



All savanna islands of fertility are not equal: colonial birds influence soil nutrient stoichiometries with consequences for tree seedling growth

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Abstract

Islands of fertility associated with tree/shrub patches in arid grasslands create spatial heterogeneity of soil nutrients. Faunal activities under these trees/shrubs may contribute to diverse characteristics of these fertile patches of soil due to different faecal inputs. This study used the tree islands of fertility (TIFs) created by camelthorn (*Vachellia erioloba*) and shepherd trees (*Boscia albitrunca*) and these species that also host sociable weavers (*Philetairus socius*) nests (bird islands of fertility; BIFs) in the Kalahari Desert to investigate the diversity in islands of fertility. We hypothesized that grasslands, the TIFs, and the BIFs differ in both the concentrations and stoichiometries of soil nutrients due to the sources of nutrients and that this subsequently determines the growth and foliar nutrient concentrations and stoichiometries of plants that grow on these soils. We predicted that seedlings grown on soils from BIFs would have greater growth, higher biomass yield, and higher foliar nutrients than those grown on soils from TIFs and grasslands. We sampled and grew camelthorn seedlings in soils from BIFs, TIFs, and matrix grasslands. Despite the higher soil nutrients in TIFs than in grasslands, there were no significant differences in seedling growth. However, we observed significantly higher seedling growth in BIF soils compared to TIF soils. Seedlings grown in soils from BIFs and grasslands allocated more growth to shoots and roots, respectively, while those grown on TIF soils were intermediate. The foliar nutrient stoichiometries of seedlings grown in BIF soils were similar to the stoichiometric ratios in BIF soils and in sociable weaver faecal matter. This shows that the faecal input of the sociable weaver accounts for the growth differences in these islands of fertility. The ecological engineering activities of the sociable weaver address nutrient limitations for camelthorn seedling growth, which TIF soils could not address despite the high faecal input of mammals.

Keywords Sociable weavers · Phytometer experiment · Foliar nutrients · Ecological stoichiometry · Ecosystem engineer

Introduction

Woody plants accumulate soil nutrients beneath their canopy via various processes, resulting in hotspots of nutrients referred to as “islands of fertility” (Schlesinger et al. 1996). Plant roots search for nutrients and transport them into the leaves of the plants, which later deposit these as leaf litter beneath the canopy enriching the soils (Schlesinger and Pilmanis 1998). Plants that shed their leaves annually (Abril et al. 2009) and those with dense canopies (Camara 2021) can deposit large quantities of nutrients below their canopies. High soil N concentrations for leguminous trees are also due to their nitrogen-fixing capacity (Schlesinger and Pilmanis 1998; Tölgyesi et al. 2020). Tree canopies also trap aeolian dust, while low-stature plants and leaf litter may trap runoff containing nutrients (Parsons et al. 1992). While islands of

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fertility may form due to the presence of trees alone, animals also contribute to the formation of islands of fertility through faecal deposition under these woody plants when they seek shade or roost (Dean et al. 1999; Prayag et al. 2020). The nutrient stoichiometry of the different sources of nutrients in the island of fertility should determine the key enhanced nutrients with potential implications for the vegetation that grows on these soils.

Ecological stoichiometry indicates ecological processes that include nutrient limitations, energy flow between trophic levels, and material cycling across different ecosystems (Elser et al. 1996). According to Liebig's law of the minimum (Marschner 2012), plant growth depends not only on nutrient availability but also on the balance between multiple nutrients. Therefore, nutrient stoichiometry determines nutrient limitations in ecosystems (Han et al. 2013; Sardans and Peñuelas 2015). The foliar nutrient stoichiometry of most plant species is somewhat plastic and influenced by the edaphic environment and several plant traits, including plant size, growth form, relative growth rate, leaf construction, and longevity (Elser et al. 2010; Peñuelas and Sardans 2009). The strong links of foliar nutrient stoichiometric variations to soil fertility have been inferred to be adaptive; hence plant foliar nutrients vary with the prevailing environmental conditions (Han et al. 2005; Elser et al. 2010). Many plant species, however, exhibit a degree of stoichiometric homeostasis through which they maintain their tissue stoichiometries relatively independently of the environment (Elser et al. 2010), resulting in nutrient concentrations and stoichiometries of plant tissues being less variable than those in the soils (Güsewell and Koerselman 2002; Neff et al. 2006). Plant nutrient stoichiometries have been reported to have stronger genotypic links than environmental links, with different taxa having evolved different nutrient stoichiometries (Neff et al. 2006; Verboom et al. 2017). It is, therefore, not clear that plant nutrient stoichiometry necessarily follows that of the soil. Investigating the extent to which the sources of nutrients (e.g., mammal and avian droppings) influence the soil and its subsequent influence on the foliar nutrient concentrations and stoichiometries of plants growing in these soils, at least within a species, may help to establish the drivers of growth responses of the plants to their edaphic environment.

Faunal nutrient input can be a significant source of soil nutrients in islands of fertility (Ellis 2005; Huang et al. 2014), resulting in localized changes in the physical and chemical properties of the soil under trees that attract animals (Schlesinger et al. 1996; Dean et al. 1999; Prayag et al. 2020). In terrestrial ecosystems, seabird faecal matter can increase available levels of N and P by 100- and 400-times, respectively (Mulder et al. 2011). The increased availability of N and P, in turn, may increase the growth of plants in this ecosystem compared to other systems (Mulder

and Keall 2001). However, high faunal nutrient input from colonial birds may not always lead to positive outcomes. For example, high guano input can result in high levels of NH_4^+ that may reach toxic levels (Kolb et al. 2010) and negatively affect the growth of mature woody plants (Dusi 1977; Haynes and Goh 1978). Since the stoichiometric composition of the animal's food, its body size, and body nutrients influence the nutrient stoichiometry (e.g., N:P ratios) in their faecal matter (Sitters and Venterink 2021; le Roux et al. 2020), mammals and birds will not have the same nutrient contributions at islands of fertility. Furthermore, the amounts of faeces/urine deposited and nutrient stoichiometry determine how plants grow in response to the faunal input (le Roux et al. 2020). The principles of eco-stoichiometry may provide a way to understand the nutrient regulation mechanism of plant-soil interaction and show the nutrient utilization strategy of different plants as influenced by their environmental factors (Tao et al. 2021). It may be expected that the nutrient stoichiometry of plants growing in islands of fertility that differ in their origins will vary based on the soil nutrient stoichiometry in these islands of fertility as influenced by the sources of faunal nutrients (e.g., mammalian or avian sources).

