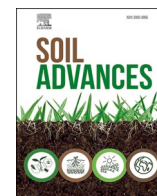


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Root traits and mineral nutrients in the rhizosphere and shoot biomass of African dryland grasses

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ABSTRACT

Seed-based ecological restoration through reseeded perennial grasses has been successfully used to combat desertification in Africa. However, studies to investigate the relationship between root traits of the native grasses and mineral nutrients in rhizosphere and plant biomass remain limited. This has limited our understand of the relationship between belowground processes and ecological restoration outcomes, especially in nutrient poor African dryland environments. This study was conducted in a long-term ecological restoration site in typical semi-arid African dryland to elucidate the relationship between root traits and mineral nutrients in the rhizosphere and shoot biomass of native perennial grasses used for seed-based ecological restoration i.e. *Cenchrus ciliaris*, *Enteropogon macrostachyus* and *Eragrostis superba*. *Cenchrus ciliaris* exhibited superior root characteristics than *E. macrostachyus* and *E. superba* in all the measured traits expect for specific root length (SRL) and root tissue density (RTD). Root trait relationships of the root economic spectrum were largely not supported. A significant negative correlation between RTD and SRL was only found in *E. superba* ($r^2 = 0.92$, $P = 0.03$). Calcium and potassium mineral concentrations in soil displayed a regular pattern where *E. macrostachyus* consistently had the highest concentrations. Total phosphorus concentrations were highest in *C. ciliaris*. Shoot biomass total calcium and phosphorus concentrations were highest in *E. superba* while total magnesium and potassium concentrations were highest in *C. ciliaris*. Correlation analysis revealed only a few significant relationships between root traits and mineral concentrations in soil and shoot biomass. African grasses used for seed-based ecological programs exhibit varying root traits and mineral nutrient concentrations in the rhizosphere and shoot biomass, underpinning their significant role in modulating soil fertility and nutrient cycling in reseeded African drylands. Integrating root traits and mineral nutrient concentrations in rhizosphere and shoot biomass can deepen our holistic understanding of the ecological restoration process using perennial grasses. This will better inform the selection of appropriate species to successfully restore degraded landscapes and support positive outcomes for future sustainability of African drylands in a changing global environment.

1. Introduction

Perennial grasses native to African drylands e.g. African foxtail/Buffel grass (*Cenchrus ciliaris* L.), Bush rye grass (*Enteropogon macrostachyus* (Hochst. ex A. Rich.) Munro ex Benth.), Maasai love grass (*Eragrostis superba* Peyr.) have been used to restore degraded African drylands through seed-based ecological restoration. Previous studies investigating and assessing the potential of using these perennial grasses for reseeded and ecological restoration have largely focused on aboveground plant morphoecological traits (Kimiti et al., 2017; Mur-eithi et al., 2014). Few studies, if any, have investigated root traits of these perennial African grasses and their relationship with soil and plant

biomass mineral nutrients composition under natural conditions. Thus, despite the expansion of seed-based ecological restoration using perennial grasses as a key tool for combating degradation and curbing biodiversity loss in African drylands, our understanding of the impact of ecological restoration on below-ground functioning and soil and plant nutrients remains limited.

Focusing only on the aboveground morphoecological traits limits our understanding of dry African rangeland ecosystems. This is because 67% of the plant biomass in grassy biomes exists belowground (Ma et al., 2022). Additionally, trait-based approaches play a critical role in understanding how plants affect different ecosystem and ecological processes e.g. ecological restoration (Garbowski et al., 2020). Root

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functional traits (e.g. morphological, physiological, architectural) studies have contributed significantly to our understanding of root trait diversity and ecosystem functioning (Freschet et al., 2021). However, numerous research and knowledge gaps still remain, limiting our understanding of trait-functioning relationships, especially applied to ecological restoration under dryland conditions, because majority of root trait studies have largely been conducted under controlled conditions (Lozano et al., 2020; Rojas-Botero et al., 2023).

There are still important gaps in our knowledge regarding the impacts of ecological restoration on soil processes and nutrient cycling in African dryland systems. Thus, advancing our knowledge of root traits of perennial African grasses used to restore degraded drylands can significantly enhance our understanding of root traits as important drivers of many ecosystem processes e.g. nutrient cycling (Bardgett et al., 2014). Incorporating root traits in selecting grass species for reseeding degraded landscapes can contribute to decreasing uncertainties of seed-based ecological restoration outcomes in dryland ecosystems. Root trait-based approach has been increasingly recognized as a useful tool in ecological restoration, considering the crucial roles of roots in controlling ecosystem processes (Garbowski et al., 2020). This is because they provide a promising avenue for improving restoration outcomes in drylands (Garbowski et al., 2025).

Root biomass and root area significantly influences the exploitative capacity of root systems to acquire resources (water and nutrients), thus, it is fundamentally important to quantify root biomass in restored dry and nutrient poor grasslands. Similarly, root length density (RLD) enhances the exploitative capacity of root systems by increasing the spatial coverage of a given soil volume (Freschet et al., 2021), which determines the probability of encountering nutrient hotspots (Chen et al., 2016). Root tissue density (RTD) is a vital trait in comparative root ecology, being increasingly used as an indicator of plant species' resource use strategies. Low-density root tissues facilitate a rapid resource acquisition, thus is a valuable ecological index that can be used to compare plant species from contrasted environmental conditions, including drought (Craine et al., 2003; 2001). For instance, drought stress, frequently coincides with nutrient deficiency resulting to an increase in RTD in some plant species (Ostonen et al., 2007). Similarly, specific root length (SRL) is also indicative of environmental changes. For instance, in their study, (Garbowski et al. (2025) demonstrated that dense roots with low SRL underpin performance of dryland restoration species.

