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RESEARCH ARTICLE

Plant functional traits can guide the regeneration of soil fertility in Kenyan grasslands

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Abstract

Background and aims In mesic areas of Sub-Saharan Africa, grassland and soil degradation is widespread and accelerating through overgrazing, alien plant encroachment, and climate change. Selection of native plant species that help to regenerate soil fertility is needed. Here we used a plant functional trait-based approach to species selection aiming to identify traits of native grassland plants that may regenerate soil fertility in degraded grasslands.

Methods We set up a mesocosm experiment with degraded and undegraded grassland soils from two contrasting locations in western Kenya. Mesocosms were planted with 18 local plant species. After six months, we harvested the plants and measured survival, plant functional traits, and a range of soil chemical and biological properties related to soil health.

Results Seedling mortality was widespread, with eleven out of eighteen species not surviving after six months when planted in the degraded soils. Carbon and nitrogen concentrations of degraded soils from both sites were lower than for undegraded soils, as was microbial biomass carbon and nitrogen. In soil of the surviving plant species, we found greater carbon and nitrogen, and enhanced enzyme activity for carbon, nitrogen and phosphorus cycling. This was linked to plant traits, including lower leaf dry matter content, high tissue nutrient content, and deep roots.

Conclusion Overall, our findings provide evidence that sowing native plant species with dense and nutrient rich tissues, such as high yielding forage grasses and slow-growing legumes, can help regenerate the fertility of degraded grassland soils in mesic tropical regions.

Keywords Restoration · Plant functional traits · Degradation · Species selection · Sub-Saharan Africa

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Introduction

Degradation of grassland is widespread and accelerating globally (Bardgett et al. 2021). In Sub-Saharan Africa, grassland degradation is largely attributed to soil erosion caused by overgrazing and extreme weather events, especially drought and periodic heavy rains, which are increasing in frequency and intensity with climate change (Tully et al. 2015). Degradation can be defined as the loss of resource potential, including the ability to produce food and economic value, which results in land that can no longer fulfil a given economic or ecological function (Mganga 2022). In mesic areas of sub-Saharan Africa, degraded soils can be characterised by a loss of plant biomass production, often resulting in patches of bare soil and increased soil erosion, with associated loss of soil fertility (van de Koppel et al. 1997). Soils that lose the ability to support plant growth are very difficult to restore, and choosing plant species to recover lost biomass requires understanding of their ability to grow and survive in degraded soils and to augment soil fertility. In subsistence farming systems, soil degradation can have catastrophic consequences for livestock keepers (Mganga 2022). Due to expansion of cropland, grazing areas are encroaching into forested lands, and degradation of soils is accelerating rapidly, mostly unchecked (Chomba et al. 2020). There is an urgent need to find practical solutions to enable restoration of these soils. Extensive research into grazing management has been undertaken in dry lands across sub-Saharan Africa and worldwide (Paul et al. 2020). However, there has been little emphasis on restoring the soils in addition to the vegetation, and there are calls for a 'whole system' approach (Bardgett et al. 2021; Mens et al. 2022).

Degradation of grasslands results in a loss of palatable forage for animals. Moreover, grassland degradation is associated with a decline in soil health, as indicated by the deterioration of soil physical structure, rates of nutrient cycling, and soil carbon content, which can be difficult to reverse. A plant species or plant trait approach has been proposed to help restore soil fertility (Bardgett 2017) and enable selection of a plant community that can balance the contrasting requirements of livestock keepers (Balazs et al. 2020). These requirements are to offer sufficient forage for grazing animals, while also maintaining cover and rooting networks that promote soil organic matter and nutrient content and reduce erosion. However, degraded soil may not support the growth and survival of some grassland plant species due to unfavourable soil conditions, such as low nutrients and poor soil structure, and a lack of potential for beneficial microbial associations (Luo et al. 2022; Wang et al. 2012). Species choice for restoring degraded lands must therefore take survival, productivity, and the functional traits of selected plant species into account. With respect to functional traits there is likely to be a trade-off between growth and survival, which will determine the success of the species chosen. Fast-growing species that can rapidly exploit resources but often do not survive when resources are low or depleted. Conversely, slow-growing species with a more conservative resource use strategy are likely to survive in low nutrient soils (Laughlin 2023). Therefore, when choosing species, or combinations of species, for restoration this balance between survival and establishment must be considered. Grazing studies have shown that shifts in plant communities with different traits that occur through heavy grazing can have further impacts on soil properties, leading to further changes in ecosystem service delivery (Li et al. 2021; Wentao et al. 2023). A trait-based approach to restoration could help with species selection for plant communities with a high likelihood of survival and establishment in degraded soils, and with the potential to improve soil fertility. The efficacy of a trait-based approach to restoration has mainly been tested in temperate regions and drylands (see reviews including Brown and Anand 2019; Carlucci et al. 2020), with little research conducted in degraded mesic grasslands of Sub-Saharan Africa (according to Carlucci et al. 2020, with only one paper reported on restoration in Kenya between 2007–2017). Here we aim to test trait-based approaches that can be employed by landowners in Kenya to find the most effective plant types that improve soil health and productivity.

There is growing evidence that plant functional traits influence soil properties that underpin soil fertility, and therefore selecting plants based on traits that boost soil fertility might accelerate initial stages of restoration (Bardgett 2017; Fry et al. 2018). In the case of restoring soils, desirable species may add more to the soil than they remove, in terms of organic matter and nutrients, and by recruiting beneficial plant-microbial associations (Yang et al. 2019; Zuo et al. 2016). When restoring grazing lands, the

growing body of evidence that plant functional traits can influence soil properties could be used to inform species choice (Carlucci et al. 2020). Across Kenya, heavy grazing leads to soil erosion and loss of organic matter (Mganga 2022; Wachiye et al. 2022). Therefore, efforts may be best targeted at species that bind the soil together with their roots and will increase soil fertility, as demonstrated by Gould et al. (2016), who showed that root length density, i.e., the total length of roots in a given soil volume, was a key driver of soil aggregate stability. Other traits that may be useful in early restoration include leaf dry matter content, a proxy for tissue density that is an excellent predictor of soil fertility (Hodgson et al. 2011), and shoot and root nutrient content, which directly link to plant resource economy. Furthermore, recent research asserts that using plant traits in a restoration framework is contingent on local climate, and by extension, local conditions (Balazs et al. 2020). By using two contrasting sites in western Kenya, we aim to identify linkages between desirable functional traits of native plant species and site conditions, which can inform restoration efforts.

Our goal was to identify a set of native plant species that can both grow and survive in degraded soils, and which have the potential to regenerate soil fertility, and further, to identify associated plant functional traits to aid future species selection for restoration. This was tested experimentally using a range of native plant species with contrasting functional traits grown in mesocosms containing degraded and undegraded soils collected from two grassland areas in west Kenya: Kuresoi, an area of formerly forested land in the Mau Forest area that has been converted to grassland; and Nyando, which is a nearby lowland area with a long history of livestock grazing. Degradation in mesic Sub-Saharan African grasslands, such as in Kuresoi and Nyando, often arises from a combination of overgrazing and climate change, including drought and irregular, intense rainfall events, which erode and remove the more fertile surface layer of soil. Our research questions are: 1) which plant species are capable of growth and survival in degraded soils? 2) how do plant functional traits of surviving species influence soil properties, and how do contrasting soil types influence these plant traits? 3) which plant species have traits that may improve soil properties in degraded lands? We measured important soil properties for the regeneration of soil fertility during initial stages of restoration. These included dissolved and total soil carbon, plant available nutrients including nitrate, ammonium and phosphate, and microbially driven properties and processes including microbial biomass carbon and nitrogen, mineralisation of nitrogen, and microbially-derived extracellular enzymes that break down complex carbohydrates, nitrogen- and phosphate-based compounds. Enzymes are exuded by microbes in response to substrate availability, and could be viewed as an initial step in building soil fertility during early stages of restoration, and are thus more important in our relatively short-term study (Feng et al. 2019; Zuccarini et al. 2023). Soil carbon, nitrogen and phosphate pools are more stable and may represent a longer-term investment by the plant species present (Hartemink 2006). A functional microbial community is likely to be key to building soil fertility and underpinning establishment and growth of plant communities in degraded lands (Farrell et al. 2020).