Sociable weavers (*Philetairus socius*) are colonial birds endemic to southern Africa that make large nests in host trees used yearly and attract numerous other animal associates (Maclean 1973; Lowney and Thomson 2021). Due to their large colonies that alter resources and ameliorate conditions in the harsh Kalahari environment, the sociable weaver acts as an ecosystem engineer (Lowney et al. 2020; Lowney and Thomson 2022). Sociable weavers defecate outside of their nests, accumulating guano under their host trees and increasing soil C, N, and P compared to grassland and tree soils (Prayag et al. 2020), which can increase biomass yield and foliar nutrients in host trees and their seedlings. Trees with and without sociable weaver nests also receive mammalian faecal input under canopies. Prayag et al. (2020) used wheat (*Triticum aestivum*) as a phytometer and found higher shoot biomass in soils influenced by the nutrient input of the sociable weaver. The nutrient concentrations and stoichiometries of the faecal inputs (of mammalian and sociable weavers) and the soil may be relevant for explaining the growth and foliar nutrient concentrations and stoichiometries of plants that grow in these soils. Documenting the effect of these islands of fertility on the growth of camelthorn (*Vachelia erioloba*) seedlings may provide insight into how the mature trees that grow in these islands of fertility benefit from the nutrient flux.

We hypothesized that the savanna grasslands, the tree islands of fertility (TIFs), and the bird islands of fertility (BIFs) differ in both the concentrations and stoichiometries of soil nutrients due to the sources of nutrients (mammalian and sociable weaver droppings) and that this subsequently

determines the growth and foliar nutrient concentrations and stoichiometries of plants that grow on these soils. We predicted seedlings grown on soils from BIFs would have greater growth, higher biomass yield, and higher foliar nutrients than TIFs. We also predicted that the nutrient stoichiometries in mammalian and sociable weaver droppings would be similar to the soils and seedling foliage from TIFs and BIFs, respectively. We tested this by sampling and analyzing mammalian and sociable weaver droppings and soil nutrients from BIFs, TIFs, and grasslands and subsequently grew camelthorn seedlings in these soils.

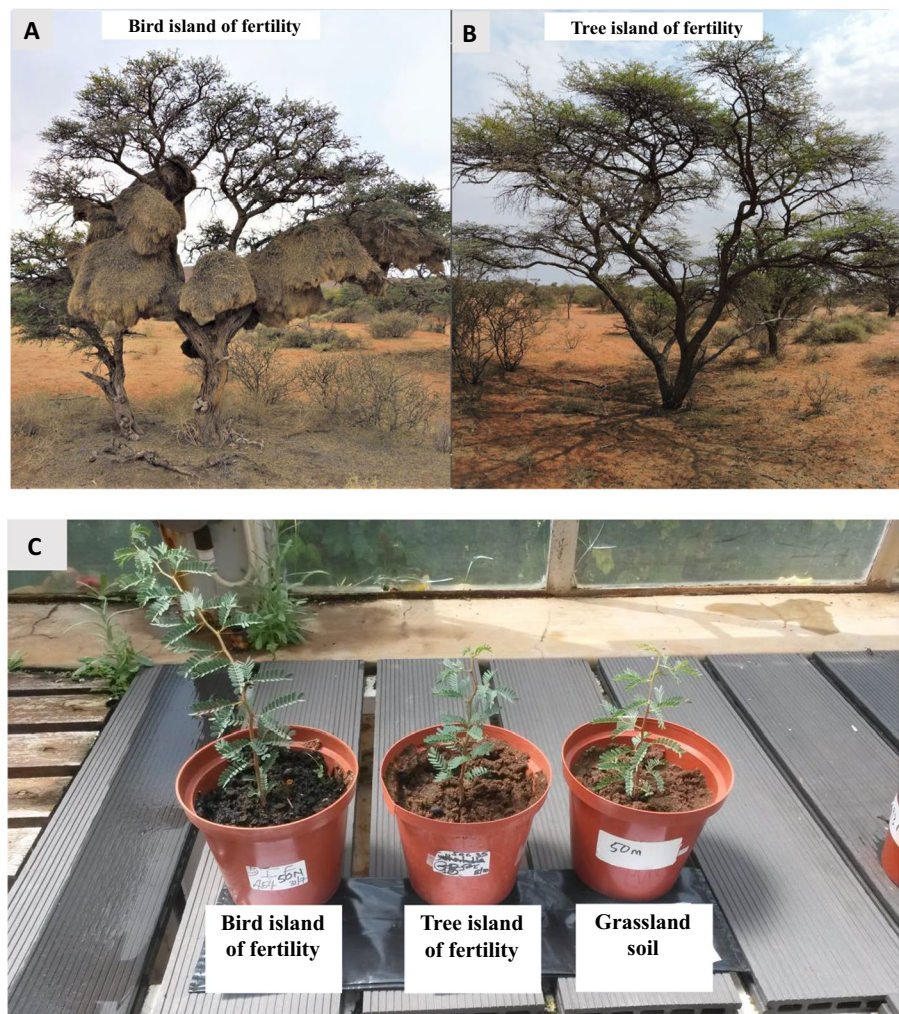
Materials and methods

Site description and experimental setup

We collected the soils and seeds used in this study from Tswalu Kalahari, a reserve in the Northern Cape Province, South Africa (27.225°S 22.478°E). The climate is typically hot and arid; the long-term annual mean temperature

is 20.3 °C, with an annual mean maximum of 29.5 °C and a minimum of 11.1 °C (Cromhout 2006). Rainfall is highly variable, occurring mainly during summer (December–March), with a mean of 325 mm per year (range 175–595 mm; Van Rooyen and Van Rooyen 2017). The soils collected for this study were within the Koranna-Langeberg Mountain Bushveld and Olifantshoek Plains Thornveld vegetation types of the study area. The soils are red Kalahari sands, with the main component of the soil classified as fine sand (Prayag et al. 2020). We obtained permission from Tswalu Kalahari Reserve to collect all samples used in this study. The sociable weavers build their nest mainly in camelthorn and shepherd trees (*Boscia albitrunca*). The camelthorn tree is a large (DBH of 42 ± 1.9 cm for nest-trees and 35 ± 1.3 cm for control trees) robust leguminous tree that is the preferred tree for sociable weavers in the Kalahari (Fig. 1A). It grows up to 5.7 m tall and begins flowering from August to September, and in February, the pods reach full size and swell in March (Barnes 2001). The shepherd tree is a non-legume tree up to 4.8 m tall. Like camelthorns, the seeds of shepherd trees are endozoochorous (Dean et al.

Fig. 1 Photos showing a camelthorn tree with a nest (bird island of fertility), a tree without a nest (tree island of fertility), and a typical example of the effect of soils from bird and tree islands of fertility and grassland sites on the growth of camelthorn seedlings



1999), but unlike the camelthorn, shepherd tree seeds are non-dormant, with a short viability period (Briers 1988) germinating quickly under other large trees that provide shade for mammals like the camelthorn (Dean et al. 1999). Since the recruitment of shepherd trees depends on large trees like the camelthorn, threats to camelthorn indirectly threaten shepherd trees (Alias & Milton 2003).

To measure the nutrient concentrations and stoichiometries of both mammalian and sociable weaver droppings, we collected fresh mammalian faecal matter under BIFs and TIFs of both tree species. We randomly selected (from the list of known nest-trees) 14 paired BIFs matched with TIFs of similar height and trunk DBH that had no nest. We removed all the old faecal matter under the canopies of these trees. After 10 d, we collected all fresh faecal matter under these trees, oven-dried it at 70 °C to constant weight, and then milled it using a ball mill (MM200, Retsch, Germany). We obtained the data on the nutrient concentrations of the sociable weaver faecal matter from Prayag et al. (2020).

To sample soils for soil nutrient analysis and the growth of camelthorn seedlings, we randomly selected 12 camelthorn and 12 shepherd trees that contained a sociable weaver nest from a list of nest-trees documented in the study area. We matched each selected nest-tree with a tree (without a nest) of a similar height and trunk diameter at breast height (DBH) to that of the paired nest-tree. We selected the paired trees without nests near nest-trees (mean 78 m; range 16 m–192 m) to control for spatial variability within the study area. We designated the midpoint between the nest-tree and the tree as the grassland site. This resulted in 72 sites (12 triplet sites; nest-tree, tree, and grassland for each species, hereafter referred to as BIFs, TIFs, and grasslands sites, respectively). We collected soil samples from these sites for nutrient analysis and to grow camelthorn seedlings in the greenhouse to investigate the seedling growth response to nutrient concentrations and stoichiometries in the islands of fertility. Soil samples (approximately 1.5 kg each) were collected directly under the nests and active chambers or from branches below that could have supported a nest in the control trees. We cleared the soil surface of the accumulated faecal matter and grass materials before taking samples using a soil auger (7 cm diameter) to a depth of 20 cm. In this study, we considered the effect of tree species because our previous study found that some soil nutrient concentrations varied depending on tree species (camelthorn vs. shepherd trees, Aikins et al. 2023).

We sieved the soils through a 1 mm sieve and then coned and quartered (Gerlach et al. 2002) to sub-sample the soils for the various tests. The dry sub-sampled soils from each sampling point were milled to a fine powder using a mortar and pestle. We determined soil pH by adding 25 ml 1 M KCl solution to 10 g air-dried soil, shaking for 20 min using an orbital shaker at 20 rpm, and after settling for 1 h, we

measured the pH. We separated the dried shoot biomass into leaves and stems. The leaves were crushed in a mortar and pestle and milled to powder using a ball mill (MM200, Retsch, Germany).

We conducted a growth experiment to determine how camelthorn seedlings perform under these soils as influenced by mammalian and sociable weaver faeces. We collected seeds from a single camelthorn tree without a nest (to limit genetic variability). One hundred seeds were scarified using sandpaper and soaked in water for 24 h before being transferred to a Petri dish in a phytotron for germination. After germination, we randomly assigned the seedlings to 72 individual pots filled with each of the 72 soil samples at a depth of 2 cm (Supplementary Fig. 1). The seedlings grew in a greenhouse at the University of Cape Town with a temperature of 25 °C. Seedlings were watered twice daily (7 am and 2 pm) for 3 min using an automatic overhead water irrigation system. We regularly changed each pot's position in the greenhouse to create uniform conditions for all plants. We immediately removed all weeds from the pots as they germinated during the experiment. We measured the initial growth parameters of each seedling 2 weeks after planting. Plant height, stem diameter, and the number of leaves were then measured once a week, every week until the 10th week, after which we harvested the plants. Roots were washed free of soil, and the number of nodules was counted. We separated the harvested plants into the shoot and root biomass and oven-dried at 70 °C for 48 h, and we weighed the dry samples to obtain their biomass.

Analysis of soil, faecal matter, and camelthorn seedling leaves

We placed the milled soil, faecal matter, and leaf samples in XRF sample cups sealed with a 4 µm Polypropylene thin film (Chemplex Industries Inc, Florida, USA) at the bottom and inserted into an Energy Dispersive benchtop X-Ray Fluorescence (ED-XRF) Spectro Xepos spectrometer (Spectro, Amatek materials analysis division, Kleve, Germany). We controlled the analysis using Spectro X-Lab Pro computer data acquisition system, which incorporates the TurboQuant software for automatic matrix effect correction. We calibrated the instrument using a certified standard GBW07312 (National Research Center for Certified Reference Materials, Beijing, China), for which elemental concentrations were obtained from the NOAA Technical Memorandum NOS ORCA 68 (1992). The focus elements for this study were P, K, Ca, and Zn, as these minerals were in higher proportions in the faecal matter of the sociable weaver and the soils under the selected trees. However, we also considered other essential elements. XRF measures total P, which according to Vona et al. (2022), detects a higher concentration of P than other methods of detecting the concentration of P,

such as ammonium lactate extraction, Mehlich 3 extraction, water extraction, and cobalt hexamine extraction. Therefore, we performed a regression analysis between soil XRF total P and citric acid extracted P for the same samples (data obtained from Prayag et al. 2020) to determine the relationship between the two measures of soil P. We used the equation of the line ($\text{Soil P}_{\text{XRF}} = 7.0991_{\text{citric acid extracted P}} + 0.0541$, $R^2 = 0.776$) to estimate the equivalent citric acid P of the soil from our XRF soil P values.