Environmental conditions and soil characteristics e.g. high nutrient availability, compaction, insufficient aeration, high temperature and soil density, don't favour root branching and increases specific root area (SRA). Thus, SRA can be considered as an ecomorphological index of soil physicochemical characteristics (Löhmus et al., 1989) to assess ecological restoration outcomes. Root diameter and branching plays a key role in determining the capacity of plant roots to penetrate through the soil to acquire water and nutrients (Wu et al., 2016). Similarly, when rhizosphere total elemental composition limits growth, plants will invest relatively more biomass in their roots compared to shoot. This can also be exemplified by an increase in the specific root length (SRL) in response to low rhizosphere total elemental composition and supply. Plants also development roots with large surface area and long length as strategies to overcome nutrient and water limitation and enhance their interactions with microbes in the rhizosphere (Ma et al., 2018).

Soil nutrients are often very limited in drylands especially in the rhizosphere where microorganisms and plants compete for the same nutrients (Kuzuyakov and Xu, 2013). Thus, understanding belowground characteristics of grasses used for ecological restoration in African drylands will greatly contribute to the selection of appropriate grass species to match the prevailing site specific environmental conditions. While the impacts of ecological restoration on above-ground plant morphoecological characteristics have been widely investigated in African drylands, there are important gaps in our knowledge regarding its impacts on soil mineral nutrients. Data on nutrient concentrations in the field at

scales comparable with variation in root traits and plant species composition (i.e. centimetre scale) are surprisingly scarce (Skálová et al., 2023). Soil mineral nutrients play essential biological functions e.g. enzyme cofactors in photosynthesis and synthesis of biomolecules. Thus, to fully understand the impact of seed-based ecological restoration and ultimately its effect on the functioning of drylands, the relationship between the perennial grasses and the abundance of soil mineral nutrients needs to be fully known.

Thus, the aim of this study was to unravel the 'hidden half of seed-based ecological restoration' using perennial grasses native to African drylands i.e. *C. ciliaris*, *E. macrostachyus* and *E. superba*. The specific objectives of this study were to determine: 1) root traits of the grasses, 2) total mineral nutrient concentrations (phosphorus, potassium, calcium and magnesium) in the rhizosphere soil and shoot biomass of the grasses and 3) relationship between the root traits and total mineral nutrient concentrations in rhizosphere soil and shoot biomass of the grasses. The study was guided by the following hypotheses 1) all the studied grasses will align to the root economic spectrum, where specific root length (SRL, an acquisitive root trait) and root diameter (D) will have a negative and positive correlation with root tissue density (RTD, a conservative root trait), respectively, 2) total mineral nutrient concentrations in the rhizosphere soil and shoot biomass will vary significantly between the studied grasses and 3) root traits will exhibit positive relationship with total mineral nutrient concentrations in the rhizosphere soil and shoot biomass.

2. Materials and methods

2.1. Study area

The study was conducted in semi-arid in Kitui County, southeastern Kenya. It is the sixth largest county in Kenya by land area, covering approximately 30496.4 km² and is among the arid and semi-arid land (ASAL) counties that cover approximately 80% of the country's land mass and characterized by sporadic rainfall and cyclic droughts. The area experiences arid to semi-arid climate which is hot and dry with erratic and unreliable rainfall. The annual rainfall average ranges between 250 and 1050 mm with 40% reliability with high temperatures throughout the year ranging from 16 °C to 34 °C (Yageta et al., 2019). Rainfall pattern is bimodal, with the long rains (LR) in March-May and short rains (SR) in October-December. Intense LR have a rain peak in April while the less intense SR have a rain peak in November. Livestock production characterised largely by a mix of largely free-ranging local livestock breeds e.g. small East African shorthorn zebu, Red Maasai sheep, small East African goat is one of the main economic activities.

2.2. Experimental and sampling design

The experimental site was established during the short-rain season of 2017 as part of a long-term ecological restoration study. The experimental design and initial site description are detailed in Mganga et al. (2022). Briefly, layout consisted of five blocks, with an area of 150 m² (15 m x 10 m), each divided into three equal plots of 50 m² (5 m x 10 m). Each of the three studied grass species i.e. *C. ciliaris*, *E. macrostachyus* and *E. superba* was established without fertilisation in one plot per block (plot per species, n = 5). Basic soil characteristics of the study site were: soil texture 68% sand, 8.6% silt, 23.40% clay, total nitrogen (N) 0.08%, total carbon 0.8%, phosphorus (P) 165 mg kg⁻¹, potassium (K) 3859 mg kg⁻¹, soil pH (determined in Milli-Q water (ratio of 1:2.5)) 5.38. The soil is a Haplic Acrisol with a sandy clay texture, based on the WRB soil classification guidelines (IUSS et al., 2022).

Sampling of root and shoot biomass was done during the early reproductive stage of the studied grasses. Roots were sampled using a soil core to determine the root traits in the rhizosphere of the selected perennial grasses (sample size per grass species, n = 5). Briefly, a soil core was taken at the center of each plot at a soil depth of 20 cm with a 5-

cm diameter auger. A total of 15 soil cores were collected (5 plots per species x 1 sampling points per plot x 3 grass species). Soil adjacent to the root segments, at 1–5 mm from the root surface, was shaken off and defined as rhizosphere soil. Thereafter, roots were washed through a sieve (2 mm mesh) and scanned. Thereafter, the scanned images of the roots were analysed using RhizoVision Explorer (open access <https://www.rhizovision.com/>) to determine root area (cm^2), root length (cm) and root volume (cm^3). Thereafter, roots were dried (60°C for 3 days) to determine root biomass (g). Categories of these traits were adapted from the Fine-Root Ecology Database (Iversen et al., 2021) classification and included: (1) morphological for root length and average root diameter and (2) root system of the standing crop for root volume, root surface area and root biomass weight.

