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The potential of the marula tree, *Sclerocarya birrea*, (A. Rich.) Horchst subspecies litterfall in enhancing soil fertility and carbon storage in drylands

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The potential of *Sclerocarya birrea* subspecies as native trees to improve agricultural productivity and combat global warming through carbon storage has not been fully explored, despite their extensive distribution across global drylands. The objective of this study was to determine the potential of litterfall from *Sclerocarya birrea* subspecies to improve soil organic carbon (OC) and fertility, and carbon storage in drylands. Leaf and fruit litterfall samples, comprising 18 samples for each subspecies, from nine trees of subspecies *birrea*, *caffra*, and *multifoliata* were collected in Tanzania. Soil samples were collected under and away from the canopies of the selected trees. The soil pH and the concentrations of organic carbon (OC) and nutrients (total Nitrogen - TN, P, K, Ca, Mg, Na, Cu, Zn, Fe, Mn, S) in the soil, fruit and leaf litterfall were determined using standard laboratory methods of analysis. The results showed that leaf OC in *S. birrea* subspecies ranged from 41.16% to 43.49%, and TN from 1.01% to 1.19%. The C:N ratio ranged from 34.58% to 41.66% in leaf, and from 52.73% to 75.12% in fruit litterfall. Phosphorus was significantly higher in fruit (0.17-0.20%) than in leaf (0.02-0.04%) for all subspecies. Ca and Mg were higher in leaf litterfall (0.54-0.89% Ca and 0.19-0.27% Mg), than in fruit litterfall (0.08-0.11% Ca and 0.10% Mg). Cu, Fe, and Mn concentrations were significantly higher in fruit, ranging from 11.71 to 31.42 mg kg^{-1}, 214.13 to 400.59 mg kg^{-1}, and 31.42 to 54.77 mg kg^{-1}, respectively, than in leaf with 3.32 to 4.39 mg kg^{-1}, 64.10 to 107.70 mg kg^{-1}, and 16.08 to 18.97 mg kg^{-1}, respectively. Contrastingly, Zn in leaf ranged from 412.97 in *multifoliata* to 499.78 mg kg^{-1} in *caffra*, which was 33 to 46 times higher than in fruit litterfall. Soils under the canopies of subsp. *birrea*, *caffra*, and *multifoliata* had significantly higher OC and K, Na, and S (p < 0.05), and numerically higher concentrations of most nutrients than soils away from the canopies. We concluded that leaf and fruit litterfall of the *Sclerocarya birrea* subspecies can improve soil fertility and carbon storage in drylands if managed properly.

Keywords: Climate Change, C:N Ratio, Carbon Sequestration, Food Security, Agroforestry, Litterfall Quality, Soil Amendment

Introduction

Innovative agroforestry systems to conserve native trees, improve crop yields, and achieve food security are critical for climate change resilience in African dryland farming systems. Sub-Saharan Africa (SSA) harbors approximately 13.9 million km^2 of drylands that support the livelihoods of more than 425 million people (Cervigni & Morris 2016). About 70 percent of the SSA dryland is used for agriculture, of which 66 percent is for cereal production (Cervigni & Morris 2016). However, the nexus of food insecurity, extreme poverty, and environmental degradation, coupled with low use of inorganic fertilizers, is the most challenging in the drylands of African countries (Jama et al. 2008). Agricultural soils in drylands are characterized by low fertility due to low nitrogen and phosphorus levels, low water-holding capacity, low organic matter content (Thomas et al. 2006), and highly variable soil fertility (Nyamangara et al. 2020). Thus, there is a need to find ways to improve soil fertility through agroforestry nutrient cycling using appropriate native tree species to complement fertilizer applications and simultaneously improve land productivity and sustain crop production.

Native trees are acknowledged as an important component of sustainable agriculture (Rode et al. 2023). Native trees have the potential to increase agricultural production by recycling nutrients through lit-

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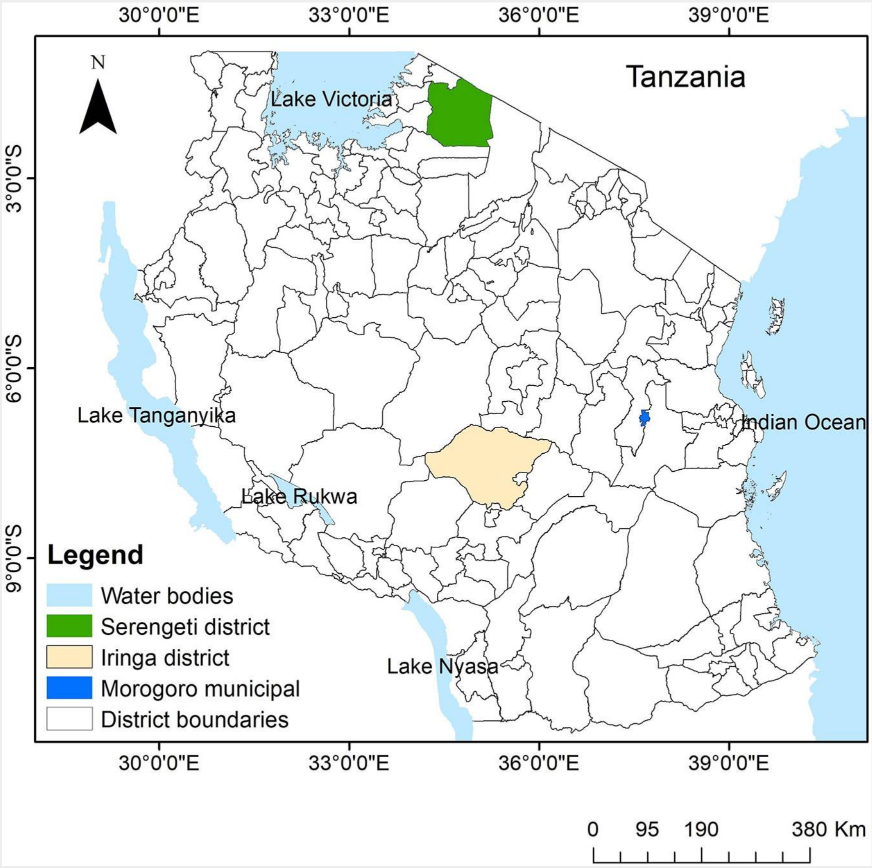

Fig. 1 - Map showing the locations of the Serengeti district, Morogoro municipal, and Iringa district, where leaf and fruit litterfall samples of *Sclerocarya birrea* subsp. *birrea, S. birrea subsp. caffra,* and *S. birrea* subsp. *multifoliata* were collected, respectively.

terfall, producing more annual litterfall with higher nutritional quality than exotic species (Valente et al. 2023). Native trees also support ecosystem connectivity, biodiversity conservation, and carbon sequestration (Somarriba et al. 2017).

Marula tree, *Sclerocarya birrea* (A. