	Invaded	Cleared	Uninvaded	*F*-values	*P*-values	*η*-values
Richness of all species	3.13 ± 0.16^{c}	5.38 ± 0.48^{b}	8.96 ± 0.40^{a}	62.53	< 0.001	0.645
Abundance of all species	16.38 ± 1.88^{c}	45.04 ± 4.90^{b}	93.88 ± 7.96^{a}	50.64	< 0.001	0.595
Shannon–Wiener index	0.28 ± 0.02^{a}	0.29 ± 0.01^{a}	0.29 ± 0.01^{a}	0.45	0.64	0.013
Evenness index	0.25 ± 0.02^{a}	0.20 ± 0.01^{b}	0.13 ± 0.01^{c}	22.25	< 0.001	0.392
Species richness by growth form						
Trees and shrubs	1.00 ± 0.09^{a}	1.41 ± 0.15^{a}	1.12 ± 0.19^{a}	2.08	0.13	0.057
Forbs	1.63 ± 0.20^{c}	2.25 ± 0.36^{b}	3.50 ± 0.30^{a}	10.47	< 0.001	0.233
Graminoids and sedges	0.46 ± 0.12^{c}	1.71 ± 0.28^{b}	4.29 ± 0.28^{a}	67.42	< 0.001	0.661

Data are means ± SE, one-way ANOVA, and Eta Squared (*η*, effect size) results are shown. Numbers with different superscript letters represent significant differences

was significantly ($P < 0.001$) higher in the uninvaded treatment compared to the cleared and invaded treatments (Table 2). Species richness for forbs was twice higher in the uninvaded compared to the invaded treatments, whereas for graminoids and sedges it was nine times higher between the above-mentioned two treatments (Table 2). Species richness for trees and shrubs showed no significant ($P > 0.05$) differences across all the treatments (Table 2). Except for the species richness of trees and shrubs ($\eta = 0.057$), the effect size for the measured richness per growth form revealed large differences among the three treatments (Table 2). Species density was significantly ($P < 0.001$) higher in the uninvaded treatment than in the invaded and cleared treatments. Generally, the density for all species was twice as high in the uninvaded treatment than in the invaded treatment (Table 3). Species density by growth form showed significant ($P < 0.001$) differences across all treatments for all growth forms (Table 3). Species density for trees and shrubs was significantly ($P < 0.05$) higher in the uninvaded treatment than in the invaded treatment (Table 3). For forbs, species density was five times higher in the uninvaded treatment compared to the invaded treatment, whereas for graminoids and sedges, it was 33 times higher in the uninvaded compared to the invaded treatment (Table 3). The effect size for the density of all species revealed a medium difference among the treatments ($\eta = 0.037$) but large effect sizes for densities of soil seed banks per growth form when the three invasion conditions were compared (Table 3).

Seedling composition

Leucosidea sericea was the only native tree species that frequently occurred across all treatments, although higher densities were observed in the cleared treatment (Table 1). Only two native trees, namely *Diospyrus* and *Searsia* species were present in the cleared and uninvaded treatments, although the frequency of occupancy was higher in the latter compared to the former treatment (Table 1). The alien forb species *Conyza* had more than 50% frequency of occurrence across all treatments (Table 1). Although the alien forbs *Pseudognaphalium obtusifolium* and *Bidens pilosa* as well as native forb *Oxalis* recorded above 50% occupancy frequency in the uninvaded treatment, they had below 30% in the cleared and invaded treatments (except for *Oxalis* species in the cleared treatment) (Table 1). The native forb *Lactuca capensis* was present only in the uninvaded treatment. For graminoids, only the alien species *Cynodon dactylon* and *Sporobolus indicus* were present across all three treatments, although densities were higher in the uninvaded compared to the cleared and invaded treatments (Table 1). The frequency of occurrence for the other graminoids, native species *Themeda triandra* and alien species *Aristida stricta* and *Paspalum dilatatum*

Table 3 Analysis of species density of seed bank communities in invaded, cleared, and uninvaded treatments