We used a mass spectrometer to analyze C, N, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$. We weighed the oven-dried and milled leaves of the camelthorn seedlings (ca. 2 mg), the mammalian faecal matter (ca. 2 mg), and the powdered soils (ca. 40 mg) into tin capsules (Elemental Microanalysis Ltd, Devon, UK). These were combusted in a Flash 2000 organic elemental analyzer (Thermo Scientific, Bremen, Germany), and the gases were passed to a Delta V Plus isotope ratio mass spectrometer (IRMS) via a ConFlo IV gas control unit (Thermo Scientific, Bremen, Germany). We calibrated the results using two in-house standards and one IAEA standard. We obtained the data on the faecal nutrients of the sociable weaver from Prayag et al. (2020).

Data analysis

We performed all statistical analyses with R (version 4.0.3). Using a linear model, we explored the characteristics of the faecal nutrients between sources (sociable weaver, mammals under nest-trees, mammals under trees). The faecal nutrient values were log-transformed before analysis. We tested the residuals of the models of the response variables (growth parameter, biomass, and foliar nutrients) for normality, and all were normally distributed. To address the issue of heteroscedasticity, we used the appropriate variance functions; model = lme ($Y \sim X$, random = ~ 1|S, data = df, weights = varIdent(form = ~ 1|X), method = "REML"). We ran linear-mixed effects models using the nlme package to test our response variables: soil nutrients, growth parameters (height, number of leaves, stem diameter, and shoot root, and total biomass), and foliar nutrients, relative to explanatory variables: sites (3 levels: BIFs, TIFs, and grasslands) and species (2 levels: camelthorn and shepherd) with random effect of the triplet identity (unique identification number for each collection site; BIFs, TIFs, and grasslands). We tested the interactions between sites and tree species. The interaction term determines whether the nest impacts the two species of trees differently. The interaction term was removed in all models if they did not explain significant variation ($p > 0.05$).

We used the Anova function in the car package to test whether the model terms explain a significant proportion of the variation in our response variables. We then performed post-hoc pairwise comparisons (Tukey's post-hoc test, using

emmeans package, version 1.3.2; Lenth 2019) to test differences between the BIFs, TIFs and grasslands when the main effect was significant. The p values in the multiple pairwise comparisons were adjusted using the Tukey method. We calculated the average concentrations of mammalian faecal nutrients from the nutrient content per species.

We fitted a generalized additive model (GAM) using the mgcv package (Wood 2017) to seedling growth parameters to compare growth over weeks ($k = 9$) grouped by sites. We represented the GAM smooth term using penalized regression splines with smoothing parameters selected by REML. We used the negative binomial distribution in our model with 95% confidence bands. To test for factors that significantly predict the total biomass of the camelthorn seedlings, we used multiple linear regression analysis followed by a forward and backward stepwise simplification using the stepAIC function (MASS package; Venables and Ripley 2002). We used soil properties (pH, N, P, K, and Ca) as response variables (predictors) and used total biomass as our explanatory variables.

Results

Soil and faecal matter nutrient concentration and stoichiometries

Soil pH was significantly higher in the soil associated with both tree species with nests (BIFs) than grassland soils. For both tree species, the soil pH of the BIFs and TIFs did not differ (Table 1). BIFs had significantly higher soil C, N, $\delta^{15}\text{N}$, P, K, and Ca for both tree species than TIFs and grassland sites. Grassland soils had higher soil $\delta^{13}\text{C}$ than BIF and TIF soils, but soil $\delta^{13}\text{C}$ did not vary between BIFs and TIFs. The TIF soils of both tree species had higher C, N, and P than the grassland soils. There were, however, lower soil C:N, K:P, and Zn:P under BIFs than under TIFs and grasslands, but N:P was higher under TIFs than under grasslands (Table 2). There was a higher N concentration in the sociable weaver's than in the mammal faecal matter (Supplementary Table 1). There were also higher levels of P, K, and Zn in the faecal matter of the sociable weaver than in the faecal matter of the mammals under TIFs. Also, due to the differences in mammal species that frequent the nest-trees and trees without nests, we found higher levels of P, K, and Zn in the faecal matter of mammals under the BIFs than TIFs. C:N and Ca:P ratios were higher in mammalian faecal matter from both BIFs and TIFs than in the sociable weaver faecal matter (Table 2). The mammal faecal C:N and Ca:P ratios were 3.2- and 5.7 times higher than the sociable weaver, respectively. N:P, K:P, and Zn:P ratios did not vary between faunal nutrient sources.

Table 1 Properties of soils used for the growth of seedlings in the greenhouse that came from sites related to camelthorn and shepherd trees

Soil sources	Soil properties (mean $\pm$ SE)								
	Soil pH	C (%)	$\delta^{13}\text{C}$ (‰)	N (%)	$\delta^{15}\text{N}$ (‰)	P (%)	Citric acid P (mg/kg)	K (%)	Ca (%)
Camelthorn tree									
Bird Islands of fertility	5.63 $\pm$ 0.22 ^b	1.95 $\pm$ 0.28 ^c	− 20.42 $\pm$ 0.18 ^a	0.29 $\pm$ 0.04 ^c	17.76 $\pm$ 0.75 ^c	0.41 $\pm$ 0.08 ^d	500 $\pm$ 110 ^d	1.23 $\pm$ 0.05 ^{bc}	0.30 $\pm$ 0.05 ^{bc}
Tree Islands of fertility	4.90 $\pm$ 0.18 ^{ab}	0.47 $\pm$ 0.05 ^b	− 21.37 $\pm$ 0.37 ^a	0.05 $\pm$ 0.01 ^b	13.04 $\pm$ 0.41 ^b	0.08 $\pm$ 0.01 ^{bc}	40 $\pm$ 10 ^{bc}	1.11 $\pm$ 0.05 ^{ab}	0.14 $\pm$ 0.02 ^a
Grassland	4.71 $\pm$ 0.13 ^a	0.25 $\pm$ 0.03 ^a	− 18.87 $\pm$ 0.39 ^b	0.03 $\pm$ 0.003 ^a	12.66 $\pm$ 0.44 ^b	0.07 $\pm$ 0.01 ^a	20 $\pm$ 10 ^a	1.10 $\pm$ 0.04 ^a	0.06 $\pm$ 0.01 ^a
Shepherd tree									
Bird Islands of fertility	5.66 $\pm$ 0.23 ^b	1.20 $\pm$ 0.17 ^c	− 20.91 $\pm$ 0.31 ^a	0.18 $\pm$ 0.03 ^c	16.74 $\pm$ 0.77 ^c	0.43 $\pm$ 0.04 ^d	530 $\pm$ 50 ^d	1.30 $\pm$ 0.05 ^{bd}	0.35 $\pm$ 0.05 ^c
Tree Islands of fertility	5.39 $\pm$ 0.15 ^b	0.42 $\pm$ 0.03 ^b	− 21.46 $\pm$ 0.24 ^a	0.05 $\pm$ 0.003 ^b	12.83 $\pm$ 0.42 ^b	0.09 $\pm$ 0.01 ^c	60 $\pm$ 10 ^c	1.18 $\pm$ 0.04 ^{ac}	0.16 $\pm$ 0.04 ^{ab}
Grassland	4.44 $\pm$ 0.07 ^a	0.18 $\pm$ 0.02 ^a	− 18.32 $\pm$ 0.22 ^b	0.02 $\pm$ 0.003 ^a	9.96 $\pm$ 0.35 ^a	0.07 $\pm$ 0.003 ^{ab}	30 $\pm$ 10 ^{ab}	1.13 $\pm$ 0.04 ^{ac}	0.12 $\pm$ 0.04 ^a

