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ORIGINAL PAPER

Impacts of *Gleditsia triacanthos* L. (Fabaceae) on soil characteristics: insights from the free state highveld grasslands of South Africa

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Abstract Invasive alien plants are one of the significant threats to ecosystems globally. These species are known to have detrimental effects, including adverse effects on biodiversity, water quality and, in some cases, soil health. Many invasive species have no adverse impact on soil health, but certain species, such as those within the Fabaceae, have distinct impacts. An invasive *Gleditsia triacanthos* (Fabaceae) is rapidly spreading and becoming an aggressive transformer of the temperate grasslands in South Africa. This species has several environmental impacts, its influence on soil properties in grassland biomes remains to be determined. We investigated the effects of *G. triacanthos* on selected soil properties across five locations within the grassland biome. At each location, soil samples were collected near the roots of *G. triacanthos* and at the same depth at an adjacent, uninvaded grassland. The soils collected under *G. triacanthos* in all the locations had significantly higher concentrations of organic C, N, P, K, Ca and Mg. Clay percentage and exchange acidity were also significantly increased under *G. triacanthos*, while soil bulk density and pH were decreased. *Gleditsia triacanthos* did not impact Zn, Mn and Cu. The results reveal the soil enrichment under *G. triacanthos*, which is detrimental to the biodiversity and, thus, the functioning and productivity of this vulnerable ecosystem. To prevent further impacts, management of the tree is recommended.

Keywords Honey locust · Invasive plant · Grassland · Soil properties

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Introduction

Plants can modify their environment in many ways, including influencing the physical and chemical aspects of the substrate they grow (Weidenheimer and Callaway 2010; Afzal et al. 2023). This includes using resources such as organic matter, water and

nutrients, as well as releasing root exudates and litter that can alter the soil's physicochemical composition, increasing or decreasing some nutrients and thus affecting the growth and development of neighbouring plants (Dassonville et al. 2008; Rusterholz et al. 2018; Afzal et al. 2023). The functional diversity of a plant community is a good predictor of ecosystem health and function. More diverse ecosystems, measured by plant traits, are known to have better nutrient recycling, resulting in higher soil fertility and plant productivity (Fornara and Tilman 2008; Teixeira et al. 2020).

Biological invasions are one of the main perturbations affecting plant diversity and, thus, ecosystem function and productivity (Stanek et al. 2020; Teixeira et al. 2020). In novel environments, invasive alien plants (IAPs) act as ecological engineers, affecting the ecosystem differently from native plants (Linders et al. 2019). They affect biodiversity and modify ecosystem function and productivity (Le Maitre et al. 2004; Linders et al. 2019; Stanek et al. 2020). Such changes lead to positive feedback loops that favour the growth and persistence of alien plants (Kulmatiski et al. 2008; Marler 2020; Teixeira et al. 2020). Generally, they can alter soil nutrient availability, causing a shift that favours the formation of invasive monocultures (Ruwanza and Shackleton 2016) and the transformation of ecosystems. For example, *Acacia mearnsii* De Wild (Fabaceae) and *Acacia dealbata* Link (Fabaceae) have been reported to modify the physicochemical parameters of the soils they invade in South Africa, leading to the detriment of surrounding native plant species (Lusizi et al. 2024).

Invasive alien trees pose the greatest threat to preserving threatened ecosystems, such as the South African grassland biome. The biome is an important centre of plant endemism; it also hosts and supports many endemic, rare and threatened animal species (O'Connor and Kuyler 2009; Prinsloo et al. 2021). The soil in the grassland biome is a medium for plant growth and biogeochemical cycling and is the most agriculturally productive in the country, with over 20% of the biome supporting both commercial and subsistent farming (Neke and Du Plessis 2004). Despite this, only about 2% of the biome is protected (O'Connor and Kuyler 2009). More than 30% of the grassland in South Africa has been transformed by exotic woody plants, leaving it with the third-highest number of IAPs (O'Connor and van Wilgen 2020; Martin 2021).

Invasive alien trees have the potential to significantly alter native plant communities, fire regimes, and water use patterns and modify soil processes (Dassonville et al. 2008; Grove et al. 2012; Stanek et al. 2020). The impacts of invasive alien trees on soil processes are often genus or species-specific, influenced by the chemicals they release (Afzal et al. 2023). Most invasive alien trees have secondary compounds, often allelopathic, defensive, or antimicrobial, that are novel, and the native plants are not accustomed to them (Weidenhamer and Callaway 2010). These compounds can disrupt biogeochemical processes, ultimately altering the soil chemistry of the grassland (Weidenhamer and Callaway 2010). Some work on the influence of invasive alien woody plants within the Fabaceae family on soil properties of the grassland biome has been undertaken in South Africa (Gwate et al. 2021; Yapi et al. 2018); however, research on Fabaceae from Northern Temperate regions, such as *Gleditsia triacanthos* L. (Fabaceae), has not been investigated in the country (Martin 2021).

Gleditsia triacanthos, commonly known as honey locust, is a fast-growing tree native to the Central and East United States of America (Blair 1990). *Gleditsia triacanthos* has rapidly expanded its range, becoming one of the nine fastest-spreading weeds in South Africa (Henderson and Wilson 2017; Martin 2021). Consequently, *G. triacanthos* is listed under Category 1b of the National Environmental Management: Biodiversity Act (NEMBA) (NEM: BA, 2004) and is currently being considered for biological control (Martin 2021).

Many plant species are known to impact the soil; for example, see Nunes et al. (2025). Plants in the family Fabaceae are known to influence nitrogen fixation, enhancing nutrient availability and phosphate solubilisation (Yuvaraj et al. 2020). Very little is known about the potential impacts of *Gleditsia triacanthos* on soil properties.

Given that substantial resources and time are spent to control invasive plants, it is essential to first test whether and how the invaded ecosystems are modified. These studies are also necessary to optimise resource allocation and devise effective management strategies to mitigate further ecological disruptions of the invaded ecosystems. To

achieve this, studies take the comparative approach by examining invaded and uninvaded areas (Dassonville et al. 2008; Ruwanza and Shackleton 2016). This study investigates the consequences of *Gleditsia triacanthos* invasion on topsoil chemistry and nutrient reserves within standing biomass across five locations in South African grasslands. These sites vary in terms of the soil type and climatic conditions. The aim of the study is to investigate the impact of *Gleditsia triacanthos* on soil physicochemical properties and provide insights into whether differences exist between sites with and without *G. triacanthos* in the grassland biome of South Africa. Similar to other invasive Fabaceae, it is hypothesised that *Gleditsia triacanthos* affects soil physicochemical properties in the South African Highveld grassland, particularly by increasing nutrient pools, including nitrogen, carbon, and phosphorus.

Methods and materials

Site description

In South Africa, *Gleditsia triacanthos* is most abundant in the Grassland biome, forming dense monocultures (Salgado Astudillo 2021; Fig. 1). Within the highveld grassland of Free State province in South Africa, we selected five locations for their homogeneity in soil type (Table 1), and the availability and abundance of *G. triacanthos* in the site. The sites were chosen based on three criteria: firstly, the number of *G. triacanthos* trees in that area had to exceed

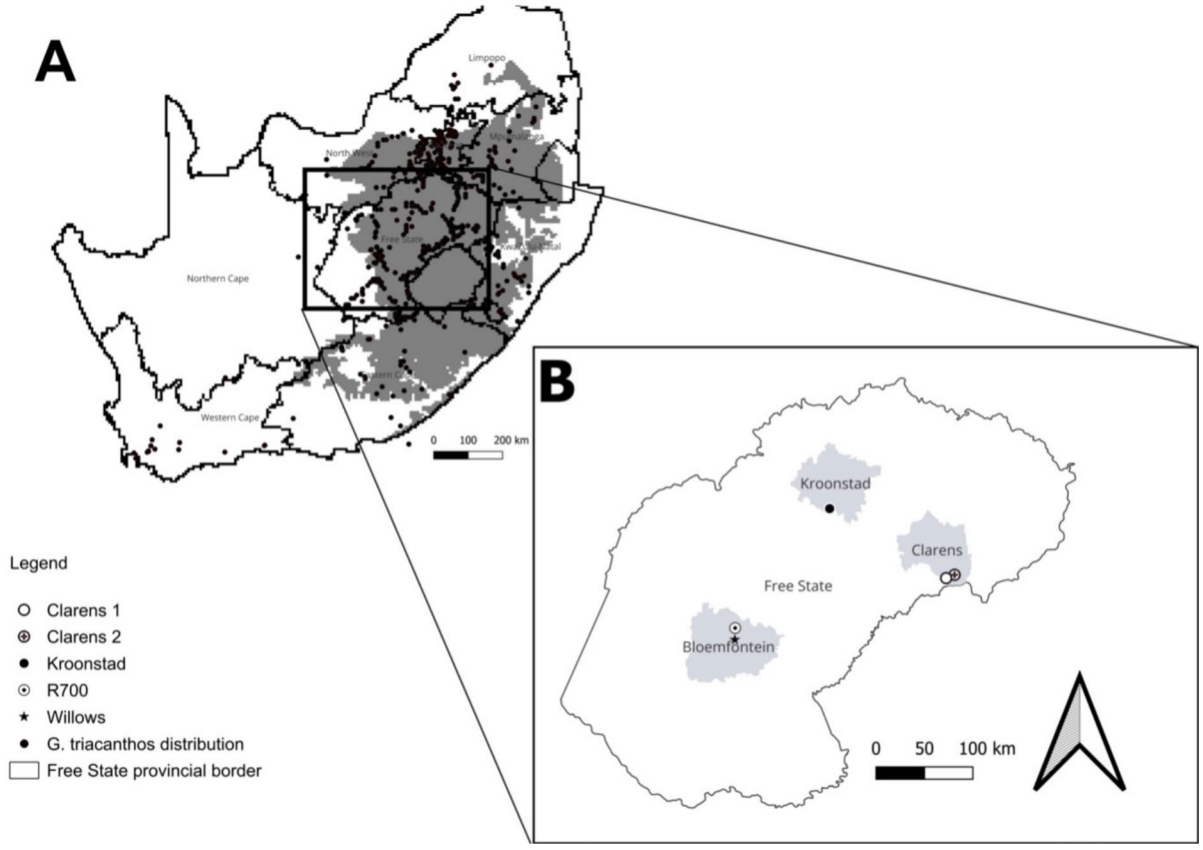

Fig. 1 Distribution of *Gleditsia triacanthos* in South Africa (**A**) and location of study areas in the Free State Province, South Africa (**B**). The *G. triacanthos* distribution map was adapted from the Southern African Plant Invaders Atlas database (SAPIA), INaturalist (2019), Global Biodiversity Information Facility (GBIF 2024) and road surveys by Salgado Astudillo (2021)

Table 1 Location, chosen names, spatial coordinates, and climatic measures of the sampled *Gleditsia triacanthos* sites within the Grassland biome in South Africa

Location	Site name	Latitude (S)	Longitude (E)	Vegetation type	Soil type	Annual mean temperature (°C)		Annual mean precipitation (mm)
						Minimum	Maximum	
Bloemfontein	Willows	− 29.1′ 1566″	26.20′359″	Dry highveld	Leptic Phaeozems	8.9	23.4	545
	R700	− 29.00′ 24″	26.12′29.5″		Rhodic Lixisols			
Kroonstad	Kroonstad	− 27.89′ 50.1″	27.20′84.9″	Dry highveld	Paraplinthic Lixisols	9.7	22.6	616
Clarens	Clarens 1	− 28.53′ 596″	28.43′89″	Mesic highveld	Chromic Lixisols	5.8	17.8	854
	Clarens 2	− 28.50′ 41.1″	28.52′9″					

20 mature trees to ensure that the invasion was well-established, allowing for the investigation of potential ecological impacts on soil properties. Secondly, there should be an adjacent uninvaded grassland to serve as a reference or benchmark site; and lastly, the site should be accessible, and landowner consent should be obtained. The exact size of each site was not measured; however, each sampling area was large enough to include eight soil sampling points per invasion status while maintaining a minimum separation of 10 m between invaded and uninvaded stands.