	Invaded	Cleared	Uninvaded	*F*-values	*P*-values	*η*-values
Density of all species (seedlings/m^2)	131.00 ± 13.04^{b}	209.50 ± 20.82^{ab}	262.33 ± 19.44^{a}	8.08	< 0.001	0.037
Density of *A. dealbata* (seedlings/m^2)	205.21 ± 29.10^{a}	190.63 ± 24.21^{a}	00.00 ± 0.00^{b}	27.45	< 0.001	0.443
Density of trees and shrubs (seedlings/m^2)	8.33 ± 4.91^{b}	41.67 ± 13.26^{ab}	60.42 ± 12.31^{a}	5.94	0.004	0.147
Density of forbs (seedlings/m^2)	147.71 ± 31.61^{b}	501.04 ± 113.77^{ab}	840.63 ± 141.32^{a}	10.62	< 0.001	0.235
Density of graminoids and sedges (seedlings/m^2)	42.71 ± 19.53^{c}	384.38 ± 77.91^{b}	1433.33 ± 151.13^{a}	53.78	< 0.001	0.609

Data are means ± SE, one-way ANOVA, and Eta Squared (*η*, effect size) results are shown. Numbers with different superscript letters represent significant differences

were more than twice higher in the uninvaded than in the cleared treatment (Table 1). The above-mentioned trend was also observed for the two sedge species of *Cyperus rotundus* (alien) and *Bulbostylis* species (native; Table 1). The PCA for all species that germinated across all treatments showed little species separation in ordination space from the first two axes, except for alien species *Galinsoga paruiflora* which assembled more in the invaded and cleared treatments (Fig. 2a). The seven trees and shrubs that germinated across all treatments assembled mostly in the uninvaded treatments (Fig. 2b). Although the PCA for forbs showed little separation across the treatments, the alien species *Erigeron* assembled more in the invaded and cleared treatments, whereas the native species *Lactuca capensis* assembled more in the uninvaded treatment (Fig. 2c). The seven graminoids and sedges that germinated across all treatments assembled more on the cleared and uninvaded treatments but not in the invaded treatment (Fig. 2d). Overall, there were more alien forbs and graminoids recruiting in the cleared treatment compared to the invaded and uninvaded treatments (Table 1).

Discussion

Effects of invasion on soil seed banks

Results of this study show that *A. dealbata* invasion affects soil seed banks of native plant species, mainly because of its persistent soil seed banks. Our results on soil seed banks underneath *A. dealbata* invasion are consistent with previous studies that have reported both high *A. dealbata* seed bank density and viability (Possos et al. 2017) as well as a decrease in native species soil seed bank diversity and composition (González-Muñoz et al. 2012; Gioria et al. 2014). Apart from that, this study confirms that *A. dealbata* invasion effects on soil seed banks of native species are growth-form specific. For example, a closer assessment of species richness and density data from this study shows that the invasion impacts were more visible on forbs and graminoids than on trees and shrubs. González-Muñoz et al. (2012) reported enhanced *A. dealbata* invasion effects on some species (bryophyte and ferns) than other species (Asteraceae and other exotic) and attributed this to the invader. Effects of *A. dealbata* invasion on soil seed banks are caused by several factors such as competition, allelopathy, and soil nutrient manipulation (González-Muñoz et al. 2012; Gioria et al. 2014). Firstly, several studies have reported that *A. dealbata* outcompetes native species and displaces them through the creation of dense mono stands (Lorenzo et al. 2010; Gouws and Shackleton 2019; Hirsch et al. 2019). Such dense *A. dealbata* mono stands prevents the growth of understory native vegetation (Yapi et al. 2018), and this is likely to result in the loss of native species' soil seed banks. The effect of *A. dealbata* mono stands on native species is likely to be more pronounced on woody plants (trees and shrubs) than on grasses since the former survives on deeper soil resources than the latter, which needs shallow soil resources. This aligns with the two-layer hypothesis on plants, suggesting that grasses are more water-use efficient on shallow soil resources due to root distribution than trees that depend on deep soil resources (Ward et al. 2013). However, it is essential to note that species-specific effects due to *A. dealbata* mono stands can also be affected