Thereafter, root functional traits were computed as follows: root length density (RLD, cm cm^{-3}) as the root length per unit of soil volume, root tissue density (RTD, g cm^{-3}) as the ratio between root dry mass and root volume; specific root length (SRL, cm g^{-1}) as the ratio between root

length and root dry mass and specific root area (SRA, $\text{cm}^2 \text{g}^{-1}$) as the ratio between root surface area and root dry mass (Bardgett et al., 2014).

Shoot biomass was harvested from 0.25 m^2 quadrats. Briefly, one quadrat was placed in each quarter of the plot and clipped to a stubble height of 2 cm. Harvested shoot biomass per plot was mixed, placed in paper bags and oven dried at 60°C for 24 h to determine the total elemental concentrations.

Total elemental concentrations of the sieved rhizosphere soil and dry shoot biomass were determined using the Bruker Tracer 5i pXRF (portable XRF) spectrometer (CIFOR-ICRAF Soil and Land Health Laboratory, Nairobi, Kenya). This method was used because pXRF provides a rapid, non-destructive and environmentally-friendly elemental analysis in soils. Additionally, there is a great expansion of pXRF applications in soil science especially in tropical countries because of its lower costs compared to conventional laboratory procedures (Silva et al., 2021). Briefly, for the pXRF analysis, scans were acquired from air-dried and milled (to pass through 75- microns mesh sieve) samples presented to

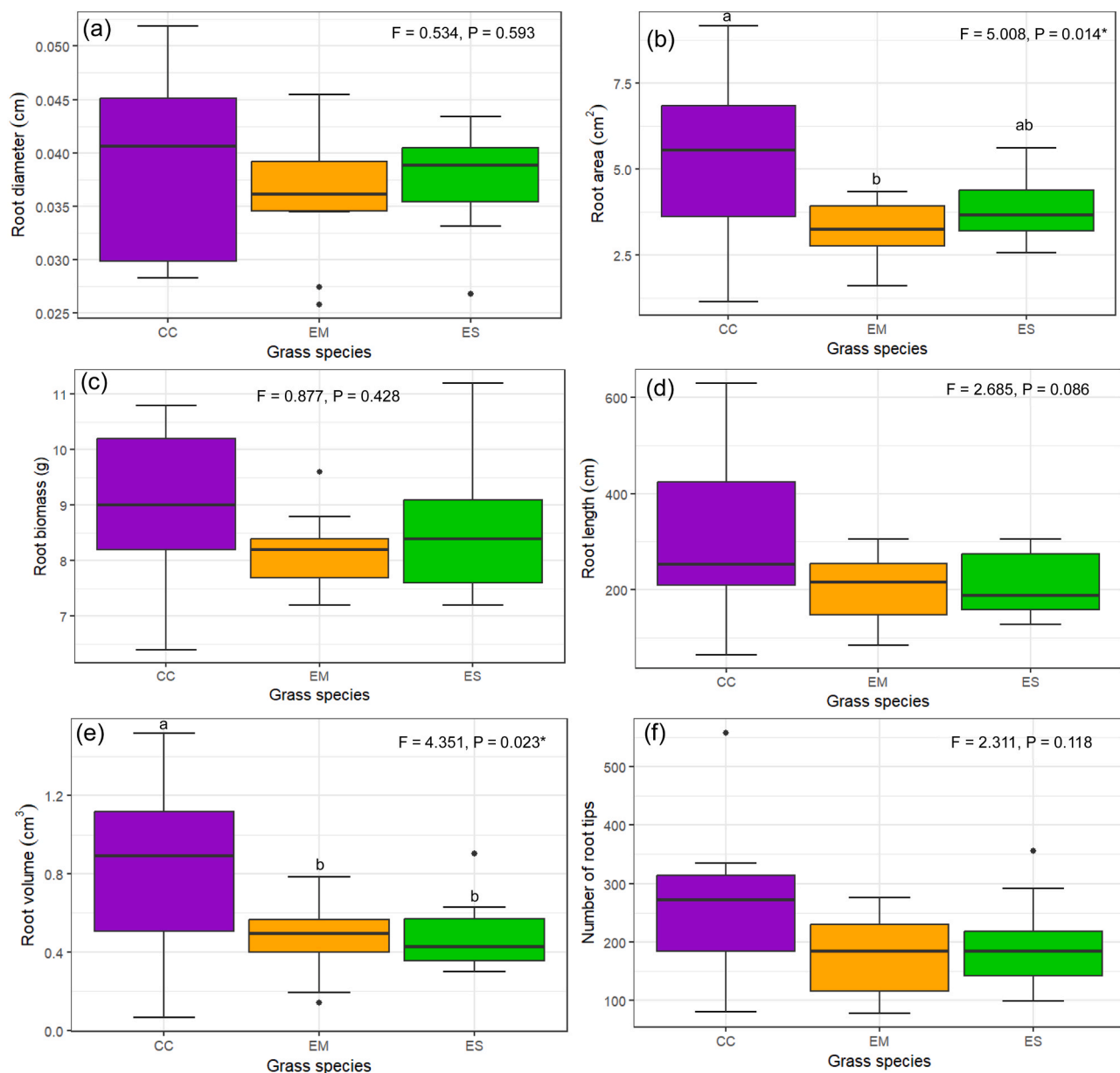


Fig. 1. (a) Root diameter (cm), (b) root area (cm^2), (c) root biomass (g), (d) root length (cm), (e) number of root tips and (f) root volume (cm^3) of selected African dryland grasses. Where CC – *Cenchrus ciliaris*, EM – *Enteropogon macrostachyus*, ES – *Eragrostis superba*. Boxplots show minimum, first quartile, median, third quartile, and maximum values. Error bars with different letters are significantly different ($P < 0.05$).

the instrument as loose powder in XRF cups lined with Prolene film. The net photon intensities were quantified using empirically developed calibrations to get total elemental concentrations in mg kg^{-1} .