Invaded and uninvaded stands were selected within the same soil type at each location to minimize the potential confounding effects of inherent soil characteristics on soil physicochemical properties (Table 1). The aim was to ensure that any observed differences in soil properties could be attributed to the presence of *Gleditsia triacanthos* rather than natural variations in soil texture across the sites.

All the reference sites were dominated by grasses, particularly Kikuyu grass (*Cenchrus clandestinus*) in Willows, while *Themeda triandra* and *Eragrostis lehmanniana* were prevalent in the other locations, along with a single layer of forb species, although these were hardly prominent. In contrast, the invaded sites were dominated by *Gleditsia triacanthos* trees, including seedlings, with some ruderal plant species present in low numbers.

Two sites were selected in Bloemfontein, two other sites were chosen near Clarens, and one other was selected in Kroonstad towns/cities (Fig. 1, Table 1). The sites selected in Bloemfontein and Clarens are located > 10 km from each other. In all the sampled locations, the uninvaded paired grassland stands were located > 10 m from the *G. triacanthos* stands. The study sites were named based on their location within the Free State province (Table 1).

Oil sampling and analysis

In each site, eight soil samples weighing 250 g were collected using a garden trowel from the invaded stands, and eight more were collected from the uninvaded paired grassland stands. After removing the surface litter, the soil samples were collected near the roots of *G. triacanthos*, less than one meter from the tree base. A soil core, approximately 15 cm in diameter and 15 deep, was removed. Reference samples were collected similarly from uninvaded paired grassland stands. The samples were collected along two 50 m transects, with four samples per transect, collected approximately 5 m apart. The invaded and uninvaded stands were situated approximately 10 m apart. The samples were stored in sealed zip lock bags, labelled, and sent to the KwaZulu-Natal Department of Agriculture and Rural Development for analysis at the Soil Fertility Laboratory, Cedara College, KwaZulu-Natal.

Upon arrival at the laboratory, the samples were air dried at room temperature at the soil fertility laboratory by spreading them on drying trays and allowing them to dry for 48 h. Once dry, the samples were crushed and passed through a 1 mm sieve to discard any stones, gravel, and other coarse materials. The soil samples were then assessed using the methods described by Manson et al. (2020). Since the soil samples are analysed on a volume rather than mass

basis, sample density was determined using a scooped volume weight.

Organic carbon, clay content and total nitrogen percentages were estimated using mid-infrared reflectance (with a Bruker Tensor 27). Exchangeable cations such as Ca, Mg, K and extractable Zn, Cu, and Mn were analysed through atomic absorption using an air-acetylene flame. Extractable phosphorus and soil pH (KCl) were analysed by using the Murphy and Riley (1962) molybdenum blue procedure with some modifications (Manson et al. 2020).

Data analysis

The data was initially analysed using a Mixed Linear Model (MLM) to test for an interaction between location and treatment (invaded vs. uninvaded) for various soil physicochemical properties. For this model, location and treatment were treated as fixed factors, and pair ID as a random factor to account for the paired design of the dataset (e.g., paired invaded and uninvaded samples within each location). Since the location by treatment interaction was significant ($p < 0.05$), each location was analysed separately, using an amalgamated data set created by pooling the eight samples. Treatment was a fixed factor, and pair ID was included as a random factor. The locations were not compared with each other. The significance level was kept at $p \leq 0.05$, and all the tests were performed using Python; data handling was done with pandas, and the model was fitted using statsmodels.

Results

Physical soil structure in invaded and uninvaded habitats

All soil samples collected under *G. triacanthos* had different physical soil structures when compared to the paired control samples. There was a significantly higher clay percentage of the soil collected under *G. triacanthos* (Fig. 2A), and bulk density was significantly decreased in these areas in all the sites sampled (Fig. 2B). The soil under *G. triacanthos* was slightly more acidic than that collected at the uninvaded control sites; the pH was significantly reduced in all invaded locations (Fig. 2C). While the exchange acidity was only significantly increased in the invaded site along the R700 route in Bloemfontein (Fig. 2D), there were no significant differences in the other sampled locations.

Soil organic carbon and macronutrients in invaded and uninvaded habitats

The soil organic carbon and micronutrient (nitrogen, phosphorus and potassium) concentrations differed in *G. triacanthos* stands compared to surrounding grassland sites. Significantly higher concentrations of organic carbon (Fig. 2E) and nitrogen percentages (Fig. 2F) were recorded in soils from all sampled sites where *G. triacanthos* was present compared to the reference sites. There was double the amount of organic carbon and nitrogen in the soils collected under *G. triacanthos*. Similarly, phosphorus (Fig. 2G) and potassium (Fig. 2H) concentrations were significantly higher in all the soils from *G. triacanthos* stands than in the soils collected from the uninvaded grasslands. In all the sites except Willows, phosphorus was more than 3 × higher under *G. triacanthos*.

Exchangeable cations and micronutrients in invaded and uninvaded habitats

Exchangeable cation concentrations also differed between the soils from the invaded and uninvaded grassland sites. Compared to the uninvaded reference sites, calcium (Fig. 2I) and magnesium (Fig. 2J) concentrations were consistently higher in all the sampled sites with *G. triacanthos*. The total cation count was also significantly higher in soils containing *G. triacanthos* (Fig. 2K).

In contrast to the macronutrients and exchangeable cations, there was no difference in micronutrient concentrations between the samples collected from the invaded and uninvaded sites across the sampled grasslands. While there was a slight numerical increase in zinc concentration in the soils collected under *G. triacanthos*, this was insignificant (Fig. 2L). Copper (Fig. 2M) and manganese (Fig. 2N) did not significantly differ between the soils from *G. triacanthos* stands and the control sites in all the sampled grasslands.