Methods

Experimental design

We found seven potential matched pairs of sites (degraded and undegraded) within two areas of western Kenya: Kuresoi and Nyando. We assessed sites visually by finding sites within 1.5 km of each other. Undegraded sites would be characterised by high plant productivity, that had a high proportion of Graminoids. Degraded sites would have a shrubby composition, fewer Graminoids, with substantial areas of bare soil. Consultation with the landowners confirmed that in the case of the undegraded sites, farming had been continuous for over six years and animal stocking rates were low, while in the degraded sites, in Kuresoi the land was adjacent to the road, with heavy cattle and sheep stocking, while in Nyando the land belonged to a dispensary, with goat browsing. We collected soils from grasslands and completed a set of soil analyses. The sites that were selected based on the greatest contrasts in soil properties are presented in Table 1 (see Figure S1 for a location map). The Mau forest region of western Kenya is characterised by a mesic climate, with regular periods of high rainfall. The soils were passed through a 4 mm sieve, then individually added to 20 l drums

Table 1 Location and initial characteristics of the soils used in the mesocosm study

Location	Soil status	Texture	pH	Dissolved organic carbon mg kg^{-1}	%carbon	%nitrogen	Carbon to nitrogen ratio
Kuresoi	Undegraded	silt loam	4.45	229.74	4.15	0.35	11.86
Kuresoi	Degraded	loam	6.30	165.89	1.40	0.11	12.73
Nyando	Undegraded	silt loam	7.06	325.28	2.13	0.18	11.83
Nyando	Degraded	loam	7.56	212.41	1.05	0.10	10.50

containing a base layer of sand and gravel (approximately 30 cm diameter × 50 cm depth).

We chose 18 plant species that were native to western Kenya (Agnew 2006): ten grass species, four forbs, and four legumes (see Table S1). Seeds were obtained from various sources, including the International Livestock Research Institute (ILRI) in Nairobi, Kenya (*Brachiaria brizantha*), the Millennium Seed Bank Project, Kew, UK (MSB), and locally collected seed stock. We created a full factorial design, with soils from two sites (Kuresoi and Nyando), two levels of degradation (degraded and undegraded), 18 plant species, and each combination was replicated four times, resulting in 288 mesocosms. We grew one individual seedling per mesocosm in a greenhouse at the University of Kabianga, Kenya, for six months (January to June 2020) to simulate initial stages of grassland restoration, before destructively harvesting the plants and sampling the soil.

Plant traits

We measured vegetative plant height and counted total leaf numbers for each plant monthly through the growing period. At harvest, we collected four healthy leaves per plant to determine leaf area. These leaves were stored in wet tissue paper and processed within 24 h before being weighed. We arranged the four leaves around a reference of known size and took a digital image from a standard focal length. We then used Image J software to calculate the average leaf area for each plant using the crop and threshold functions (Martin et al. 2020; Schneider et al. 2012). We could calculate specific leaf area (SLA) by dividing leaf area by dry weight according to standard protocols (Pérez-Harguindeguy et al. 2016). When the protocol was complete, the leaves were placed in a drying oven at 80˚C for 48 h and then weighed again to determine leaf dry matter content (LDMC). These were then packaged and sent to The University of Manchester for further processing. The rest of the plant was cut at the soil surface level and the aboveground part was also weighed fresh then reweighed after drying to determine aboveground dry matter content (AGDMC) and total aboveground biomass. The roots were carefully washed and weighed to determine belowground biomass, and rooting depth was also determined by measuring the deepest extent of the roots. The dried roots and leaves were analysed to determine carbon and nitrogen content using an elemental combustion analyser (Elementar Vario EL, Hanau, Germany).

Soil properties

Soils were collected from each mesocosm after harvest and passed through a 2 mm aperture sieve. First, pH from each mesocosm was measured using a ratio of 5 g soil to 5 ml distilled water, and a pH probe (Mettler Toledo FE20, Salford, UK). Soil moisture content was determined gravimetrically by weighing 5 g moist soil, drying for 48 h at 105˚C and reweighing, calculating the proportion of water lost. Extractable carbon and nitrogen were measured as follows: 5 g of fresh soil was weighed and shaken at 150 rpm with 35 ml Milli-Q water for 10 min, then filtered through a Whatman 42 filter paper. Total dissolved carbon (TC), total organic carbon (TOC) and total inorganic carbon (IC) were determined using an Aurora 1030 W TOC analyser (OI Analytical, UK). The filtrate was also used to determine total extractable nitrogen and nitrate (NO_3) using an AA3 autoanalyser (Seal Analytical, Wrexham, UK). We then extracted ammonium (NH_4) using a solution of 1 M KCl and shaking for one hour at 150 rpm, before filtering through a Whatman number 1 filter paper (Allen 1989). The filtrate was also run on the AA3 autoanalyser. Data were adjusted for soil moisture and

exact soil weights. Potential nitrogen mineralisation and nitrification were determined by incubating 5 g of soil at 20˚C for 14 days, then extracting and measuring the nitrogen with the AA3. Data were divided by 14 to calculate the daily accumulation of nitrate and ammonium (Bardgett et al. 2003). We determined total soil phosphorus using the Kjeldahl acid digestion method (Kjeldahl 1883). Briefly, 420 ml concentrated sulfuric acid and 12 g lithium sulfate were mixed to create a reagent. We then added 51 ml of the reagent to 25 mg of dried soil in glass tubes, then 0.5 ml of 30% hydrogen peroxide. These mixtures were then heated on a digestion block for two hours at 360 ˚C, before cooling, adding a further 0.5 ml hydrogen peroxide, and heating to 360 ˚C for a further two hours. When complete, the samples were diluted to 25 ml with deionised water. Samples were quantified using a colourimetric method in a microplate, read at 880 nm (Kuo 1996). Plant available phosphate was measured by mixing 2 g of dry soil with 50 ml 0.5 M sulfuric acid, shaking for 16 h on an orbital shaker at 120 rpm, then filtering using Whatman 42 filter paper. Quantification was carried out using the same method as for total P.

We measured microbial biomass carbon and nitrogen using the chloroform-fumigation method (Vance et al. 1987). Briefly, for each mesocosm two replicates of 5 g of soil were weighed. One replicate was fumigated with chloroform for 24 h to lyse microbial cells. Both replicates were extracted for carbon and nitrogen using 25 ml 0.5 M K2SO4, mixing on an orbital shaker for 30 min and filtering through Whatman 42 paper, and analysing on the Aurora and Seal AA3 as before. Fresh soil values were subtracted from lysed soil values and adjusted for extraction efficiency using K_{EC} (0.35) and K_{EN} (0.45) factors respectively (Joergensen and Mueller 1996).

Extracellular enzyme activity was assayed colourimetrically in each soil for carbon, nitrogen and phosphate-based molecules. For *p*NP-linked enzymes, the protocol was based on that of Jackson et al. (2013). These included *N*-acetylglucosaminidase (NAG), β-glucosidase (GLC), cellobiohydrolase (CBH), phosphatase (PHO) and β-xylosidase (XYL). We further measured urease (URE) activity using the protocol of Cordero et al. (2019), and phenol oxidase (POX) and peroxidase (PER) using Kaisers method (Kaiser et al. 2010) with the modifications described in De Long et al. (2019). Total carbon and nitrogen were determined in dried, ground soil using an elemental combustion analyser (Elementar Vario EL, Hanau, Germany).