The mean and standard error (SE) of the soil pH, C, $\delta^{13}\text{C}$, N, $\delta^{15}\text{N}$, P, K, and Ca are provided ($n = 12$). Different letters on mean values in the same column across species and sites indicate significant differences ($p < 0.05$) as determined by Tukey's post-hoc pairwise comparisons of the different levels within the explanatory terms of the LMM

Table 2 Soil nutrient stoichiometry (w/w) of soils from BIF, TIF, and grassland sites

Soil sources	Nutrient stoichiometry (mean $\pm$ SE)				
	C:N ratio	N:P ratio	K:P ratio	Ca:P ratio	Zn:P ratio
Bird islands of fertility ($n = 24$)	6.5 $\pm$ 0.24 ^a	0.86 $\pm$ 0.21 ^{ab}	3.9 $\pm$ 0.5 ^a	0.82 $\pm$ 0.07 ^a	0.012 $\pm$ 0.001 ^a
Tree islands of fertility ($n = 24$)	8.4 $\pm$ 0.19 ^b	0.67 $\pm$ 0.06 ^b	13.8 $\pm$ 0.64 ^b	1.57 $\pm$ 0.15 ^b	0.021 $\pm$ 0.002 ^b
Grassland ($n = 24$)	7.9 $\pm$ 0.37 ^b	0.42 $\pm$ 0.04 ^a	17.0 $\pm$ 0.7 ^c	1.51 $\pm$ 0.44 ^{ab}	0.029 $\pm$ 0.005 ^b
Faunal nutrient sources					
Sociable weaver	7.05 $\pm$ 0.53 ^a	5.89 $\pm$ 1.04 ^a	1.34 $\pm$ 0.04 ^a	1.22 $\pm$ 0.13 ^a	0.025 $\pm$ 0.003 ^a
Mammals (BIFs)	23.32 $\pm$ 2.98 ^b	4.42 $\pm$ 0.71 ^a	2.24 $\pm$ 0.45 ^a	7.80 $\pm$ 1.53 ^b	0.024 $\pm$ 0.004 ^a
Mammals (TIFs)	21.51 $\pm$ 1.98 ^b	10.29 $\pm$ 2.28 ^a	1.65 $\pm$ 0.36 ^a	6.09 $\pm$ 0.93 ^b	0.028 $\pm$ 0.004 ^a

Nutrient stoichiometry of sociable weavers and mammalian faecal matter are also given (sociable weaver data were obtained from Prayag et al. 2020). The mean $\pm$ SE is reported for each soil and faecal nutrient source and the nutrient stoichiometries. The means of soil ratios with the same letters in columns did not significantly differ

Bird and tree islands of fertility effects on the growth of camelthorn seedlings

There was a slight variation in size (29.0 ± 0.11 mm, mean $\pm$ SE) and mass (0.30 ± 0.01 g) of camelthorn seeds used for this study (Supplementary Table 2; seed germination rate was 79%). There was generally poor nodulation in the roots of all the seedlings in this experiment; only two out of the 72 camelthorn seedlings formed root nodules (a seedling grown in soil from a TIF formed seven nodules, while a seedling grown in grassland soil formed 11). None

of the seedlings grown in the soils from BIFs formed root nodules.

The identity of the tree species (camelthorn vs. shepherd) associated with the source soils for the study did not explain significant differences in the height of camelthorn seedlings, the number of leaves, stem diameter, shoot biomass, root biomass, root-to-shoot ratio, and total biomass (Supplementary Table 3). The site term (BIFs, TIFs, and grasslands) explained significant variation in the height of the camelthorn seedlings and the number of leaves but not the stem diameters (Fig. 1C; Table 3; Supplementary

Table 3 Linear mixed model analysis of growth and biomass parameters of camelthorn seedlings grown in soils from BIFs, TIFs, and grassland sites

Response variables	BIFs	TIFs	Grassland	χ^2	<i>p</i> value
Height (mm)	191 ± 11.7 ^b	141 ± 11.2 ^a	139 ± 7.2 ^a	18.22	< 0.001
Number of leaves (#)	40 ± 2.4 ^b	30 ± 1.6 ^a	28.5 ± 1.6 ^a	18.98	< 0.001
Stem diameter (mm)	3.30 ± 0.12 ^a	3.13 ± 0.11 ^a	2.99 ± 0.08 ^a	4.62	0.099
Shoot biomass (g)	1.29 ± 0.11 ^b	0.83 ± 0.07 ^a	0.77 ± 0.05 ^a	18.05	< 0.001
Root biomass (g)	0.68 ± 0.08 ^a	0.52 ± 0.05 ^a	0.51 ± 0.05 ^a	3.89	0.143
Root-to-shoot ratio	0.50 ± 0.04 ^a	0.63 ± 0.05 ^{ab}	0.66 ± 0.05 ^b	9.30	0.010
Total biomass (g)	1.97 ± 0.18 ^b	1.35 ± 0.11 ^a	1.28 ± 0.09 ^a	12.36	0.002