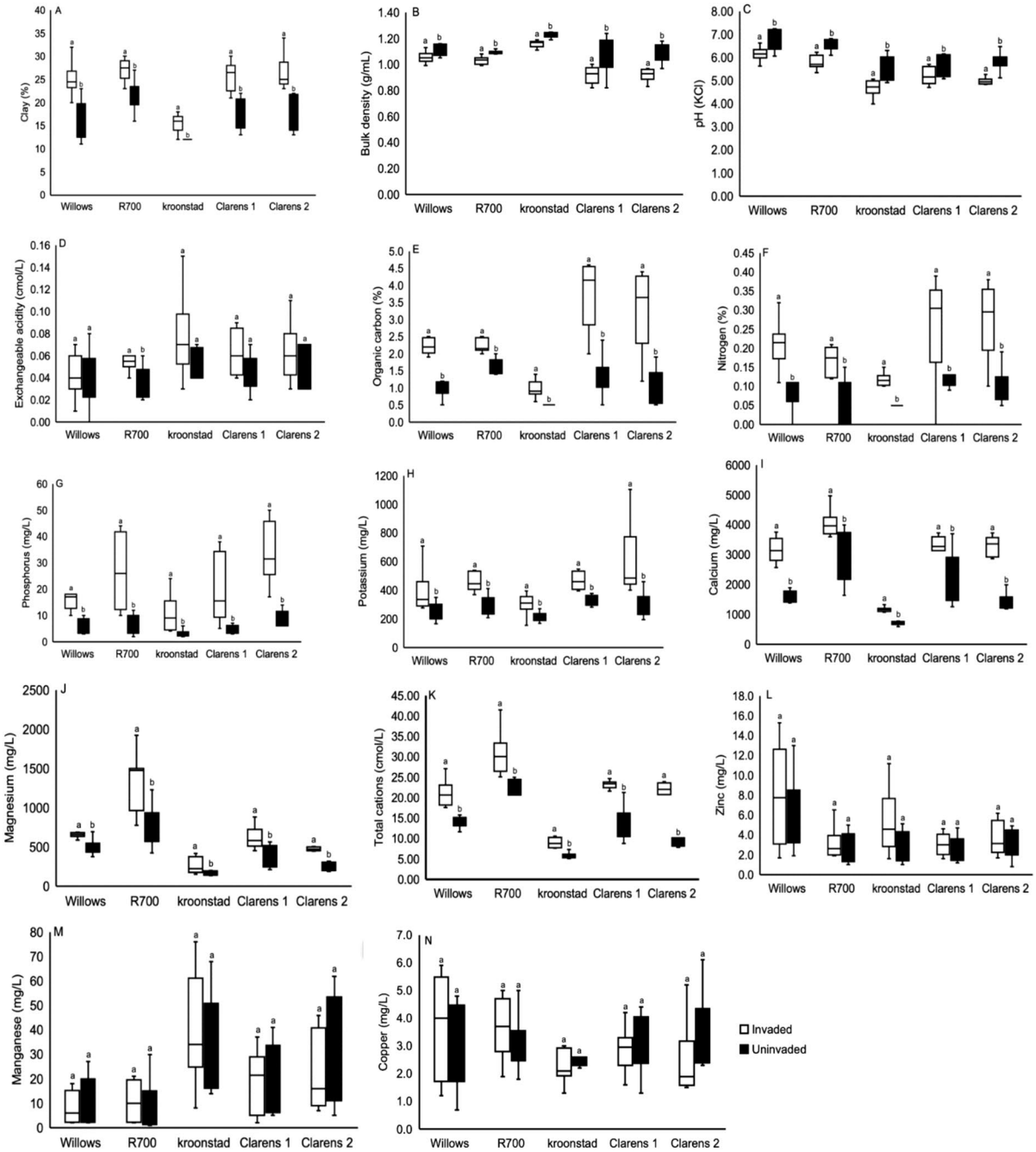

Fig. 2 Comparison of **A** clay percentage, **B** bulk density, **C** pH, **D** exchangeable acidity, **E** organic carbon, **F** nitrogen, **G** phosphorus. **H** potassium. **I** calcium, **J** magnesium, **K** total cations, **L** zinc, **M** manganese and **N** copper between uninvaded and grasslands invaded by *Gleditsia triacanthos* across five locations in the Grassland biome. Bars and lines represent the interquartile range, and the data's spread and different superscript letters denote a significant difference ($p < 0.05$) between the invaded and uninvaded areas

Discussion

This study was conducted across five locations within the dry highveld Grassland biome of South Africa, and it compared soil properties between grasslands and areas invaded by *Gleditsia triacanthos*. The variation in the soil properties among the sampled grasslands, coupled with the diverse climatic conditions across the chosen locations, indicated the adaptability of *G. triacanthos*, showing that the tree can thrive in a wide range of environmental conditions.

In this study, the clay content increased in areas with *G. triacanthos* while bulk density decreased. Araya et al. (2022) reported similar findings in the invaded ranges of *Tamarix* (Tamaricaceae) species. Clay particles bind more water and have more cation space, explaining the higher total exchangeable cation concentration observed in invaded soils (Simba et al. 2017; Araya et al. 2022). Bulk density, which refers to soil compaction, was lower in the soils with *G. triacanthos*. Differences in soil texture have often been observed where invasive plants are present; for example, May and Attiwill (2003) and Vargas-Lomelín et al. (2023) reported that the invasion of *Acacia dealbata* Link. (Fabaceae) and *Prosopis juliflora* (Sw) DC. (Fabaceae), respectively, was associated with decreased soil bulk density. Notably, even within its native range in Virginia, *G. triacanthos* was found to decrease soil bulk density in silvopasture plots (DeBruyne 2009).