Statistical analysis

All statistical analyses were carried out using R version 4.3.1 (R Development Core Team 2023). We determined differences between degraded and undegraded soil properties in the two sites after harvest by calculating Hedges' *g* with 95% confidence intervals (Hedges 1981, 1982) using the undegraded sites as the control, and the degraded sites as the treatments. Kuresoi and Nyando sites were assessed separately, as they had differing starting values. All data were standardised by calculating z-scores using the scale function in base R. Hedges' *g* values over 0.8 were considered large effects, 0.4–0.8 were medium sized effects, and 0.2–0.4 were considered small effects (Trepel et al. 2024). We additionally carried out one-way analysis of variance to determine statistical significance of these effects, taking each soil property in turn and looking at the two sites separately.

To test whether there was a relationship between trait values with site and soil degradation status, we used zero-inflated Gaussian mixed models in the NBZIMM package in R (lme.zig function, Yi 2024). These models determine the log-likelihood of the zero state then fit a mixed effects model to the non-zero data. We used NBZIMM models because mortality meant that trait data was not available for all site and degradation combinations. This model assesses whether the zeros are due to treatments and then models the non-zero entries with a Gaussian error distribution. Where no zero data existed in the dataset, linear mixed effects models were fitted. The time series trait data (plant height and leaf number) were used as response variables and a three-way interaction was modelled between date, site and degradation status. Pot number was included as a random effect.

To include the most effective species for restoration, we eliminated species that achieved lower than 75% survival at harvest in both degraded sites, as these are unlikely to be successful in restoration efforts. This left us with seven species in Kuresoi, and six species in Nyando. We condensed the soil properties into two main axes using Principal Components Analysis (PCA) in the *factoextra* package in R (Kassambara and Mundt 2024). The separation of

the two degraded *vs* undegraded soil properties, and the two different sites, were determined using two-way ANOVA on the axis values for PCA1 and PCA2. Following this, we conducted a three-way ANCOVA with PCA1 as the response, with each plant functional trait in turn, degradation status and plant species in the mesocosm as interacting explanatory variables. We also included site as an additive effect to account for variation between the sites, but we did not include their interaction with other variables, given this was not the main aim of our analysis. We used a model selection approach on the global model using the MuMin package in R (Bartón 2024). If a trait was retained in one of the top models (those within Δ2 AICc of the top model), we presented this graphically. We repeated this process with the PCA2 axis.

Finally, we complemented the above analyses by examining the Pearson's correlation coefficients between plant traits and soil properties separated by site and degradation status. This analysis yields further information on the raw relationships between traits individual soil properties outside of variation collapsed by the PCA analyses and provides a plant-species agnostic assessment of how trait-soil property relationships. The Pearson's correlation coefficients were estimated and evaluated with t-tests using the *Hmisc* package (Harrell Jr. 2024). Most variables were natural log or logit transformed to meet normality assumptions.

Results

Soil degradation indicators

Total soil carbon and nitrogen (%) were lower in degraded soils at the start of the study (Table 1). At harvest, microbial biomass carbon and nitrogen were also significantly lower in degraded relative to undegraded soil taken from both Kuresoi and Nyando irrespective of planted species, shown using Hedges' *g* effect sizes (Figure S2). Soil properties such as plant available nutrients, dissolved organic carbon concentration, and extracellular enzyme activities showed more variable responses to degradation. While degraded soils generally had lower values for soil nutrients and enzyme activities relative to undegraded soil, dissolved organic carbon concentrations were greater in degraded than undegraded soil (Figure S2).

Plant species potential for accelerating restoration

Due to extensive seedling mortality, we completed the experiment with 139 plants out of 288 planted in mesocosms, after planting the healthiest seedlings available. Survival rates of the plant species in the experiment were generally lower (by about 25%) in the degraded soils of both sites (Fig. 1). We did not observe a pattern of survival according to plant functional group, i.e., grass, forb, legume, and while there were some species that were successful in both sites (*Sporobolous superba, Trifolium cheranganiense, Themeda triandra*), there were others that were only successful in one site, such as *Ipomoea obscura* in Nyando. Some species were more successful in soils taken from degraded sites, which may mean they are more viable candidates for early restoration efforts. These included the grasses *Brachiaria brizantha* in Kuresoi and *Cynodon dactylon* in Nyando. The species that achieved 75% survival or more at harvest in the degraded soils were assessed for leaf and root traits.

Plant trait response to soil types

Analysis of plant height over the growing period, accounting for zero inflation, was strongly linked to both site and degradation status (for statistical output, see Table S2; Figure S3a,b). We did not observe strong, consistent differences in plant height between the species that survived in degraded soils and those that were eliminated. For the eight species that showed 75% or more survival at least one degraded site (hereafter surviving species), there was no clear pattern of effects. While there was a significant effect of date, signalling growth for *C. mimosoides, C. dactylon* and *T. triandra,* the other five species did not grow significantly taller throughout the study. We also did not see an interaction of date with site or degradation status, indicating that the trends remained stable through the study. We observed an interaction between site and degradation status in *C. mimosoides, C. dactylon, I. obscura, S. superba* and *T. cheranganiense*. While undegraded soils tended to have taller plants than degraded, which varied with site, this was not the case for *C. dactylon*, which had markedly larger plants in degraded soils from Nyando than the undegraded soils.