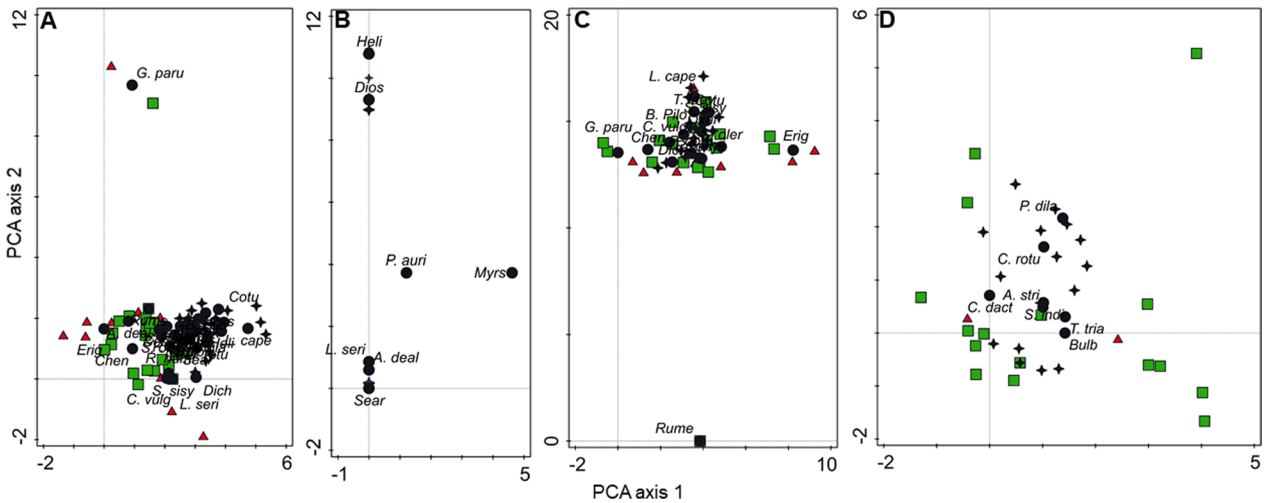


Fig. 2 Principal component analysis (PCA) bi-plots of the 30 most frequently occurring seed bank species (black circle) at the invaded (red up-pointing triangle), cleared (green square), and uninvaded (black star) treatments for **A** all plant species, **B** Trees and Shrubs, **C** Forbs, and **D** Graminoids and sedges. The first four letters of the species names are presented with full names in Table 1

by the ability of plants to survive as understory vegetation, i.e., the notion that understory plants compete with invaders for nutrient resources and are shade tolerant. Secondly, *A. dealbata* is allelopathic, implying it releases allelochemical that can affect the seed of native plants (Lorenzo et al. 2013; Aguilera et al. 2015). Although not extensively studied for *A. dealbata*, it is possible that the released allelochemicals may prevent native species seed germination through autotoxicity and disrupting the physiological processes of other plants, e.g., cell division, plant hormone production, enzymatic activity, photosynthesis, and respiration as shown in other plants (Patanè et al. 2023). Other studies have shown that allelochemicals released by other plants inhibit seed germination of other plants through disrupting subcellular structure and disturbing the metabolism process in other plants (Mamude and Asfaw 2023). In contrast, other studies have shown enhanced plant germination under different allelopathic compounds (Ruwanza et al. 2015), likely due to hormesis (Duke et al. 2006). Hormesis refers to the adaptive response of plant cells and organisms to stress, e.g., low doses of allelopathic compounds can positively stimulate plant growth, compared to high doses that could inhibit plant germination and growth. Therefore, allelopathic effects could be species specific, which likely explains why soil seed banks of some native species were present underneath *A. dealbata* invasion, yet others were not. Lastly, *A. dealbata* fixes atmospheric nitrogen in the soil (Lorenzo et al. 2013; Hirsch et al. 2019), thus manipulating soils to promote its growth. The ability of plants to manipulate soil properties causes native plant displacement, which ultimately results in loss of native species seed rain and soil seed banks. Nitrogen fixation by invasive alien plants is likely to have more displacement effects on slow-growing native species than on fast-growing species. This is because root quality (total surface area of the roots) and activity (root nutrient content and enzyme activities) could be affected under high soil nitrogen content, alternately affecting plant root nutrient uptake. This could be more visible on slow-growing plants (mostly trees and shrubs) whose nutrient uptake would be negatively impacted compared to fast-growing plants like grasses.