Lorenzo et al. (2010), Araya et al. (2022), and Unger et al. (2022) reported a decrease in soil pH in invaded sites. This is in line with the findings of the current study. This decrease can be attributed to the release of carbon dioxide and the addition of organic acids from the decaying leaf litter (Araya et al. 2022). Invasive alien plants have been reported to have high leaf litter that decomposes and mineralises faster than native plants, releasing organic acids and thus acidifying the soil. For instance, *Fraxinus uhdei* (Wenz) Lingelsh. (Oleaceae), invasive in Hawaii (Rothstein et al. 2004), and *Eucalyptus camaldulensis* Dehnh. (Myrtaceae), invasive in South Africa (Hirsch et al. 2020), have shown a similar influence on the soil pH. However, this is not the same for all invasive species; other studies reported non-significant results in soil pH (Dassonville et al. 2008; Marler 2020; Comole et al. 2021); while others reported an increase in the pH of invaded soils (Gibbons et al. 2017; Keet et al. 2021). Moreover, the same species can have varying influences depending on the ecosystem it invades. Leicht-Young et al. (2009) reported an increase in soil pH in the grassland and shrubland and the opposite for the pineland ecosystem, all invaded by *Celastrus orbiculatus* Thunb. (Celastraceae). This indicates that the influence can be species- or site-specific.

The soil in the studied sites invaded by *G. triacanthos* had significantly higher concentrations of organic carbon, nitrogen, phosphorus and potassium. Additionally, increased calcium and magnesium concentrations were observed in the invaded soils, aligning with other studies that reported increased nutrient availability under invaded soils (Lorenzo et al. 2010; Sardans et al. 2017; Gibbons et al. 2017; Simba et al. 2017; Keet et al. 2021; Xiao-Qi et al. 2019). This accumulation of nutrients under *G. triacanthos*, particularly nitrogen, shows the soil enrichment properties of this tree, a trait shared by other invasive Fabaceae trees such as *Prosopis velutina* (Comole et al. 2021) and *Acacia mirensii* and *A. dealbata* (Lusizi et al. 2024). While *G. triacanthos* lacks the nodules found in other fabacean species, some studies have reported the presence of bacteroids and ethylene evolution in the roots of *G. triacanthos*, which indicates nitrogenase activity (Bryan et al. 1997; Dent and Cocking 2017). Interestingly, DeBruyne (2009) also observed this soil enrichment effect of *G. triacanthos* within its native range at the silvopasture plots of Virginia Tech's Kentland Research Farm (Virginia, USA).

The fertility islands created by invasive plants have been shown to affect plant diversity, functional species composition, and soil microbial communities (Nsikani et al. 2018; Ruwanza and Tshililo 2019; Ludwig et al. 2004; Chikowore et al. 2021; Erckie et al. 2022). These changes often favour the spread of invaders, replacing native species (Weidenhamer and Callaway 2010). Some effects persist even after the trees have died or been cleared (Ludwig et al. 2004; Nsikani et al. 2018). Similarly, in Argentina, *G. triacanthos* woody patches had higher soil fertility, which, along with the tree canopy, promoted the growth of exotic C_3 grasses, which displaced native C_4 grasses (Ferraina et al. 2021).

Invasive plants also create dense stands that impact grazing systems in rangelands (Chikowore et al. 2021), with some invasive plant species offering unpalatable feed (O'Connor and Wilgen, 2020).

While *G. triacanthos* has palatable pods, they can be harmful in large quantities, and their consumption has contributed to its spread (O'Connor and Wilgen, 2020). *Gleditsia triacanthos* also has thorns that reduce access to palatable pods and can cause physical damage to livestock, as seen with *Prosopis* species (Bekele et al. 2018).

The lower levels of organic matter in the adjacent open grasslands are attributed to the predominant grasses' lower quality of litter, which is resistant to decay because of the high cellulose concentration (Birouste et al. 2012). South African grasslands are herbaceous systems dominated by grasses from the Poaceae family and forbs (Carbutt et al. 2011). These grasslands have low resource availability, particularly nitrogen and phosphorus (Carbutt and Kirkman 2022). Additionally, this study was conducted within the highveld grassland bioregion; these grasslands are present in leached soils with low nutrient statuses (Carbutt and Kirkman 2022). Consequently, increasing nutrient availability in these grasslands can promote and favour the accumulation of competitive species, leading to a decline in native species richness (Critchley et al. 2002; Carbutt and Kirkman 2022).

In these ecosystems, invasive alien plants can employ different strategies to modify the soil and increase nutrient pools, creating feedback loops that favour their success. Deep-rooted plants, such as *G. triacanthos* with its deep roots and root suckers (Blair 1990; Kebbas et al. 2018), can aerate soils and uplift nutrients from deep soil layers, and such efficient nutrient mobilisation is likely to occur in nutrient-poor soils (Dassonville et al. 2008). Deep roots also alter soil structure, influencing permeability, compactness, and cohesiveness in the soil (Wang et al. 2018; Araya et al. 2022). By disrupting compacted layers, *G. triacanthos* can improve soil porosity, allowing finer particles, including clay, to accumulate over time.

Invasive alien plants can also release unique combinations of chemicals through leaf chelates, higher-quality leaf litter, root exudates and volatiles (Weidenhamer and Callaway 2010). Sardans et al. (2017) reported that the photosynthetic tissues of IAPs have higher concentrations of bioactive compounds, improving their litter quality. For example, Yelenik et al. (2004) showed that areas invaded by *Acacia saligna* (Labill.) H.L. Wendl (Fabaceae) had increased litterfall, with greater nitrogen concentrations. Additionally, studies have shown that IAPs decompose faster than native species, making the nutrients readily available for uptake (Rothstein et al. 2004; Prescott and Zukswert 2016; Hu et al. 2022).