2.3. Statistical analyses

The statistical analyses were performed using R (R Core Team). The Shapiro–Wilk test was used to validate normality, and Leven's test was used to confirm homogeneity of variance. Fisher's Least Significant Difference (LSD) test and one-way analysis of variance (ANOVA) were used to assess for significant differences across the measured root traits. Significant differences were considered at the $p < 0.05$. Linear Pearson's correlations of selected root traits were calculated in R program (R Core Team, 2020). Additionally, a correlation analysis between the root traits and soil mineral nutrients was conducted using R version 4.0.3 (2020–10–10) (R Core Team, 2020) within RStudio (RStudio Team, 2018) and the correlation matrix was generated using the corplot package (Wie et al., 2017). Significant correlations were considered at $p < 0.05$ level.

3. Results

3.1. Root traits of the studied African dryland grasses

Root diameter ($F = 0.534$, $P = 0.593$) of the studied grasses varied and were in the order $C. ciliaris > E. superba > E. macrostachyus$ (Fig. 1a). Similarly, $C. ciliaris$ had a significantly higher root area ($F = 5.008$, $P = 0.014$) compared to $E. superba$ and $E. macrostachyus$ that were ranked second and third, respectively (Fig. 1b). Total root biomass ($F = 0.877$, $P = 0.428$) and root length ($F = 2.685$, $P = 0.086$) of the grasses also varied and were higher in $C. ciliaris$ than $E. superba$ and

$E. macrostachyus$ ranked second and third, respectively (Figs. 1c and 1d). Root volume ($F = 4.351$, $P = 0.023$) and the number of root tips ($F = 2.311$, $P = 0.118$) displayed a similar pattern (Figs. 1e and 1f).

$Cenchrus ciliaris$ had higher root length density (RLD, $F = 1.844$, $P = 0.200$) (5.54 cm cm^{-3}) than $E. macrostachyus$ (3.32 cm cm^{-3}) and $E. superba$ and (3.30 cm cm^{-3}) (Fig. 2a). Similarly, $Cenchrus ciliaris$ exhibited higher specific root area (SRA, $F = 2.789$, $P = 0.101$) ($0.68 \text{ cm}^2 \text{ g}^{-1}$) than $E. superba$ ($0.46 \text{ cm}^2 \text{ g}^{-1}$) and $E. macrostachyus$ ($0.40 \text{ cm}^2 \text{ g}^{-1}$) (Fig. 2b) and higher specific root length (SRL, $F = 1.101$, $P = 0.364$) (0.36 cm g^{-1}) (Fig. 2c) than $E. superba$ (0.24 cm g^{-1}) and $E. macrostachyus$ (0.24 cm g^{-1}). The mean root tissue density (RTD, $F = 1.491$, $P = 0.264$) of the grasses did not vary significantly and ranged between 10.68 and 23.77 g cm^{-3} in the order $E. macrostachyus > E. superba > C. ciliaris$ (Fig. 2d).

3.2. Total elemental concentrations of rhizosphere soil depending on grass species

Rhizosphere total elemental concentrations of the studied grasses varied between the species (Fig. 3). Total phosphorus concentrations were higher in $C. ciliaris$ compared to $E. superba$ and $E. macrostachyus$ that were ranked second and third, respectively (Fig. 3a). Total potassium ($F = 4.03$, $P = 0.046$) and calcium ($F = 3.54$, $P = 0.062$) exhibited a similar pattern where $E. macrostachyus$ consistently had higher total elemental concentrations compared to $C. ciliaris$ and $E. superba$ that were ranked second and third, respectively (Figs. 3b and 3c). Total magnesium concentrations were very low and below the limit of detection ($< \text{LOD}$), thus data not presented in Fig. 3.