The mean ± SE is reported for each soil source and the growth and biomass parameters. Wald Chi-square values (χ^2) and *p* values are provided for each analysis. Means with the same letters in rows did not differ significantly

Table 3). There was also a significantly greater mean seedling height (1.4 times) and the number of leaves (1.4 times) in soils from BIFs than in TIFs and grasslands sites. The interaction between the tree species and sites did not explain significant variation in our growth response variables. Time-course analysis of seedling growth showed that ‘site’ significantly influenced the weekly growth in height ($\chi^2 = 48.46$, $p < 0.001$) and number of leaves ($\chi^2 = 83.31$, $p < 0.001$; Fig. 2A, B). Seedlings grown in soils from BIFs were taller and had more leaves than in TIF and grassland soils. The stem diameter, however, did not vary between sites (Fig. 2C).

Seedling shoot biomass and total biomass varied significantly with ‘site’ (Table 3, Supplementary Table 3). There were significantly higher mean shoot biomass and total biomass of plants grown on BIF soils than TIF and grassland soils. Still, there were no significant differences in the mean shoot biomass between the TIFs and grassland soils. The mean shoot biomass of seedlings grown in BIF soils was about 1.6 times higher than those grown in soils from TIF and 1.7 times higher than those grown in the grassland soils. The mean total biomass of seedlings grown in soils from BIFs was approximately 1.5 times higher than the TIFs soils and 1.5 times higher than the grassland soils. Seedling root biomass did not vary significantly with the site, but the root-to-shoot ratio varied significantly with the site. Camelthorn seedlings grown in grassland and TIF soils increased biomass partitioning to the roots. There was a significantly higher root-to-shoot ratio in seedlings grown in grassland soils than in BIFs, but there was no significant difference between grassland soils and TIF soils. Furthermore, there were no significant differences in the root-to-shoot ratio in seedlings grown in soils from TIFs and BIFs (Table 3). The mean root-to-shoot biomass in seedlings grown in soils from grasslands was approximately 1.3 times higher compared to the seedlings grown in soils from the BIFs.

The results also show that 25% of the variance in total seedling biomass can be explained by two predictors (i.e., soil N/P and K; $F_{(2, 69)} = 11.33$, $p < 0.001$). We found Soil

N and P to be collinear; hence our fitted regression model was: Total biomass = $0.03 + 2.28 * (\text{soil N/P}) + 1.07 * (\text{soil K})$. Soil N/P ($\beta = 2.28$, $p < 0.001$) and K ($\beta = 1.07$, $p = 0.021$) significantly predicted total biomass. Soil N and P was the most important soil property that predicted total biomass.

Bird and tree islands of fertility affect the foliar nutrients of camelthorn seedlings

The foliar N and $\delta^{15}\text{N}$ were significantly higher in the plants grown on soils from BIFs compared to TIFs and grasslands (Table 4, Supplementary Table 4). There was a significant difference in $\delta^{15}\text{N}$ between the seedlings grown in TIF and grassland soils, but there was no significant difference in foliar N between BIF and grassland seedlings. There were also significant differences in foliar P between sites, but foliar K, Ca, and Zn did not vary (Table 4, Supplementary Table 4). There was significantly higher foliar P (1.8-times) in seedlings grown in BIFs compared to the grassland soils but not different from the TIFs soils (Table 4). The foliar nutrients of the camelthorn seedlings did not vary between the tree species that were associated with the soils collected for the experiment (Supplementary Table 4). There were also no significant interactions between the tree species and the sites.

The seedling foliar nutrient stoichiometry differed between sites for C:N, K:P, Ca:P, and Zn:P, but not for N:P ratios. Foliar C:N and Ca:P ratios decreased in the order of grassland = TIFs > BIFs (Table 5). Seedling foliar K:P and Zn:P ratios were higher in seedlings grown in grassland soils than in TIFs and BIFs. K:P was also higher in TIFs seedlings than BIFs seedlings, but there was no difference between BIFs and TIFs for Zn:P ratios. There was, however, a significant positive correlation between foliar N and P concentrations of seedlings grown in the soil from BIFs ($y = 2.37 + 1.38x$, $p = 0.008$, $R^2 = 0.28$) but not for TIFs ($p = 0.071$, $R^2 = 0.14$) and grassland ($p = 0.110$, $R^2 = 0.11$) soils.