In this study, macronutrients (Zn, Mn, and Cu) were not significantly different between areas with and without *G. triacanthos*, and this was consistent for all the sampled locations. The impacts of IAPs on soil macronutrients vary widely; for example, in Guam cobbly clay soils, *Leucaena leucocephala* (Lam.) De Wit (Fabaceae) significantly increased manganese but had an insignificant influence on copper and zinc, while *Vitex parviflora* Juss. (Lamiaceae) increased both manganese and copper but had no impact on zinc; manganese and zinc were increased by *Spathodea campanulata* P Beauv. (Bignoniacea) invasion, but copper was not significantly affected (Marler 2020). While beneficial and necessary for plant growth, plants require macronutrients in low concentrations, as a significant increase in their concentrations may result in plant toxicity (Chrysargyris et al. 2022).

Conclusion

The findings of this study highlight differences in the physicochemical properties of soils between native, uninvaded grasslands and those that are invaded by *Gleditsia triacanthos*. The mechanism driving the differences is assumed to be the deep root access and the addition of leaf litter and root exudates of *G. triacanthos*. These changes could substantially influence the biomass, function, and productivity of the grassland it invades. The variation in the strength of *G. triacanthos* influence in the different grasslands shows that the impact is site dependent. Still, the results highlight the need to prioritise controlling and removing *G. triacanthos* from this ecosystem. Future studies should compare the physicochemical properties of soils between *G. triacanthos* and native Fabaceae, research the mechanisms that drive the differences observed in grasslands with *G. triacanthos* and develop strategies to mitigate nutrient enrichment effects in South African grasslands.

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Author contribution Thandeka Mahlobo: Funding acquisition, Methodology, Investigation, Data curation, Formal analysis, Writing—original draft. Sandisiwe Zondo: Sample analysis, Resources, Writing—review and editing. Grant Martin: Conceptualization, Funding acquisition, Resources, Writing—review and editing. Caswell Munyai: Resources, Writing—review and editing. Nontembeko Dube: Conceptualization, Funding acquisition, Resources, Project administration, Methodology, Writing—review and editing.

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Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Afzal MR, Naz M, Ashraf W, Du D (2023) The legacy of plant invasion: impacts on soil nitrification and management implications. Plants 12(16):2980. https://doi.org/10.3390/plants12162980

Araya T, Mlahlwa AV, Elbasit MAA, Newete SW (2022) The impact of Tamarix invasion on the soil physicochemical properties. Sci Rep 12(1):5750. https://doi.org/10.1038/s41598-022-09797-3

Bekele K, Haji J, Legesse B, Shiferaw H, Schaffner U (2018) Impacts of woody invasive alien plant species on rural livelihood: generalised propensity score evidence from *Prosopis* spp. invasion in Afar region in Ethiopia. Pastor Res Policy Pract. https://doi.org/10.1186/s13570-018-0124-6

Birouste M, Kazakou E, Blanchard A, Roumet C (2012) Plant traits and decomposition: Are the relationships for roots comparable to those for leaves? Ann Bot 109(2):463–472. https://doi.org/10.1093/aob/mcr297

Blair RM (1990) *Gleditsia triacanthos* L., honeylocust. In: Burns RM, Honkala BH (eds) Silvics of North America Volume 2: Hardwoods. United States Department of Agriculture, Forest Service, Washington DC, pp 358–364

Bryan JA, Berlyn GP, Gordon JC (1997) Toward a new concept of the evolution of symbiotic nitrogen fixation in the Leguminosae. In: Elkan GH, Upchurch RG (eds) Current issues symbiotic nitrogen fixation. Springer, Dordrecht, pp 151–159. https://doi.org/10.1007/978-94-011-5700-1_21

Carbutt C, Kirkman K (2022) Ecological grassland restoration—a South African perspective. Land 11(4):575. https://doi.org/10.3390/land11040575

Carbutt C, Tau M, Stephens A, Escott B (2011) The conservation status of temperate grasslands in southern Africa. Grassroots 11(1):17–23

Chikowore G, Mutamiswa R, Sutton GF, Chidawanyika F, Martin GD (2021) Reduction of grazing capacity in high-elevation rangelands after Black locust invasion in South Africa. Rangeland Ecol Manag 76:109–117. https://doi.org/10.1016/j.rama.2021.02.006

Chrysargyris A, Höfte M, Tzortzakis N, Petropoulos SA, Di Gioia F (2022) Micronutrients: the borderline between their beneficial role and toxicity in plants. Front Plant Sci 13:840624. https://doi.org/10.3389/fpls.2022.840624

Comole AA, Malan PW, Tiawoun MAP (2021) Effects of *Prosopis velutina* invasion on soil characteristics along the riverine system of the Molopo River in north-west province, South Africa. Int J Ecol 2021:1–11. https://doi.org/10.1155/2021/6681577

Critchley CNR, Chambers BJ, Fowbert JA, Sanderson RA, Bhogal A, Rose SC (2002) Association between lowland grassland plant communities and soil properties. Biol Conserv 105(2):199–215. https://doi.org/10.1016/s0006-3207(01)00183-5

Dassonville N, Vanderhoeven S, Vanparys V, Hayez M, Gruber W, Meerts P (2008) Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. Oecologia 157:131–140. https://doi.org/10.1007/s00442-008-1054-6

DeBruyne SA (2009) Effects of black walnut and honey locust on forage growth, soil water, and soil quality indicators. MSc thesis, Virginia Tech

Dent D, Cocking E (2017) Establishing symbiotic nitrogen fixation in cereals and other non-legume crops: the greener nitrogen revolution. Agric Food Secur 6(1):7–15. https://doi.org/10.1186/s40066-016-0084-2

Ferraina A, Molina CD, Mazía N, Piñeiro G, Miranda I, Chaneton EJ (2021) Tree invasion in secondary grasslands diminishes herbaceous biomass and diversity: A study of mechanisms behind the process. J Veg Sci 32(5):e13074. https://doi.org/10.1111/jvs.13074

Fornara DA, Tilman D (2008) Plant functional composition influences rates of soil carbon and nitrogen accumulation. J Ecol 96(2):314–322. https://doi.org/10.1111/j.1365-2745.2007.01345.x