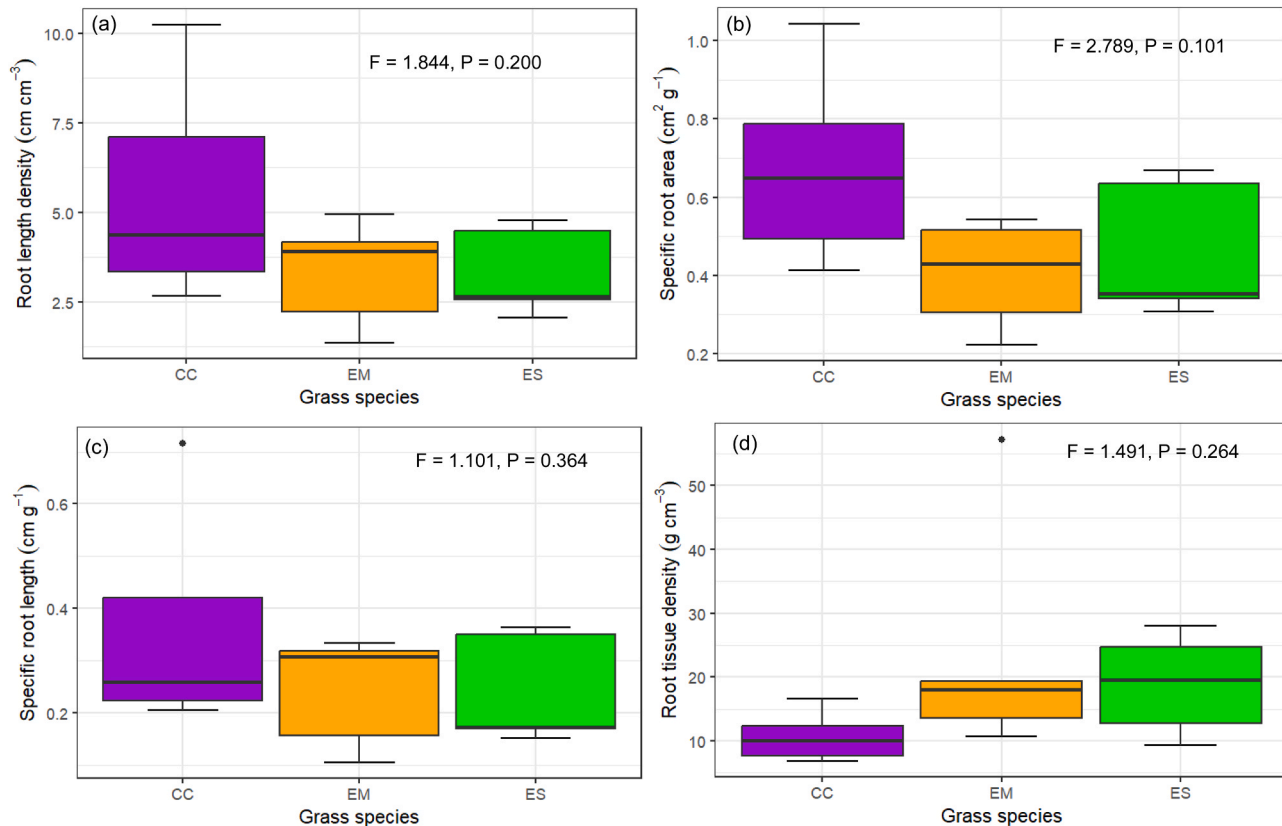


Fig. 2. (a) Root length density (RLD) (cm cm^{-3}), (b) specific root area (SRA) ($\text{cm}^2 \text{ g}^{-1}$), (c) specific root length (SRL) (cm g^{-1}) and (d) root tissue density (RTD) (g cm^{-3}) of selected African dryland grasses. Where CC – *Cenchrus ciliaris*, EM – *Enteropogon macrostachyus*, ES – *Eragrostis superba*. Boxplots show minimum, first quartile, median, third quartile, and maximum values. Error bars with different letters are significantly different ($P < 0.05$).

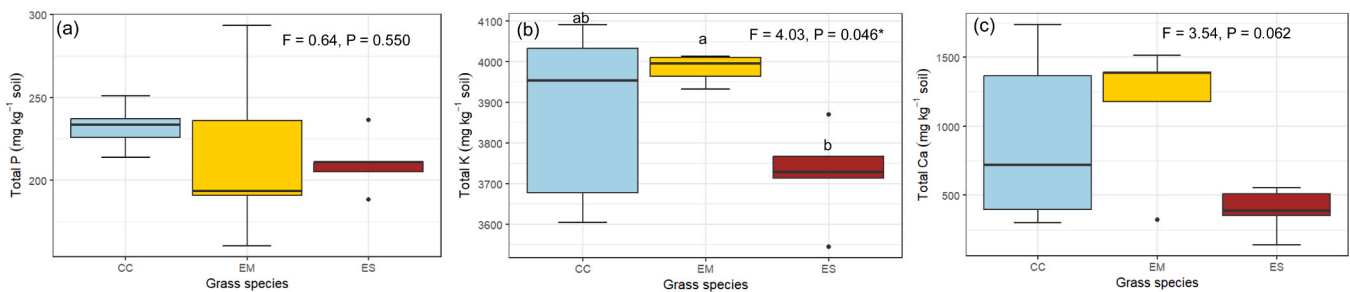


Fig. 3. Rhizosphere soil total concentrations of selected macronutrients of selected African dryland grasses. Where CC – *Cenchrus ciliaris*, EM – *Enteropogon macrostachyus*, ES – *Eragrostis superba*. Boxplots show minimum, first quartile, median, third quartile, and maximum values. Error bars with different letters are significantly different ($P < 0.05$).

3.3. Total elemental concentrations of shoot biomass depending on grass species

Total elemental concentrations of shoot biomass also varied between the studied grasses. Total phosphorus concentrations ($F = 0.401$, $P = 0.678$) were higher in *E. macrostachyus* than *C. ciliaris* and *E. macrostachyus* that were ranked, second and third, respectively (Fig. 4a). On the other hand, total potassium concentrations ($F = 11.71$, $P = 0.001$) were significantly higher in *C. ciliaris* and *E. macrostachyus* than *E. superba* (Fig. 4b). Conversely, total calcium concentration ($F = 18.09$, $P = 0.0002$) in *E. superba* shoot biomass was significantly higher than in *E. macrostachyus* and *C. ciliaris*, ranked second and third, respectively (Fig. 4c). Magnesium concentrations in shoot biomass ($F =$

0.918, $P = 0.426$) were highest in *C. ciliaris*. *Eragrostis superba* and *E. macrostachyus* were ranked second and third, respectively (Fig. 4d).

3.4. Relationship between root traits and total elemental concentrations in soil and shoot biomass of grass species

Root length of *C. ciliaris* exhibited significant positive correlations with phosphorus ($r^2 = 0.89$, $P = 0.04$), magnesium ($r^2 = 0.93$, $P = 0.02$) and calcium ($r^2 = 0.93$, $P = 0.02$) concentrations in shoot biomass (Fig. 5a). RTD ($r^2 = 0.89$, $P = 0.04$) and root area ($r^2 = 0.92$, $P = 0.03$) of *C. ciliaris*, displayed a significant negative and positive correlation with total calcium concentration in the shoot biomass, respectively (Fig. 5a). Root area of *C. ciliaris* also displayed a significant positive