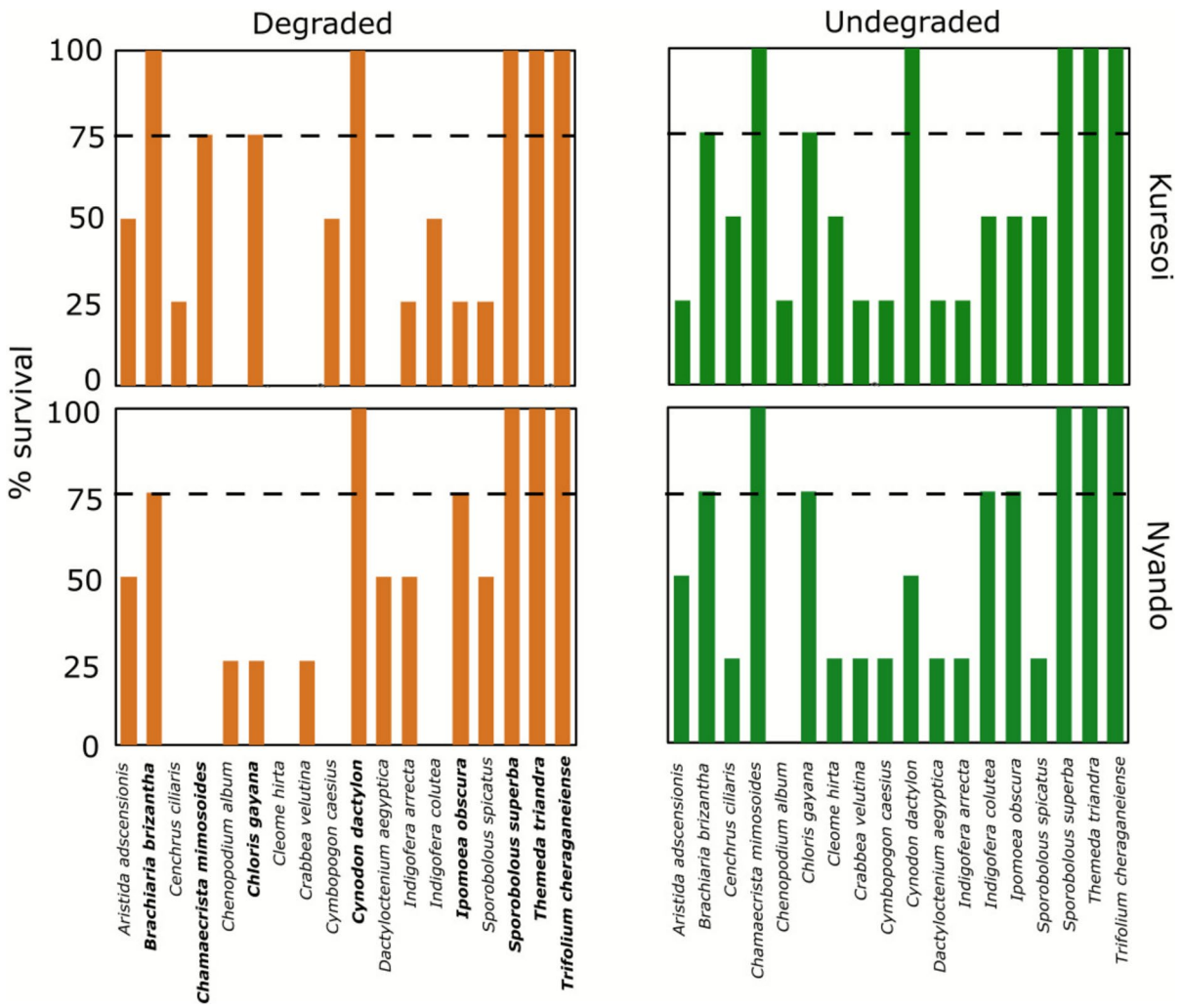


Fig. 1 Survival rates of the species used in the experiment ($n=4$). The cut off of 75% survival rate (3 out of 4 surviving seedlings) is marked with a dashed line, and the species retained are marked with bold text. Those that did not achieve this threshold in the degraded soils are removed from further analysis

Leaf number was more sensitive to site and degradation status than plant height. There was a significant effect of date for *B. brizantha, C. mimosoides, C. dactylon, S. superba T. triandra,* and *T. cheranganiense,* which again did not interact with site or degradation status. While this was mostly a steady increase in leaves through the study, for *C. dactylon, S. superba* and *T. cheranganiense* there were losses of leaves in the beginning of August, with later increases. There were again interactions between site and degradation status for *C. dactylon, I. obscura, S. superba, T. triandra* and *T. cheranganiense*, In the case of *C. dactylon, T. triandra* and *T. cheranganiense* this was because the plants with the highest leaf numbers were those in degraded Nyando soils, followed by both undegraded soils, then the degraded Kuresoi.

For the species that did not survive to 75% or more in any degraded soils, we did not observe clear patterns of plant height or leaf number across treatments. For many species there was widespread failure to establish, with many seedlings not establishing at all or dying rapidly. In Figure S3, it is clear that some individuals thrived and grew, but these were often few and growth was mostly better in undegraded soils. Correlations between the traits of the surviving species showed some changes

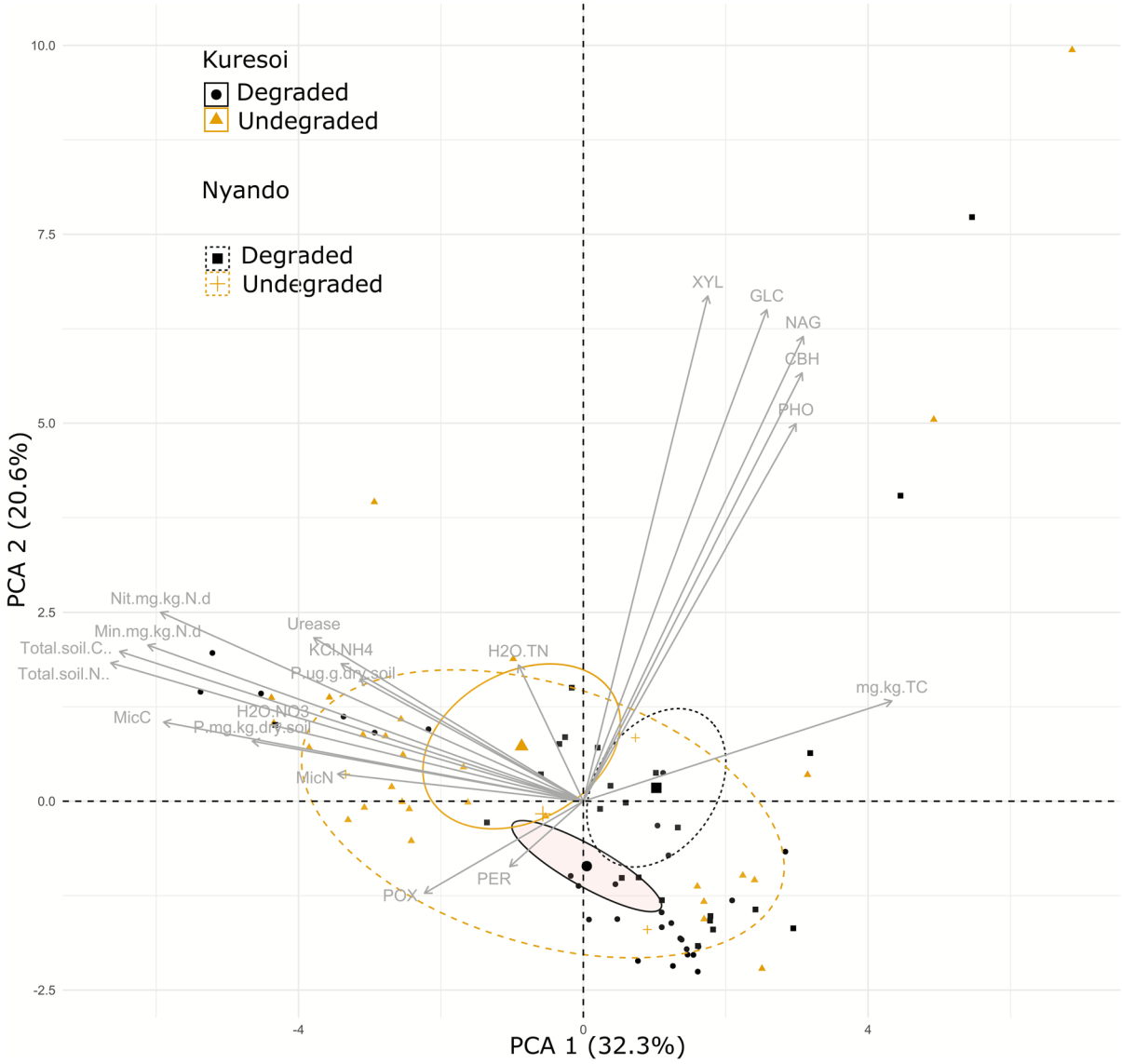


Fig. 2 Principal Components Analysis of soil properties, showing divergence between degraded and undegraded soils using all surviving species from degraded soils. PCA1: significant interaction between site and degradation status ($F_{1,79}=7.49$, $p=0.008$); PCA2: significant difference between site and degradation status ($F_{1,79}=5.57$, $p=0.021$)

between degraded and undegraded soils; LDMC and belowground biomass became more weakly linked under degraded soils than undegraded, as well as root C:shoot N, and shoot N:root N. Some root traits, such as root depth and root N, became more strongly linked in degraded soils than undegraded (Figure S4).

Alignment of soil properties with soil type

The PCA of the soil properties, based only on the surviving species from Fig. 1, revealed two main axes. The first axis represented 32.3% of the variation and negatively aligned with total soil carbon and nitrogen, microbial biomass carbon, urease activity and variables representing nitrogen cycling processes (Fig. 2). Higher values of these soil properties appeared more

negative on PCA1. We also observed a significant interaction between site and degradation status, where degraded soils in Kuresoi and Nyando were statistically similar to each other, but the undegraded sites were different to the degraded sites and different from each other ($F_{1,78} = 39.38$, $p = 0.008$). Similarly to the effect size analysis, degraded sites had lower values of soil nutrients and enzymes than undegraded sites (higher values of these soil properties resulted in more negative values on PCA1). PCA2 accounted for 20.6% of the variation and was positively aligned with extracellular enzyme activity including CBH, NAG, GLC, XYL and PHO, and negatively aligned with the enzymes PER and PHO. There was a significant interaction between site and degradation status ($F_{1,79} = 5.57$, $p = 0.021$). Tukey's Honest Significant Difference test revealed that this was because degraded soils in Kuresoi had significantly lower PCA2 axis values than the other three treatments (both undegraded soils, and degraded Nyando soils).