Few species, namely the forb species *Conyza* sp., and the grass species *C. dactylon* had seedling frequency occupancies of greater than 50% in soils collected underneath *A. dealbata*, indicating that these species can co-occur with the invader. Although co-occurance has been reported in the past (Leger and Espeland 2010), it mostly occurs between invaders with similar invasion traits, but rarely between invaders and native plant species. The ability of *Conyza* and *C. dactylon* to co-occur with *A. dealbata* could be explained by factors such as gene frequency, competition, and high species tolerance to invasion (Leger and Espeland 2010). For example, *C. dactylon* is highly tolerant and can compete with other plants by allocating nutrient resources to its stolons and leaves to enhance its growth (García et al. 2023). Apart from that, plant species that compete with the invader tend to co-occur as understory vegetation which become remnant species when clearing is done effectively to avoid their removal. Remnant species tend to produce seeds that can remain in the soil during and after the invader is removed, in this case occurring underneath *A. dealbata*. However, the ability of remnant and understory plant species to co-occur with the invader is also influenced by invasion extent. For example, Tererai et al. (2015) reported high native species soil seed banks underneath *E. camaldulensis* light and moderate invasion conditions compared to high invasion conditions and attributed this to canopy cover opening which allows light penetration to benefit fast-growing remnant and co-occurring forbs and graminoids compared to trees and shrubs.

Effects of alien plant clearing on soil seed banks

The cleared treatment had high seed banks of native plant species compared to the invaded treatment, indicating that the removal of *A. dealbata* can allow seeds from various species to recruit. Previous studies have reported that the removal of invasive alien trees could facilitate the germination and growth of native species seed banks (Vosse et al. 2008; Tererai et al. 2015). This could be linked to competition exclusion following invader removal which allows dormant seed banks to germinate. In addition, alien plant removal increases resource (e.g., nutrients and light) availability, which could benefit native seed banks and create opportunities for dispersed seeds from nearby intact to cleared areas to germinate. Previous studies have provided evidence suggesting that seed banks of native species exist in the cleared soil and tend to germinate a few years after alien plant clearing (Ruwanza et al. 2013; Ndou and Ruwanza 2016). Once the invader is removed, dormant seed banks can germinate provided germination conditions are suitable. Moreover, nutrient resources may be unused and available in access following clearing thus allowing seed banks of native species to take advantage and enhance their germination. Nevertheless, environmental factors like natural seed dispersal could also explain the availability of native species soil seed banks in the cleared areas. Seed dispersal by wind or ungulate-mediated plant dispersal could explain seed movement from intact to cleared areas, as observed in old agricultural fields (Ruwanza 2020). However, Nsikani et al. (2017) reported that excessive