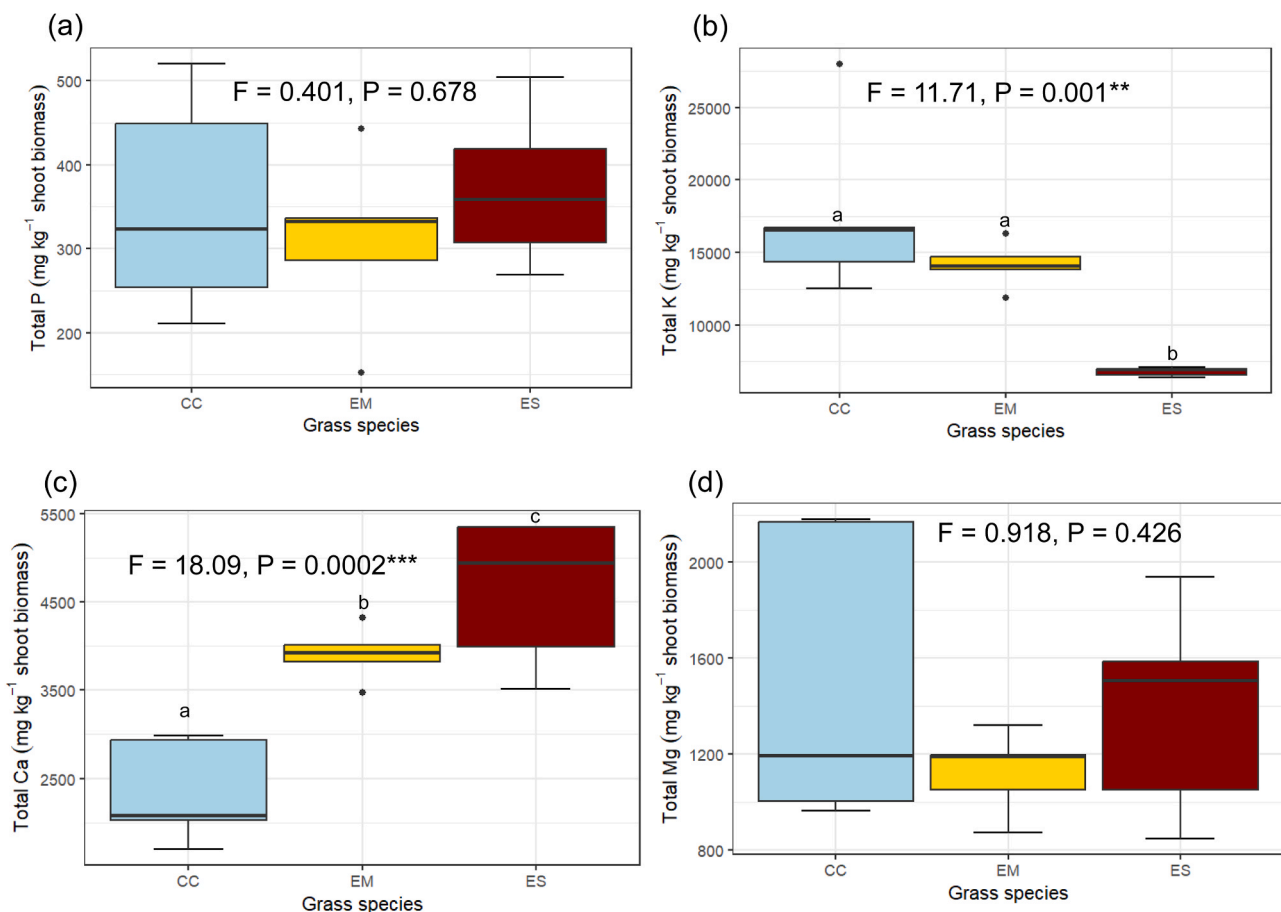


Fig. 4. Shoot biomass total mineral nutrient concentrations of selected African dryland grasses. Where CC – *Cenchrus ciliaris*, EM – *Enteropogon macrostachyus*, ES – *Eragrostis superba*. Boxplots show minimum, first quartile, median, third quartile, and maximum values. Error bars with different letters are significantly different ($P < 0.05$).

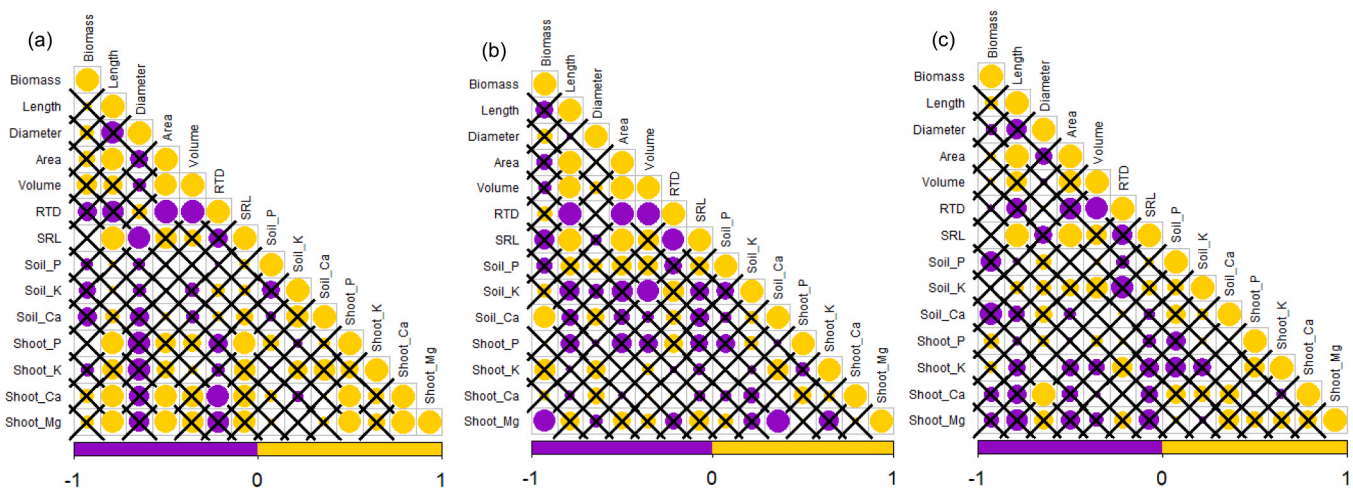


Fig. 5. Correlorgram showing the correlations between root traits and elemental concentrations in shoot biomass and rhizosphere soil of (a) *Cenchrus ciliaris*, (b) *Eragrostis superba* and (c) *Enteropogon macrostachyus*. Significant correlation coefficients ($P < 0.05$) are displayed in gold (positive) and purple (negative) coloured circles, respectively. Crossed (X) circles depict insignificant correlations. The size of the circles is proportional to the correlation coefficients. Where RTD – Root tissue density, SRL – Specific root length.