Plant functional traits associated with soil degradation

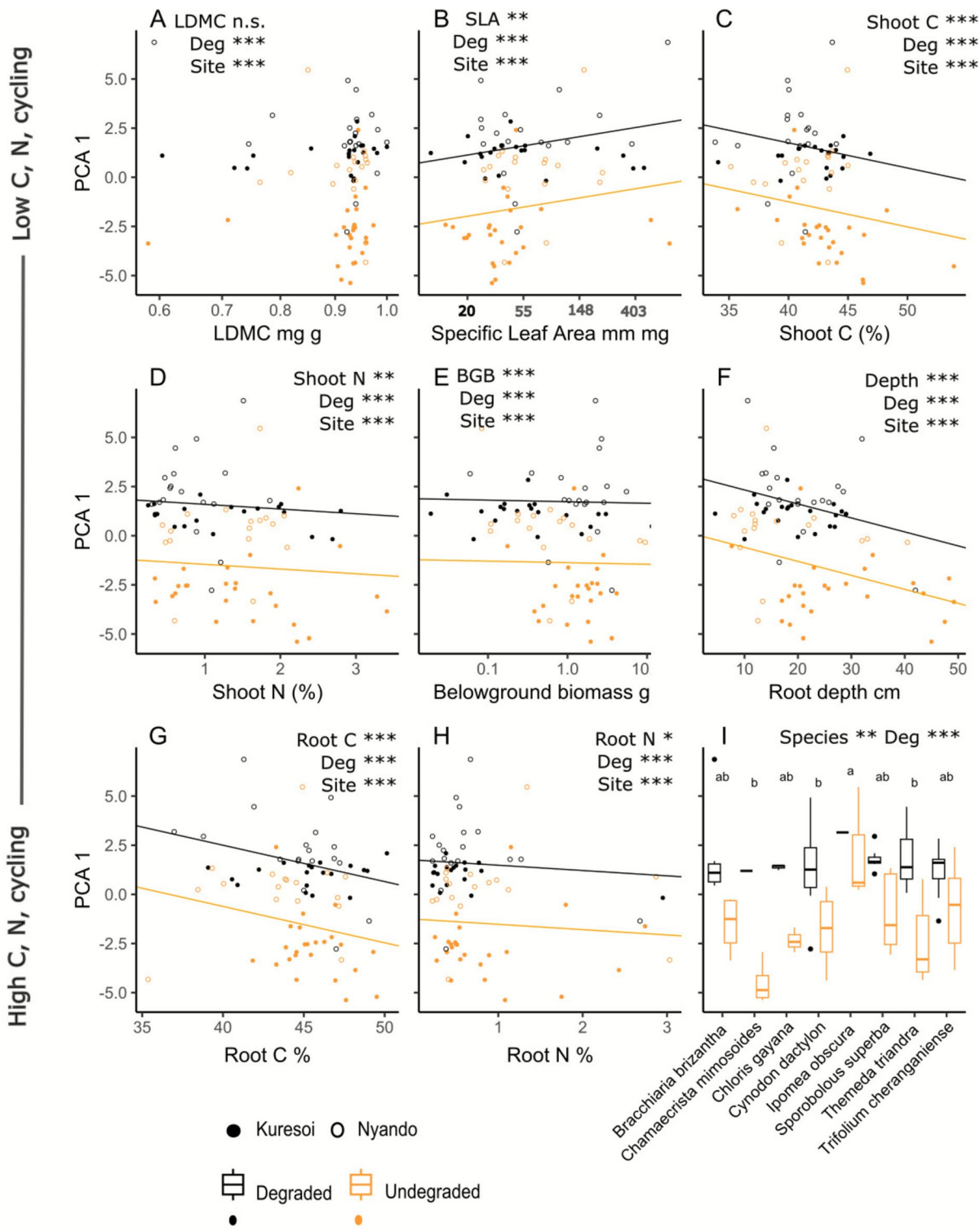
Soil property loadings on the first PCA axis were highly dependent on plant species identity. A Tukey's HSD test revealed that the legume *Chamaecrista mimosoides* (a legume) had the most negative values on PCA1, meaning the highest values of soil properties in the surviving species pool, while *Ipomoea obscura* (a forb) had the lowest values and the other species were intermediate between the two (Fig. 3I; $F_{7,73} = 4.59$, $p < 0.001$). For PCA2, we did not observe a significant species effect, indicating no effect on microbial-derived enzyme activity (Fig. 3I).

Eight traits were significantly associated with the soil properties represented by PCA1, according to model selection (Table S3; Fig. 4). This arose through trait shifts of individual species, as we could not detect individual species effects on traits. The shoot traits, leaf dry matter content (Fig. 3A), specific leaf area (Fig. 3B) and shoot tissue nitrogen content (Fig. 3D) all showed a positive relationship with PCA1, with higher values for the degraded sites. Since the axis is negatively associated with soil properties, this indicates that degraded sites have lower nutrient and nutrient cycling levels, and that low leaf dry matter content, specific leaf area, and % shoot nitrogen are associated with higher soil nutrient contents and nutrient cycling. Shoot C concentration was positively linked with soil nutrient concentration (Fig. 3C).

For root traits, higher values were generally associated with higher soil nutrient values (i.e. lower PCA1). Therefore, deeper roots (Fig. 3F), with higher tissue carbon and nitrogen (Fig. 3G and H, respectively), were associated with higher soil nutrient values in both degraded and undegraded soils. While there was a species effect on each of these traits, these species effects did not change with changing trait values, i.e., there was no interaction term, and for clarity, species effects on PCA1 are shown in Fig. 3I.

PCA axis 2 was associated positively with extracellular soil enzyme activity and correlated with only three plant attributes: LDMC, shoot C and shoot N. In each instance, there were higher values of PCA2 in undegraded soils, and no effect of species, with the exception of shoot N (Fig. 4I). We observed marginal effects of site, but these were not strongly linked with enzyme activity. For the shoot traits, higher values of leaf dry matter content (denser tissues) had lower PCA2 values (Fig. 4A), while higher values of specific leaf area and shoot carbon were all related to higher values of PCA2 (Fig. 4B, and C respectively). Shoot nitrogen showed a significant interaction with species identity to influence PCA2. For the root traits, while individual traits were retained in the model, there were no significant effects on slope.

Oddly, there were no consistent patterns of traits and individual soil properties across the degradation states (Fig. 5). That is, by way of example, if LDMC was significantly negatively correlated with GLC activity in the degraded soils, there was a similar pattern in the undegraded soils, but it was non-significant (Fig. 5). The only consistent, significant relationship between traits and soil properties in the degraded and undegraded soils was that higher plant SLA led to lower nitrate in the soils (Fig. 5). Additionally, there was no single trait in the degraded soils that was regularly significantly related to many soil properties. The highest number of significant trait – soil property correlations in the degraded soils was three, where SLA was positively related to POX and GLC activity and negatively related to soil nitrate concentration, while LDMC was positively related to nitrate concentration and negatively related to GLC and XYL activity (Fig. 5). In the undegraded soils, belowground biomass (BGB) and root depth were related to many


Low C, N, cycling
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Species ** Deg ***
PCA 1
Bracchiaria brizantha
Chamaecrista mimosoides
Chloris gayana
Cynodon dactylon
Ipomea obscura
Sporobolus superba
Themeda triandra
Trifolium cheranganiense
Kuresoi
Nyando
Degraded
Undegraded