soil nutrient availability after *Acacia* removal can benefit seeds of secondary alien plant invaders more than native woody species, thus the proliferation of secondary invaders. In the above-mentioned study, recruitment of alien graminoids and forbs from seed banks after *Acacia* removal was attributed to increased nutrient availability and reduced competition. Indeed, fast growing pioneer species (mostly forbs and graminoids) could benefit from the excessive post clearing nutrient resources, which likely explains why the occurrence of forbs and graminoids seed banks was high in the cleared treatment. Since clearing was completed in 2018, seed dispersal could have happened prior to sampling in 2021 thus explaining the high number of native species soil seed banks in the cleared treatment. Seed dispersal by bird and animals to the alien plant cleared areas has been shown to increase native species seed banks and recruitment; however, this is influenced by the type of plant species existing in the dispersal donor natural area and the distance between the donor and cleared area (Ruwanza et al. 2013). Given that passive restoration is focused on soil seed banks, movement of seeds from intact donor natural areas to cleared receiver areas is an important step in initiating restoration. Contrary to the above, this study observed seedlings of several native species such as *Diospyrus* sp., *Searsia* sp., *Aristida stricta*, and *Themeda triandra* that were present in the cleared but not in the invaded treatment. This seems to suggest that native vegetation recovery can happen in the future, an observation that has been reported in other studies where plant recruitment from seed banks is possible in cleared areas (Blanchard and Holmes 2008; Fill et al. 2017). Since these native species are not present in the invaded treatment, it is plausible to assume that these were dispersed after *A. dealbata* clearing since the cleared and invaded treatments are adjacent. For forage grasses such as *A. stricta,* it is possible that dispersal by livestock could have happened since the cleared treatments are susceptible to grazing. Apart from recruiting native species and secondary invaders in the cleared treatment, seedlings of *A. dealbata* were also abundant. *Acacia dealbata* produces seeds that remain persistent in the soil and remain viable several years after the plant's removal (Le Maitre et al. 2011; Nsikani et al. 2017; Passos et al. 2017). Passos et al. (2017) enumerated approximately 4608 seeds/m^2 underneath *A. dealbata* invaded areas, of which 90% were considered viable. Seeds of *A. dealbata* can easily germinate under high soil temperatures and fire, as these conditions tend to break seed dormancy. Therefore, the conditions mentioned above (high soil temperatures and fire), which are common in grasslands, could have substantial negative impacts on the passive restoration of native vegetation after *A. dealbata* removal.

Conclusions and management implications

This study provides compelling evidence that *A. dealbata* invasion in grasslands of upper Tsitsana communal area displaces native species seed banks, but its removal can potentially facilitate passive restoration of native species through soil seed banks. However, the post-clearing recruitment of fast-growing secondary invaders (mostly forbs and graminoids) from seed banks can hamper the passive restoration process. The study also demonstrates that the effects of *A. dealbata* invasion on soil seed banks are growth-form dependent, with trees and shrubs notably absent in the invaded treatment. These findings have several management implications for vegetation recovery after *A. dealbata* removal. Firstly, the removal of *A. dealbata* is encouraged as it has potential to facilitate the recruitment of native species through soil seed banks. Secondly, re-invasion by *A. dealbata* seedlings and secondary invaders from soil seed banks needs to be managed once the invader is removed. This can be done through effective clearing follow-up programmes aimed at removing re-invaders and secondary invaders. Although clearing agents in South Africa conduct follow-up treatments after alien plant removal, these efforts appear insufficient, necessitating improvements. Current clearing follow-up treatments tend to concentrate on re-invasions by the invaders and other recruiting woody invasive alien plants, yet this study highlights that forbs and graminoids germinating from soil seed banks are the most problematic secondary invaders. Therefore, follow-up clearing treatments should prioritise the removal of invasive forbs and graminoids to address the problem of secondary invasion. This approach may potentially increase clearing costs; therefore, clearing agents should budget for long-term follow-up treatments before initiating invasive alien plant clearing programmes. Alternatively, seed bank-driven re-invasion after *A. dealbata* clearing could be reduced by controlling the plant using biocontrol agents that prevent flowering and pod production, thus limiting seed rain, which is the driver of post-clearing re-invasion. Recent reports suggest that the wasp *Perilampella hecataeus* can control *A. dealbata* through flowering prevention (Impson and Martin 2024). Lastly, the availability of some native species seed banks in the cleared treatment indicates the potential for passive vegetation recovery. To achieve passive restoration from soil seed banks in grasslands that are prone to grazing, measures such as fencing of cleared areas to form exclusion grazing plots should be explored to protect recruiting native species. However, implementation of

exclusion grazing plots requires stakeholder engagement since these grasslands are used for communal grazing by local people.

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S.R is the sole author and did everything.

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Availability of data and materials
The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

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Consent for publication
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The author declare that they have no competing interests.

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