correlation ($r^2 = 0.91$, $P = 0.03$) with total magnesium concentration in shoot biomass (Fig. 5a). Root tissue density of *C. ciliaris* was negatively and positively correlated with SRL ($r^2 = 0.70$, $P = 0.19$) and root diameter ($r^2 = 0.41$, $P = 0.49$) (Fig. 5a). Root biomass of *E. superba* displayed a significant positive and negative relationship with total calcium ($r^2 = 0.94$, $P = 0.02$) in soil and total magnesium ($r^2 = 0.93$, $P = 0.02$) in shoot biomass, respectively (Fig. 5b). Root tissue density of *E. superba* was negatively and positively correlated with SRL ($r^2 = 0.92$, $P = 0.03$) and root diameter ($r^2 = 0.01$, $P = 0.98$) (Fig. 5b). *Enteropogon macrostachyus* displayed a significant relationship between root diameter and total calcium concentration in shoot biomass ($r^2 = 0.96$, $P = 0.01$). Root tissue density of *E. macrostachyus* was negatively and positively correlated with SRL ($r^2 = 0.77$, $P = 0.13$) and root diameter ($r^2 = 0.06$, $P = 0.92$) (Fig. 5a).

4. Discussion

4.1. Root traits of the selected African dryland grasses

The measured root traits highlighted the different strategies employed by the studied African perennial grasses to variable environmental conditions (Nippert et al., 2012). Larger average root diameter and higher root length of *C. ciliaris* suggests its competitive advantage and ability to access more soil resources compared to *E. macrostachyus* and *E. superba*. This is because root diameter and root system length have often been assumed to be proportional to resource acquisition and have closely been linked to the capacity of plants to acquire below-ground resources (Fantozzi et al., 2024). Root penetration ability is crucial for ensuring normal plant growth and development. Root systems of *C. ciliaris* characterized by a large average diameter enhances its ability to penetrate the soil and break through soil resistance significantly improving its capacity to reach water and soil mineral resources for growth (Chen et al., 2022). Additionally, longer roots enables *C. ciliaris* to access and explore deeper water reserves and possibly contributing to higher drought tolerance under water stress conditions. Thinner roots of *E. macrostachyus* and *E. superba* suggest that they have short lifespans or faster turnover rates and significantly contribute to C and nutrient cycles in semi-arid grassland ecosystems (Gu et al., 2014). Slower turnover of coarser *C. ciliaris* roots due to a larger diameter suggest an increased likelihood for high AMF root colonisation (Ngugi et al., 2025). Thus, coarse roots of *C. ciliaris* may provide a more stable environment for mycorrhizal fungal proliferation following entry than *E. macrostachyus* and *E. superba*, linked to the longevity of the

habitat i.e. the root cortex (Reinhardt and Miller, 1990).

Large root biomass of *C. ciliaris* in the upper soil layers suggests that it may also be prolific belowground and provide more C inputs for soil C sequestration than the other studied grasses under semi-arid African dryland conditions. Higher root biomass of *C. ciliaris* than *E. macrostachyus* and *E. superba* in the top soil layer highlights its adaptation to respond to pulses in resource availability in the surface soil layers or intense competition for soil resources (minerals and water) (Nippert et al., 2012; Craine et al., 2003). This morphological adaptation allows *C. ciliaris* to swiftly respond to seasonal rainfall and efficiently scavenge available soil moisture, especially during lean periods (Yu et al., 2007). Thus, high root biomass production in surface soils is advantageous to *C. ciliaris* as it enhances quicker response to increased water availability especially at the onset of the rainy season and exploit available soil moisture between rainfall episodes, making it uniquely suited to survive harsh conditions of African drylands characterized by high rainfall variability (Marshall et al., 2012). Similar to our results, *C. ciliaris* had a significantly higher root biomass than *E. macrostachyus* and *E. superba* which displayed comparable belowground biomass (Ngugi et al., 2025). *Cenchrus ciliaris* vigorous root system enables it to remain productive and competitive under harsh environmental conditions such as prolonged droughts in drylands.

Similarly, *C. ciliaris* exhibited higher root area and volume compared to *E. macrostachyus* and *E. superba*. This may be a reflection of the different ecological drought resilience strategies of these grasses. Larger root area and volume of *C. ciliaris* than *E. macrostachyus* and *E. superba* demonstrates its ability to access a larger volume of soil for water and minerals, enabling it to maintain growth, perhaps contributing to superior photosynthetic performance under water-deficit conditions. This architectural advantage of *C. ciliaris* to explore and utilize soil resources may not only increase its productivity but also outcompete other plant species, which may have negative impact on plant diversity, especially for seed-based ecological restoration programs using multiple species (Baer et al., 2003).