◂**Fig. 3** Associations between plant traits, degradation status and soil properties, here represented as PCA1. Low values of PCA1 indicate high C, N and N cycling values, while high values indicate low C, N and N cycling. These were identified by model selection using AICc. PCA1 was primarily driven by soil total C, N, microbial C and N, N mineralisation and nitrification rates (see figure S3). **A**) Leaf dry matter content + degradation + site (LDMC: $F_{1,78} = 2.52$, $p = 0.117$, Degradation: $F_{1,78} = 67.41$, $p < 0.001$, Site: $F_{1,78} = 28.10$, $p < 0.001$); **B**) Specific leaf area + degradation + site (SLA: $F_{1,77} = 8.64$, $p = 0.004$, Degradation: $F_{1,77} = 64.35$, $p < 0.001$, Site: $F_{1,77} = 24.37$, $p < 0.001$); **C**) Shoot carbon + degradation + site (Shoot C: $F_{1,76} = 11.80$, $p < 0.001$, Degradation: $F_{1,76} = 56.59$, $p < 0.001$, Site: $F_{1,76} = 24.62$, $p < 0.001$); **D**) Shoot nitrogen content + degradation (Shoot N: $F_{1,76} = 8.13$, $p = 0.006$, Degradation: $F_{1,76} = 57.04$, $p < 0.001$, Site: $F_{1,76} = 27.60$, $p < 0.001$); **E**) Belowground biomass + degradation (BGB: $F_{1,78} = 13.39$, $p < 0.001$, Degradation: $F_{1,78} = 64.56$, $p < 0.001$, Site: $F_{1,78} = 31.32$, $p < 0.001$); **F**) Root depth + degradation + site (Depth: $F_{1,79} = 27.75$, $p < 0.001$, Degradation: $F_{1,79} = 61.78$, $p < 0.001$, Site: $F_{1,79} = 21.68$, $p < 0.001$); **G**) Root carbon content + degradation + site (Root C: $F_{1,74} = 5.94$, $p < 0.001$, Degradation: $F_{1,74} = 63.21$, $p < 0.001$, Site: $F_{1,74} = 22.85$, $p < 0.001$); **H**) Root nitrogen content + degradation + site (Root N: $F_{1,74} = 5.86$, $p = 0.020$, Degradation: $F_{1,74} = 56.11$, $p < 0.001$, Site: $F_{1,74} = 28.03$, $p < 0.001$); **I**) Species and degradation effects on soil properties (Species, $F_{7,74} = 3.27$, $p = 0.004$, Degradation, $F_{1,74} = 63.77$, $p < 0.001$)

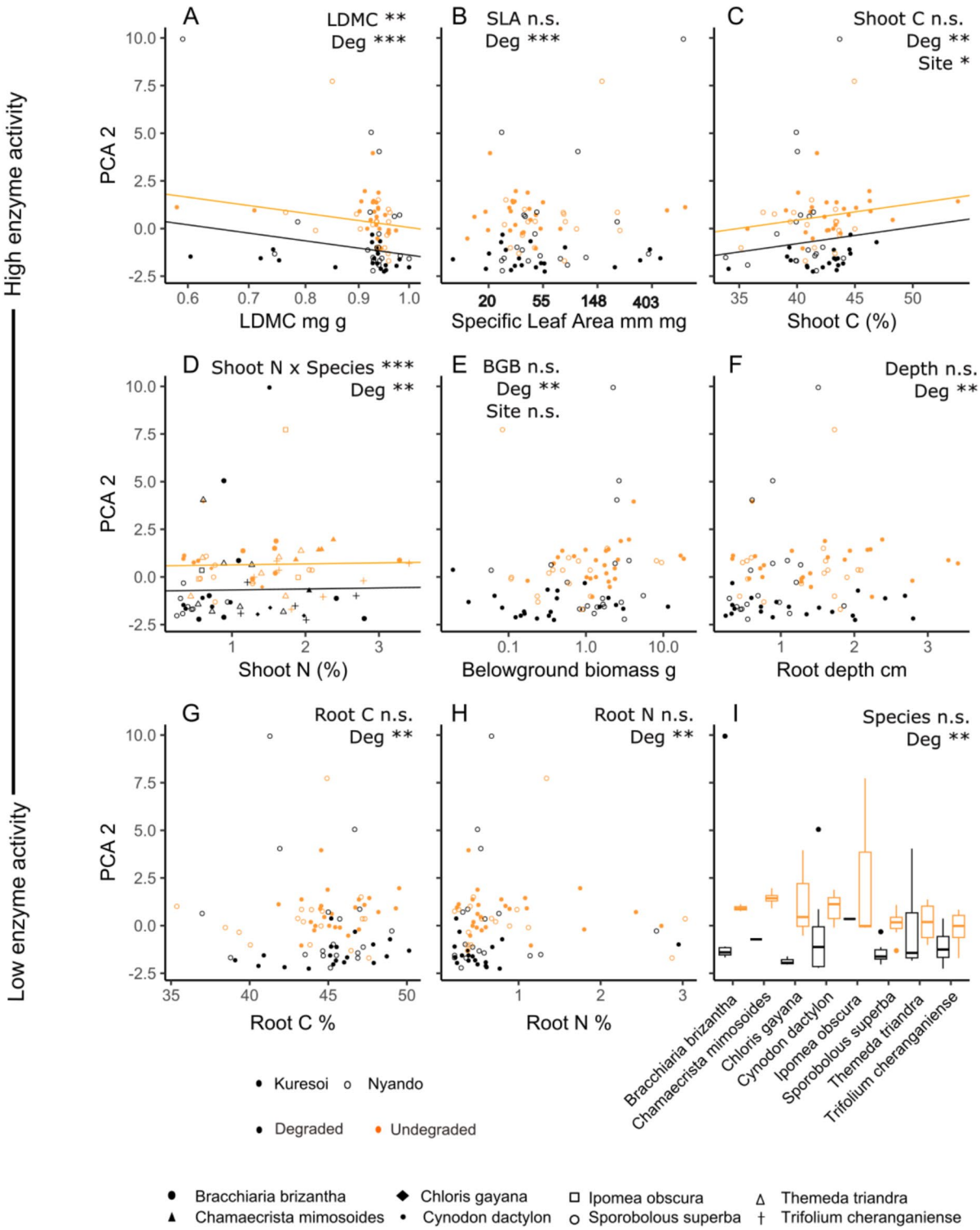
soil properties. BGB and root depth were positively related to ammonia, soil C and N, microbial C and nitrification, while BGB alone was negatively related to soil C:N.

Discussion

We aimed to identify plant species that could help restore soil fertility during initial stages of restoration of degraded grassland soils in two mesic areas in Kenya. We approached this goal by first identifying native plant species that can survive and establish in degraded soils and then evaluated their effect on a range of soil properties and associated plant functional traits. We found that while several plant species established and survived in degraded soils, there was no clear link with plant height or leaf number throughout the study. We further showed that degraded soils had lower soil carbon, nitrogen, and enzyme activity, but that this could be enhanced by growing plant species with traits associated with slow growth rates and high tissue nutrient contents, including forage grasses and legumes.