GBIF.org (2024) GBIF occurrence download https://doi.org/10.15468/dl.588y7n

Gibbons SM, Lekberg Y, Mummey DL, Sangwan N, Ramsey PW, Gilbert JA (2017) Invasive plants rapidly reshape soil properties in a grassland ecosystem. Msystems 2(2):10–1128. https://doi.org/10.1128/msystems.00178-16

Grove S, Haubensak KA, Parker IM (2012) Direct and indirect effects of allelopathy in the soil legacy of an exotic plant invasion. Plant Ecol 213:1869–1882. https://doi.org/10.1007/s11258-012-0079-4

Gwate O, Mantel SK, Gibson LA, Munch Z, Gusha B, Palmer AR (2021) The effects of *Acacia mearnsii* (black wattle) on soil chemistry and grass biomass production in a South African semi-arid rangeland: implications for rangeland rehabilitation. Afr J Range Forage Sci 38(4):270–280. https://doi.org/10.2989/10220119.2021.1875048

Henderson L, Wilson JR (2017) Changes in the composition and distribution of alien plants in South Africa: an update from the Southern African Plant Invaders Atlas. Bothalia-Afr Biodivers Conserv 47(2):1–26. https://doi.org/10.4102/abc.v47i2.2172

Hirsch H, Allsopp MH, Canavan S, Cheek M, Geerts S, Geldenhuys CJ, Harding G, Hurley BP, Jones W, Keet JH, Klein H, Ruwanza S, van Wilgen BW, Wingfield MK, Richardson DM (2020) *Eucalyptus camaldulensis* in South Africa–past, present, future. Trans R Soc S Afr 75(1):1–22. https://doi.org/10.1080/0035919x.2019.1669732

Hu X, Arif M, Ding D, Li J, He X, Li C (2022) Invasive plants and species richness impact litter decomposition in riparian zones. Front Plant Sci 13:955656. https://doi.org/10.3389/fpls.2022.955656

Kebbas S, Benseddik T, Makhlouf H, Fatiha AID (2018) Physiological and biochemical behaviour of *Gleditsia triacanthos L.* young seedlings under drought stress conditions. Not Bot Horti Agrobo 46(2):585–592. https://doi.org/10.15835/nbha46211064

Keet JH, Ellis AG, Hui C, Novoa A, Le Roux JJ (2021) Impacts of invasive Australian acacias on soil bacterial community composition, microbial enzymatic activities, and nutrient availability in fynbos soils. Microb Ecol 82(3):1–18. https://doi.org/10.1007/s00248-021-01683-1

Kulmatiski A, Beard KH, Stevens JR, Cobbold SM (2008) Plant–soil feedbacks: a meta-analytical review. Ecol Lett 11(9):980–992. https://doi.org/10.1111/j.1461-0248.2008.01209.x

Le Maitre DC, Richardson DM, Chapman RA (2004) Alien plant invasions in South Africa: driving forces and the human dimension: working for water. S Afr J Sci 100(1):103–112

Leicht-Young SA, O'Donnell H, Latimer AM, Silander JA Jr (2009) Effects of an invasive plant species, *Celastrus orbiculatus*, on soil composition and processes. Am Midl Nat 161(2):219–231. https://doi.org/10.1674/0003-0031-161.2.219

Linders TEW, Schaffner U, Eschen R, Abebe A, Choge SK, Nigatu L, Mbaabu PR, Shiferaw H, Allan E (2019) Direct and indirect effects of invasive species: biodiversity loss is a major mechanism by which an invasive tree affects ecosystem functioning. J Ecol 107:2660–2672. https://doi.org/10.1111/1365-2745.13268

Lorenzo P, Rodríguez-Echeverría S, González L, Freitas H (2010) Effect of invasive *Acacia dealbata* Link on soil microorganisms as determined by PCR-DGGE. Appl Soil Ecol 44(3):245–251. https://doi.org/10.1016/j.apsoil.2010.01.001

Ludwig F, de Kroon H, Berendse F, Prins HH (2004) The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. Plant Ecol 170:93-105. https://doi.org/10.1023/b:vege.0000019023.29636.92

Lusizi Z, Motsi H, Nyambo P, Elephant D (2024) Black (*Acacia mearnsii*) and silver wattle (*Acacia dealbata*) invasive tree species impact on soil physicochemical properties in South Africa: a systematic literature review. Heliyon 10(2):e24102. https://doi.org/10.1016/j.heliyon.2024.e24102

Manson AD, Bainbridge SH, Thibaud GR (2020) Methods used for analysis of soils and plant material by Analytical Services at Cedara. KwaZulu-Natal Dep Agric Rural Dev, KwaDukuza, South Africa

Marler TE (2020) Three invasive tree species change soil chemistry in Guam forests. Forests 11(3):279. https://doi.org/10.3390/f11030279

Martin GD (2021) Prospects for the biological control of Northern Temperate Weeds in South Africa. Afr Entomol 29:791–808. https://doi.org/10.4001/003.029.0791

May BM, Attiwill PM (2003) Nitrogen-fixation by *Acacia dealbata* and changes in soil properties 5 years after mechanical disturbance or slash-burning following timber harvest. For Ecol Manag 181(3):339–355. https://doi.org/10.1016/s0378-1127(03)00006-9

Murphy J, Riley JR (1962) A modified single solution method for the determination of phosphate in natural waters. Anal Chim Acta 27:31–36. https://doi.org/10.1016/s0003-2670(00)88444-5

Neke KS, Du Plessis MA (2004) The threat of transformation: quantifying the vulnerability of grasslands in South Africa. Conserv Biol 18(2):466–477. https://doi.org/10.1111/j.1523-1739.2004.00157.x

Nsikani MM, van Wilgen BW, Gaertner M (2018) Barriers to ecosystem restoration presented by soil legacy effects of invasive alien N2-fixing woody species: implications for ecological restoration. Restor Ecol 26(2):235–244. https://doi.org/10.1111/rec.12669