The hypothesised trait correlations of the root economic spectrum were largely not supported. Root diameter of all the studied grasses were not significantly positively correlated with RTD. Only SRL of *E. superba* was significantly negatively correlated with RTD as also observed in other studies (e.g. Freschet et al., 2021; O'Keefe et al., 2022; Wang et al., 2026). Thus, this study demonstrates that root trait relationships of the root economic spectrum vary significantly depending on the species and prevailing environmental conditions as also observed in other studies (e.g. Weemstra et al., 2016).

4.2. Linking total mineral concentrations in rhizosphere and shoot biomass to root traits of studied grasses

The rhizosphere of *E. macrostachyus* exhibited higher total calcium and potassium concentrations than *C. ciliaris* and *E. superba*. Mass flow of soil solution is an important mechanism in the supply of mobile cations such as calcium and potassium to the rhizosphere. Thus, high RTD of *E. macrostachyus* might have played a key role in increasing its potential for calcium and potassium uptake. This is depicted by it relatively high total calcium and potassium concentrations in shoot biomass. Thus, a probable explanation for the high calcium and potassium concentration in the rhizosphere of *E. macrostachyus* is that the calcium and potassium uptake rates in the surface soils may not be as high as the release rates through soil organic matter mineralization (Dijkstra and Smits, 2002). This is because, if the soil mineral supply from e.g. mass flow (the movement of mineral elements with soil moisture) exceeds its depletion, those soil mineral elements will increase and accumulate in the rhizosphere (York et al., 2016).

High mineral concentrations in the rhizosphere of has been associated with strong soil organic matter decomposition and mineralization rate — i.e. the rhizosphere priming effects that increases nutrient mineralization and their concentrations (Pausch et al., 2013). On the other hand, although *E. superba* displayed a comparable RTD to *E. macrostachyus*, it exhibited low calcium concentration in the rhizosphere and high calcium concentration in shoot biomass. Thus, it is plausible that *E. superba* calcium uptake was higher than its release to the rhizosphere through soil organic matter decomposition and mineralization rate. Magnesium accounts for ~0.05–0.7% of plant tissue and is an essential mineral nutrient for plant growth (Farhat et al., 2016). The extremely low total magnesium concentration (below the level of detection, <LOD) in the rhizosphere surface soils (0–20 cm) of all the studied grasses is indicative of possible leaching, common in acidic and dryland soils (Liu et al., 2026). Thus, a possible explanation for the magnesium concentrations in shoot biomass is that the studied African grasses accessed the leached magnesium in much deeper horizons. This suggests that perennial African grasses have great potential for improving nutrient cycling processes to support and enhance successful ecological restoration outcomes.

Cenchrus ciliaris exhibited superior root traits compared to *E. macrostachyus* and *E. superba*. Thus, the high total phosphorus concentration in the rhizosphere of *C. ciliaris* can be attributed to the possible release of high amounts of organic acids and phosphatases that accelerated mineral weathering and fuelled microbial processes to increase phosphorus concentration in the rhizosphere through e.g. mineralization of soil organic phosphorus. Plant roots secrete organic acids that accelerate mineral weathering. The rhizosphere of tropical grasses has been described as a driver of soil weathering (Ruiz et al., 2022). Tropical grass species have been reported to release compounds (e.g. organic acids and phosphatases) that increase soil phosphorus bioavailability into the rhizosphere, due to solubilization and mineralization of organic phosphorus.

Tropical grasses e.g. *Urochloa ruziziensis* and *Urochloa brizantha* are able to exude high amounts of organic acids (Ishikawa et al., 2000) that may stimulate rhizosphere microorganisms to produce phosphatases (Menezes-Blackburn et al., 2016). This microbial process enables tropical grasses to acquire phosphorus from soil recalcitrant phosphorus sources which could enhance phosphorus concentrations in the rhizosphere (Almeida et al., 2018) and alleviate phosphorus deficiency (Ma et al., 2022). In their study, Patidar et al. (2023), reported a 73% improvement of soil phosphorus status in soils under *C. ciliaris* over fallow soils. This is significant for seed-based ecological programs using perennial tropical grasses, especially in dry grasslands characterised by low mineral nutrient concentrations and availability that limit plant growth (Moreno-Jiménez et al., 2019). These results reiterate that African dryland grasses play a significant role in regulating soil mineral nutrient concentrations in the rhizosphere (Lambers et al., 2008).

Specifically, soil conditions affect root traits and plasticity (Bardgett et al., 2014) and in return, roots modify the rhizospheric soil to increase uptake of soil mineral nutrients (Dakora and Phillips 2002; Nourgholipour et al., 2022). Rhizosphere soil mineral concentration of tropical grasses vary suggesting that extent of nutrient uptake and depletion in soil is not uniform. This indicates that root systems of tropical grasses have different absorptive strategies for nutrients from soils (Yang et al., 2015).

5. Conclusions

Perennial African dryland grasses exhibit distinct root traits that influenced the total mineral concentration in rhizosphere soil and plant biomass. Root trait relationships of the root economic spectrum were largely not supported and varied between the grass species. *C. ciliaris* displayed more superior root traits suggesting its competitive advantage for acquiring soil resources compared to the other grasses. This study provides new insights into the intricate relationship between root traits of perennial African grasses used for seed-based ecological restoration and rhizosphere soil mineral nutrient concentrations. Unravelling root traits of African grasses used for seed-based ecological restoration can inform the selection of species combinations with complementary functional traits. Integration of species with distinct morphological traits will subsequently lead to a larger variance and increase their adaptation to varied African dryland environments. Thus, integrating root traits and total mineral nutrient concentrations in rhizosphere soil and shoot biomass can deepen our holistic understanding of the ecological restoration process using perennial grasses. This will better inform the choice of appropriate species to successfully restore degraded landscapes and support positive outcomes for future sustainability of African drylands in a changing global environment.

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CRedit authorship contribution statement

Kevin Z. Mganga: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare no conflicts of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.soilad.2026.100126.

Data availability

Data will be made available on request.

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