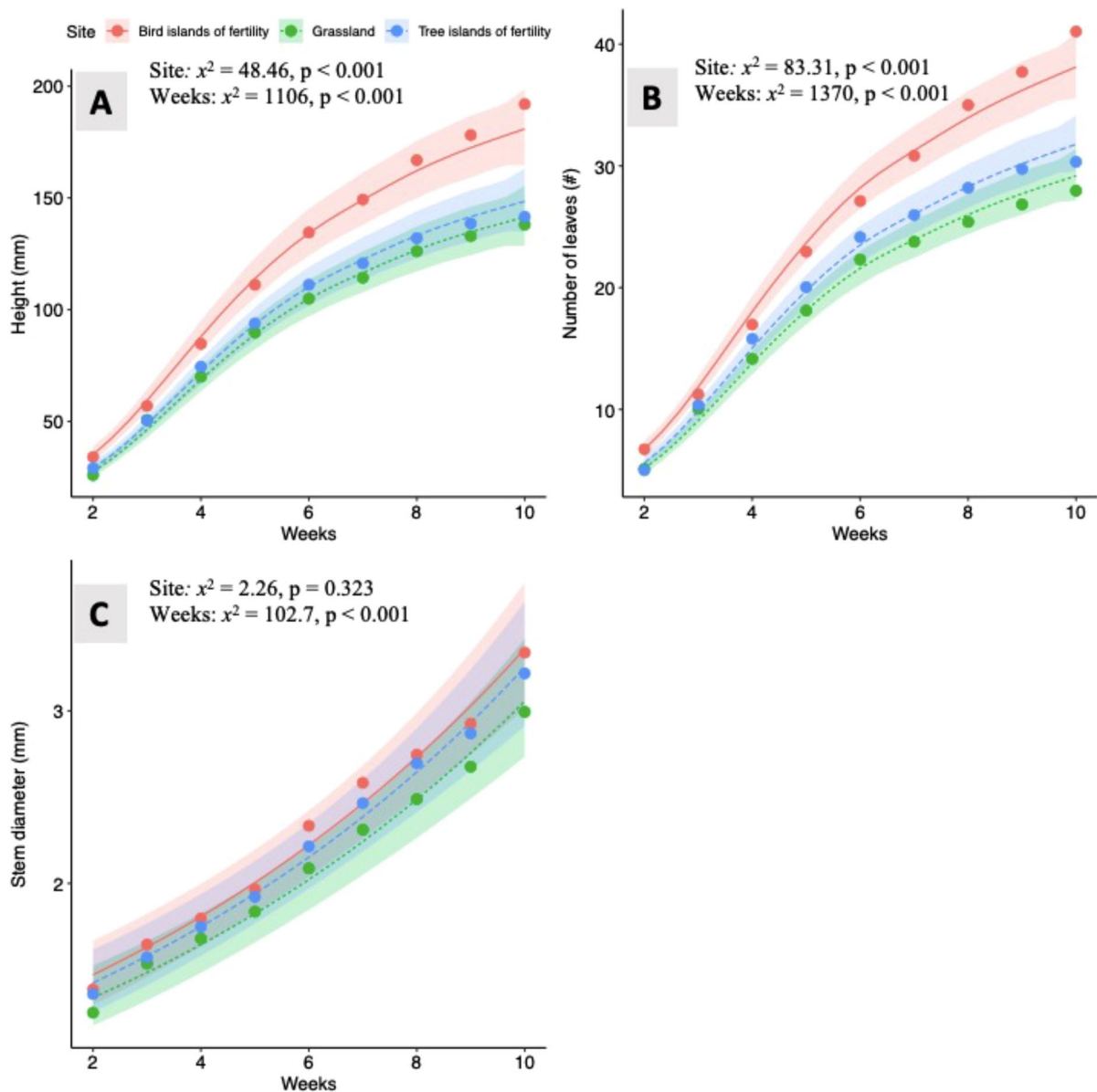


Fig. 2 Time-course analysis of the height (A), number of leaves (B), and stem diameter (C) of camelthorn seedlings grown in soils from the BIF, tree islands of fertility, and grasslands. The bands represent

the 95% confidence bands fitted with a generalized additive model (GAM) using a negative binomial distribution

Which nutrients drive the seedling growth in bird islands of fertility?

The foliar N, P, and Mg of the seedlings grown on BIF soils were higher than those found in mature camelthorn tree leaves (Supplementary Table 5) and other *Vachellia* species (Supplementary Table 6). Similarly, we found that the soil N, P, K, and Ca in the BIFs were significantly higher than in the TIFs and the grassland soils (Table 1). Since only N and P were higher in seedling foliage and soil, soil N and P could be the nutrients that drive increased seedling growth in BIF soils.

Discussion

The presence of the sociable weaver nest increased the growth of camelthorn seedlings grown on soils from those sites more than that in soils from below trees without nests. The greater height, number of leaves, and shoot biomass of seedlings grown in the BIF soils could be due to the soil nutrients derived from the faunal nutrient input of the sociable weaver. Although both the BIFs and the TIFs receive input of faunal nutrients, the differences in growth between the two are probably due to a combination of the amount/availability of faecal matter deposited and the nutrient

Table 4 Linear mixed model analysis of foliar nutrients and isotopes of camelthorn seedlings grown in soils from BIFs, TIFs, and grassland sites

Response variables	BIFs	TIFs	Grassland	χ^2	<i>p</i> value
Foliar N (%)	3.05 ± 0.16 ^b	2.33 ± 0.09 ^a	2.19 ± 0.07 ^a	25.96	< 0.001
Foliar $\delta^{15}\text{N}$ (‰)	13.53 ± 0.67 ^c	9.25 ± 0.47 ^b	7.76 ± 0.35 ^a	74.94	< 0.001
Foliar $\delta^{13}\text{C}$ (‰)	− 28.9 ± 0.16 ^a	− 29.1 ± 0.16 ^a	− 28.8 ± 0.13 ^a	2.19	0.334
Foliar P (%)	0.46 ± 0.05 ^b	0.38 ± 0.05 ^{ab}	0.28 ± 0.05 ^a	8.75	0.013
Foliar K (%)	2.11 ± 0.19 ^a	2.35 ± 0.19 ^a	2.22 ± 0.19 ^a	0.95	0.623
Foliar Ca (%)	2.07 ± 0.16 ^a	2.43 ± 0.25 ^a	1.92 ± 0.08 ^a	4.81	0.090
Foliar Zn (%)	0.0055 ± 0.0005 ^a	0.0045 ± 0.0005 ^a	0.0046 ± 0.0005 ^a	2.62	0.269

The mean ± SE is reported for each soil source and the foliar nutrients. Wald Chi-square values (χ^2) and *p* values are provided for each analysis. Means with the same letters in rows did not differ significantly

Table 5 Foliar nutrient stoichiometry (w/w) of camelthorn seedlings grown in soils from BIFs, tree islands of fertility, and grassland sites

Soil sources	Foliar nutrients stoichiometry of camelthorn seedlings (mean ± SE)				
	C:N ratio	N:P ratio	K:P ratio	Ca:P ratio	Zn:P ratio
Bird islands of fertility (<i>n</i> = 24)	16.5 ± 0.89 ^a	7.37 ± 0.43 ^a	5.06 ± 0.36 ^a	4.91 ± 0.42 ^a	0.012 ± 0.001 ^a
Tree islands of fertility (<i>n</i> = 24)	20.8 ± 0.80 ^b	8.24 ± 0.74 ^a	7.19 ± 0.49 ^b	8.22 ± 0.55 ^b	0.013 ± 0.001 ^a
Grassland (<i>n</i> = 24)	21.7 ± 0.61 ^b	9.02 ± 0.55 ^a	8.69 ± 0.47 ^c	8.33 ± 0.51 ^b	0.018 ± 0.001 ^b

The mean ± SE is reported for each soil source and the nutrient stoichiometries. Means with the same letters in columns did not differ significantly

stoichiometry in the faecal matter. This also suggests that the faunal input from the sociable weaver nests did not make the soils toxic and thus toxicity does not explain the fact that the soil below the nests is commonly barren (Prayag et al. 2020). The higher root biomass relative to shoot biomass at grassland sites than at BIFs could be explained by the fact that plants in these low soil nutrient conditions (characteristic of these grassland soils) develop roots that enhance their ability to forage for more nutrients to facilitate growth (e.g., Kang and Van Iersel 2004; Kołodziejek 2019). We attribute the infrequent nodulation to the lack of competition between camelthorn seedlings and other plants in the pots (e.g., Cramer et al. 2007) since we immediately removed all other plants as soon as they germinated.