Nunes EA, Cassiano GH, da Silveira APD, de Andrade SAL (2025) Soil legacies left by a 20-year eucalypt plantation and a secondary vegetation covers on young eucalypt plants and plant-soil feedback. Biol Fertil Soil 61(2):187–210. https://doi.org/10.1007/s00374-024-01880-3

O'Connor TG, Kuyler P (2009) Impact of land use on the biodiversity integrity of the moist sub-biome of the grassland biome, South Africa. J Environ Manage 90(1):384–395. https://doi.org/10.1016/j.jenvman.2007.10.012

O'Connor TG, van Wilgen BW (2020) The impact of invasive alien plants on rangelands in South Africa. In: van Wilgen B, Measley J, Richardson DM, Wilson R, Zengeya TA (eds) Biological invasions in South Africa. Springer Nature, Cham. https://doi.org/10.1007/978-3-030-32394-3_16

Prescott CE, Zukswert JM (2016) Invasive plant species and litter decomposition: time to challenge assumptions. New Phytol 209(1):5–7. https://doi.org/10.1111/nph.13741

Prinsloo H, Reilly B, Myburgh W (2021) Identifying potential protected areas in the grassland biome of South Africa. S Afr J Sci 117(34):1–6. https://doi.org/10.17159/sajs.2021/7507

Rothstein DE, Vitousek PM, Simmons BL (2004) An exotic tree alters decomposition and nutrient cycling in a Hawaiian montane forest. Ecosystems 7:805–814. https://doi.org/10.1007/s10021-004-0009-y

Rusterholz HP, Schneuwly J, Baur B (2018) Invasion of the alien shrub *Prunus laurocerasus* in suburban deciduous forests: effects on native vegetation and soil properties. Acta Oecol 92:44–51. https://doi.org/10.1016/j.actao.2018.08.004

Ruwanza S, Shackleton CM (2016) Effects of the invasive shrub, *Lantana camara*, on soil properties in the Eastern Cape South Africa. Weed Biol Manag 16(2):67–79. https://doi.org/10.1111/wbm.12094

Ruwanza S, Tshililo K (2019) Short term soil and vegetation recovery after *Acacia mearnsii* removal in Vhembe biosphere reserve, South Africa. Appl Ecol Environ Res 17(2):1705–1716. https://doi.org/10.15666/aeer/1702_17051716

Salgado Astudillo SE (2021) Evaluation of *Megabruchidius tonkineus* (Coleoptera: Chrysomelidae: Bruchinae), a candidate biological control agent for *Gleditsia triacanthos L.* (Fabaceae) in South Africa. MSc thesis, Rhodes University, South Africa

Sardans J, Bartrons M, Margalef O, Gargallo Garriga A, Janssens IA, Ciais P, Obersteiner M, Sigurdsson BD, Chen HY, Peñuelas J (2017) Plant invasion is associated with higher plant–soil nutrient concentrations in nutrient-poor environments. Glob Change Biol 23(3):1282–1291. https://doi.org/10.1111/gcb.13384

Simba YR, Kamweya AM, Mwangi PN, Ochora JM (2017) Impact of the invasive shrub, *Lantana camara L.* on soil properties in Nairobi National Park, Kenya. Int J Biodivers Conserv 5(12):803–809

Stanek M, Piechnik Ł, Stefanowicz AM (2020) Invasive red oak (*Quercus rubra L*)modifies soil physicochemical properties and forest understory vegetation. For Ecol Manag 472:118253. https://doi.org/10.1016/j.foreco.2020.118253

Teixeira LH, Yannelli FA, Ganade G, Kollmann J (2020) Functional diversity and invasive species influence soil fertility in experimental grasslands. Plants 9(1):53–67. https://doi.org/10.3390/plants9010053

Unger IM, Kremer RJ, Veum KS, Goyne KW (2022) Immediate and long-term effects of invasive plant species on soil characteristics. Soil Ecol Lett. https://doi.org/10.1007/s42832-021-0104-4

Vargas-Lomelín JG, Macías-Rodríguez MÁ, Zarazúa-Villaseñor P, Rodríguez-Zaragoza FA, Neri-Luna C, Albuquerque F (2023) The effect of *Prosopis juliflora* (Fabaceae) on the physical and chemical properties of coastal dune soil in Western Mexico. J Coast Res 39(1):63–72. https://doi.org/10.2112/jcoastres-d-22-00017

Wang W, Sardans J, Wang C, Asensio D, Bartrons M, Peñuelas J (2018) Species-specific impacts of invasive plant success on vertical profiles of soil carbon accumulation and nutrient retention in the Minjiang River tidal estuarine wetlands of China. Soil Syst 2(1):5–30. https://doi.org/10.3390/soils2010005

Weidenhamer JD, Callaway RM (2010) Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. J Chem Ecol 36:59–69. https://doi.org/10.1007/s10886-009-9735-0

Xiao-Qi Y, Ya-Nan Y, Ming W, Fei-hai Y (2019) High capacity of nutrient accumulation by invasive *Solidago canadensis* in a coastal grassland. Front Plant Sci 10:575. https://doi.org/10.3389/fpls.2019.00575

Yapi TS, O'Farrell PJ, Dziba LE, Esler KJ (2018) Alien tree invasion into a South African montane grassland ecosystem: impact of *Acacia* species on rangeland condition and livestock carrying capacity. Int J Biodivers Sci Ecosyst Serv Manag 14(1):105–116

Yelenik SG, Stock WD, Richardson DM (2004) Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. Restor Ecol 12(1):44–51. https://doi.org/10.1111/j.1061-2971.2004.00289.x

Yuvaraj M, Pandiyan M, Gayathri P (2020) Role of legumes in improving soil fertility status. In: Hasanuzzaman M (ed) Legume Crops-prospects, production and uses. InTech Open, Rijeka, Croatia