Survival of plant species in degraded soil is site-specific

Our study showed a fairly low number of surviving species in degraded soil, mostly comprising fodder grasses and legumes. However, our results suggest that planting leguminous species is potentially most effective for the initial stages of restoration. As well as fixing nitrogen and fertilising the surrounding soil, they will also have highly palatable nitrogen-rich tissues, which will be an advantage for grazing animals. The species *Chamaecrista mimosoides* had the strongest relationship with soil properties on PCA axis 1 and is a small leguminous shrub that fixes nitrogen, has a woody stem and extrafloral nectary, which would deliver benefits to invertebrates (Nemoto et al. 2016). Given that it has a high survival rate in degraded soils in Kuresoi, our results suggest *that C. mimosoides* is a good candidate for inclusion in species mixes for restoring degraded soils in upland regions. Further, it is consumed by browsing animals, has high drought tolerance, and is thought to facilitate the establishment of other plant species through the provision of plant-available nitrogen, making it an excellent candidate for targeted restoration of both soil and plant assemblages (Siebert and Scogings 2015; Zaré et al. 2022). In the Nyando soils, of the six plant species that achieved the survival threshold, four were grasses, one was a legume, and one was a forb. From these species, the best candidate species for restoration in these soils was the perennial grass *C. dactylon*. Of the surviving species in Nyando, *C. dactylon* had the most negative values for the PCA axis 1, which indicates high values of soil carbon and nitrogen, as well as more rapid nitrogen cycling. *Cynodon dactylon* is a highly productive forage species, with high resilience to drought, deep roots and can withstand high stocking rates (Hacker and Jank 1998; Heuzé et al. 2015). Importantly, this species has been shown in other regions of the world to be useful for erosion control because it is both rhizomatous and stoloniferous, forming dense mats of biomass, which is a critical consideration for restoration in Kenya. Finally, *C. dactylon* can withstand both drought and flooding, which occur frequently in the degraded soils of mesic areas in western Kenya (Cook et al. 2005). While the species presented here are merely an illustration of the characteristics of plant species required for restoring degraded lands, they can also form the


High enzyme activity
Low enzyme activity
A
LDMC **
Deg ***
PCA 2
LDMC mg g
B
SLA n.s.
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Specific Leaf Area mm mg
C
Shoot C n.s.
Deg **
Site *
Shoot C (%)
D
Shoot N x Species ***
Deg **
Shoot N (%)
E
BGB n.s.
Deg **
Site n.s.
Belowground biomass g
F
Depth n.s.
Deg **
Root depth cm
G
Root C n.s.
Deg **
Root C %
H
Root N n.s.
Deg **
Root N %
I
Species n.s.
Deg **
Bracchiaria brizantha
Chamaecrista mimosoides
Chloris gayana
Cynodon dactylon
Ipomea obscura
Sporobolous superba
Themeda triandra
Trifolium cheranganiense
Kuresoi
Nyando
Degraded
Undegraded
Bracchiaria brizantha
Chamaecrista mimosoides
Chloris gayana
Cynodon dactylon
Ipomea obscura
Sporobolous superba
Themeda triandra
Trifolium cheranganiense

◂**Fig. 4** Significant associations between plant traits, degradation status and soil properties, here represented as PCA2. PCA2 was primarily driven by extracellular soil enzymes, where high values of PCA2 indicate high enzyme cycling, and low PCA2 is low enzyme cycling (see figure S3). Model output shown here is from the minimum adequate model as shown by model selection. **A**) Leaf Dry Matter Content + degradation (LDMC: $F_{1,78} = 7.44$, $p = 0.008$, degradation: $F_{1,79} = 12.60$, $p < 0.001$), **B**) Specific leaf area + degradation (SLA: $F_{1,78} = 3.57$, $p = 0.063$, Degradation: $F_{1,78} = 11.25$, $p = 0.001$), **C**) Shoot carbon content + degradation + site (Shoot C: $F_{1,76} = 3.22$, $p = 0.077$, Degradation: $F_{1,76} = 8.16$, $p = 0.006$, Site: $F_{1,76} = 5.30$, $p = 0.024$), **D**) Shoot nitrogen content x species + degradation (Shoot N x Species: $F_{7,63} = 4.53$, $p < 0.001$, Degradation: $F_{1,63} = 9.93$, $p = 0.003$), **E**) Belowground biomass + degradation + site (BGB: $F_{1,78} = 2.99$, $p = 0.088$, Degradation: $F_{1,78} = 7.93$, $p = 0.006$, Site: $F_{1,76} = 8.51$, $p = 0.131$). **F**) Root depth + degradation + site (Depth: $F_{1,79} = 1.13$, $p = 0.291$, Degradation: $F_{1,79} = 9.26$, $p = 0.003$, Site: $F_{1,79} = 3.43$, $p = 0.068$), **G**) Root carbon content + degradation (Root C: $F_{1,74} = 0.26$, $p = 0.613$, Degradation: $F_{1,74} = 7.44$, $p = 0.008$, Site: $F_{1,74} = 2.58$, $p = 0.112$), **H**) Root N content + degradation + site (Root N: $F_{1,74} = 0.23$, $p = 0.630$, Degradation: $F_{1,74} = 7.29$, $p = 0.009$, Site: $F_{1,74} = 2.76$, $p = 0.101$). I) Species + degradation (Species: $F_{7,74} = 1.34$, $p = 0.243$, Degradation: $F_{1,74} = 10.20$, $p = 0.002$)

basis of recommendations for interventions in Sub-Saharan Africa.

While we found that only root dry matter content was associated with survival in degraded soils, this was only evident in Nyando where it was not associated with soil nutrients. Root dry matter content is a trait that acts as a proxy for tissue density (Birouste et al. 2013), and low values are associated with rapid growth, high root exudation, and an exploitative growth strategy, characteristics that may reduce the ability of species to survive in a degraded soil (Williams et al. 2022). However, we found higher survival rates for plant species with lower root dry matter content, in contrast with past work. This contradictory finding could potentially occur because in these lands species are highly plastic and show compensatory growth, which has been shown in other studies (Bahia et al. 2020). The low tissue density may make the roots more palatable to root-feeding herbivores, which may reduce fitness in field conditions. Additionally, low root tissue density may translate to low tensile strength, which is important for withstanding erosion in regions that receive high rainfall intensities, such as Kuresoi and Nyando. We showed a shift in root architectural relationships with root chemistry in degraded soils compared with undegraded, which may indicate a change in resource allocation in the plant in response to degradation. Undegraded soils had very highly correlated traits both above and belowground. While this remained largely true in degraded soils, there were small changes, in particular a negative relationship between aboveground dry matter content and other traits, which could indicate the plant species in this study were mainly aligned with the resource economics spectrum, with some intra-specific trait plasticity in response to external conditions (Wright and Sutton-Grier 2012). In a study that looked at plant traits across a gradient of soil erosion, the strongest indicator trait was root length density, a trait that measures the total length of all roots in a given volume of soil. This trait is akin to root dry matter content, as they both characterise resource allocation and tissue density belowground (Hao et al. 2020). Root length density was highly sensitive to erosion, demonstrated by increased soil exploration: the authors attributed this to a combination of physical parameters that are impacted by erosion, including aggregate stability and shear strength, and the availability of nutrients for fine root exploration. Root traits are highly responsive to soil conditions and the plant may reduce root inputs in depleted soils with low nutrients, favouring aboveground biomass with higher potential for sunlight capture.

Restoration of soil properties is associated with small plants with dense tissues, but high tissue nitrogen content

We observed a strong link between soil properties and plant functional traits. Our first PCA axis described soil carbon and nitrogen pools. While we did not see a link between plant species and traits to drive this axis, there was a significant species effect in both degraded and undegraded soils. We showed that the important forage grasses *C. dactylon* and *T. triandra*, and the large legume *C. mimosoides* increased soil carbon, nitrogen and enzymatic activity relative to the other species that survived, while the creeper *Ipomoea obscura* had relatively lower values of soil properties. However, the influence of these species was mainly observed in the undegraded soils, and they did not make notable differences in the degraded soils. The key traits linked with PCA1 were those that determine size and volume of the plant, tissue quality and