The higher concentrations of N in the foliar tissue of seedlings grown on BIF soils relative to TIF and grassland soils are a positive response to high concentrations of soil N from BIFs derived from the sociable weaver faeces. Indeed, the sociable weaver faeces had *ca.* 1.9–2.3 times more N than mammalian faeces (Supplementary Table 1). The elevated $\delta^{15}\text{N}$ values in the leaves of seedlings grown on the BIFs compared to seedlings grown on the TIFs and the grassland sites suggest assimilation of faunal-derived N since the $\delta^{15}\text{N}$ in the BIF soils also had high $\delta^{15}\text{N}$ values (Table 1; Prayag et al. 2020; Aikins et al. 2023). This enrichment of soil $\delta^{15}\text{N}$ in BIFs relative to TIFs and grassland soils occurred despite sociable weaver and mammalian faeces having similar $\delta^{15}\text{N}$ values, indicating that the mammalian faeces did not contribute strongly to either the soil or foliar $\delta^{15}\text{N}$ in TIFs or

BIFs. The availability of N from mammalian faeces is thus questionable.

Elevated foliar P of the seedlings grown in soils of BIFs relative to grasslands was consistent with the differences in soil P between BIFs and grasslands. This together with the intermediate concentration of foliar P in seedlings grown on TIF soils suggests that sociable weaver faeces also contribute P. The high soil P determined by XRF analysis in soils from this study compared to other savanna soils in Africa (Table 1; Supplementary Table 7), is due to the XRF measuring total P. The calculated citric acid extractable P levels in grassland and TIF soils (Table 1) were, however, low relative to that of the BIFs in the aeolian sand at our study site. The P derived from sociable weaver faeces together with some contribution from mammalian faeces thus likely contributed to increased seedling growth on soil BIFs.

The similar growth and foliar nutrient concentration between TIFs and grasslands, despite some differences in these soils, could be attributed to the fact that the concentration of nutrients in the soils of TIFs did not address the real limitations that the seedlings had, while the BIF soils did. This was unexpected because we found an accumulation of mammalian faecal matter under the TIFs, and therefore expected it to influence the growth of the seedlings. Furthermore, the mammalian faecal matter had substantial concentrations of nutrients that could increase the growth of seedlings in soils from TIFs. The lack of difference in the growth between the TIFs and grassland seedlings could mean that nutrients in this faecal matter were not available in soils. Indeed, the faecal matter

under these trees is dry and hard (field observation) in this relatively arid environment, and consequently may not readily decompose or be washed into the soil to supply nutrients. Additionally, according to Brust (2019), the C:N ratio of the organic substrate between 1 and 15 has rapid mineralization and release of N for the uptake of plants. However, a ratio of 20 to 30 results in an equilibrium state between mineralization and immobilization (Brust 2019). The C:N ratios of the mammalian faecal matter under TIFs and BIFs were 22 and 25, respectively, compared to 7.1 in the sociable weaver faecal matter. This implies that N in the faecal matter of the sociable weaver would be more readily released in BIF soils than N in the faecal matter of mammals in soils from TIFs and BIFs. Sociable weaver faecal matter is thus the primary source of nutrients under the BIFs and drives the growth of the seedlings as this N is readily mineralized and released, while N in the mammalian faecal matter under TIFs and BIFs may not be. A source of N that is unaccounted for in this analysis is mammalian urine which we were unable to analyse, although if this was co-deposited with the faecal material it also did not result in a distinct N concentration of $\delta^{15}\text{N}$ in TIF relative to grassland soils.

Foliar concentrations of individual nutrients are difficult to interpret since the concentration depends on both the availability in the soil and the demand for growth, where the demand may be determined by other nutrient limitations or non-nutrient limitations (e.g. water availability, root access, nutrient allocation). For example, the accumulation of P in the leaves of seedlings grown on BIF soils could result from “luxury” uptake (Wookey et al. 1995). The lack of differences between BIF, TIF and grassland soil grown seedlings in foliar N:P indicates, however, that these two elements were in balance. Lower values of foliar K:P and Ca:P in BIF than in TIF or grassland soil grown seedlings is consistent with the soil ratios of these elements. This means, firstly, that camelthorn seedlings do not exhibit strong stoichiometric homeostasis for K and Ca, but rather their tissue nutrient stoichiometries partially depend on soil nutrient stoichiometries (e.g., Han et al. 2005; Elser et al. 2010). Secondly, the elevated availability of N and P from sociable weaver faeces is not matched by elevated K and Ca, possibly resulting in these elements limiting further responsiveness of seedling growth to the input of sociable weaver faeces. For example, Le Roux et al. (2020) have highlighted the importance of nutrient stoichiometry in mammalian faecal matter for plant growth. The lack of differences in foliar K, Ca, and Zn between sites, despite higher levels of these nutrients in the soils of BIFs, may be due to the higher soil P and N in these soils, enabling growth dilution of K, Ca, and Zn.

Conclusion

We found that savanna islands of fertility differ in constituents and support for plant growth. We also found that sociable weavers as ecological engineers bring resources together under trees in these nutrient-poor arid sandy soils that ameliorate nutrient limitations for camelthorn seedling growth that soils from TIFs could not address despite the high mammalian faecal input. N and P in BIFs derived from sociable weavers are the main nutrients that apparently drive the growth of seedlings. Our findings thus provide empirical evidence for colonial birds enhancing the growth of host tree seedlings and, by implication, possibly mature trees, in this savanna ecosystem.

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Data availability Data are available from: Aikins Khan, Timothy (2023). All savanna islands of fertility are not equal: colonial birds influence soil nutrient stoichiometries with consequences for tree seedling growth. University of Cape Town. Dataset. <https://doi.org/10.25375/uct.23261621.v1>.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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