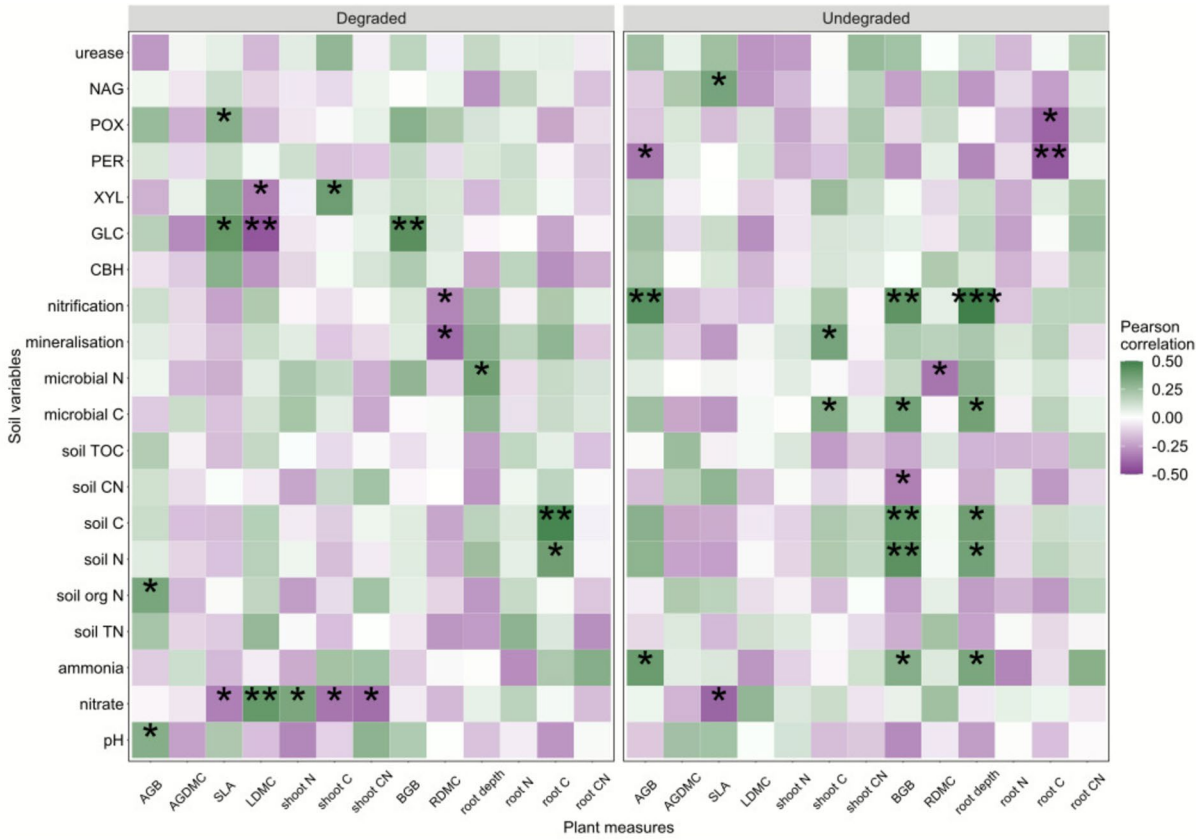

Fig. 5 Pearson correlation matrix between plant traits (x-axis) and soil properties (y-axis). The panels are split between degraded and undegraded soil. Colours are based on the strength and direction of the correlation and the panels share the legend to the left. Stars indicate significance levels based on t-tests for a given relationship ("*" is $0.05 \geq P > 0.01$, "**" is $0.01 \geq P > 0.001$, "***" is $P \leq 0.001$)

resource economy including leaf dry matter content and specific root length, and root and shoot carbon and nitrogen, which was associated with more stable carbon and nitrogen concentrations. As the main requirement of soil restoration is to build soil organic matter and nutrients to encourage microbial community growth and soil fertility, these traits are expected to enable growth with addition of soil organic matter (Carlucci et al. 2020). However, we showed that the most desirable species from a restoration context have characteristics that fall both on the 'fast' and 'slow' ends of the resource economy spectrum, with deep roots, high tissue carbon and small stature. We infer that the reason for this is that plants add nutrients and carbon to the soil through sloughed tissue and exudates, while having relatively low resource requirements themselves to complete their life cycle and reproduce. Hence, the desired plants would have high tissue density, the potential for deep rooting and high tissue nitrogen, traits which combine to improve soil properties.

While we did not observe any link with aboveground biomass with our PCA axes, we could speculate that in degraded lands, plants with large aboveground biomass can take too much resource from the soil, leading to asynchrony of plant demand and soil supply, and localised depletion of nutrients (Fontaine et al. 2024). In our study the tallest species (*C. mimosoides* and *C. gayana*) had the largest disparity in soil nutrients seen on PCA1 between degraded and undegraded soils, indicating these plants did not improve the soil in degraded sites in the same way that they did undegraded. Similarly, in a heavily degraded low nutrient chalk grassland in

the UK, we observed a need for smaller plants which will add dense and nutrient rich tissue to the soil, as large plants tended to remove nutrients and were highly susceptible to drought (Fry et al. 2018). This study also showed that deeper rooting is aligned with increased soil nutrient concentrations and nutrient cycling. Root density, and tensile strength is critical here to anchor the plant in soils with depleted organic matter. Research shows that deeper rooting is linked with more conservative resource economies, which would be beneficial for soil aggregation and preservation given that an important objective is to build organic matter (Poirier et al. 2018; Fry et al. 2021). Many degraded lands will be sparsely vegetated, and in the case of our study sites, vulnerable to irregular inputs of heavy rain. Potential for a deep rooting strategy would be useful to secure the plants in place, even though in our study plants had shallower roots in degraded soils. A potential recommendation for restoring degraded lands, therefore, would be to begin with smaller, deep rooted plant species to encourage building stocks of soil carbon and nitrogen, and bind the soil, reducing erosion (Garbowski et al. 2020).

By adopting a plant functional trait approach, restoration practitioners can become more prescriptive, selecting plants with traits that generate desired extracellular enzyme and nutrient cycling. However, some traits will be more useful than others for a specific goal (Laughlin 2014). In degraded soils, the balance of resources between the plants and the soil is of critical importance, and therefore the understanding of resource economy should be an important consideration (Saba et al. 2026). Our second PCA axis was linked with extracellular enzyme activity, which responds to resource inputs. These enzymes break down organic inputs and make nutrients available to plants and the soil food web. In our study we observed much stronger links with aboveground than belowground traits, which was surprising given the lack of a direct interface between aboveground organs and soil. We showed that the two traits concerned with resource economy, leaf dry matter content and specific leaf area, were the key drivers of enzyme activity. Dry matter content is a more stable and reliable predictor of resource use strategy than specific leaf area, which is susceptible to external variation such as shade (Hodgson et al. 1999). While we found a stronger link with the soil properties, represented by the PCA axes, for leaf dry matter content, both traits showed the same negative trend, i.e. that high values of the trait (very dense tissues) were associated with low enzyme activity. This is in line with other studies, which find that denser tissues are often associated with a more fungal dominated microbial community, which in turn, produce a wide range of extracellular enzymes that break down carbon and nitrogen-based molecules, potentially increasing nutrients available to plants (Wan et al. 2022; Weil et al. 2021). To jumpstart restoration, therefore, we recommend a mixture of small fast-growing species and those that build dense, carbon-rich structures over a longer period of time.

In sum, we show that sowing shrubby legumes and productive forage grasses can drive early restoration efforts for both soil fertility and overall sward productivity degraded soils. We have shown that plant species with dense tissues and high tissue carbon and nitrogen are crucial to steer degraded soil properties toward those of undegraded soils during initial stages of restoration. This is likely to be a balancing act in practise, not least because grazing is likely to continue on degraded grasslands. If grazing can be controlled, it is possible that plasticity of plant traits might play an important role in both improving soil properties and supporting grazing animals, in a sustainable manner (Sandel et al. 2011). However, when selecting plant species to include in Kenyan degraded grazed grasslands, a balance must be found between palatable and unpalatable species in order to maintain ground cover and nutrition, as well as a balance between growth and depletion of the soil. These considerations are critical to success of restoring degraded grasslands for sustainable use.

Author contributions MR, JQ, JH, RDB conceived the research and obtained funding, ELF, RDB designed the experiment, ELF, YO, BN carried out the research, ELF and JSL analysed the data and wrote the paper in close consultation with all authors.

In fond memory of Professor Joseph Hitimana and Professor Mariana Rufino, who passed away shortly before the submission of this paper, but whose support and contributions were invaluable. Sadly missed.

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Data availability Data are accessible at the Open Science Framework, https://doi.org/10.17605/OSF.IO/FNKHS.

Declarations

Competing interests The authors declare no competing interests.

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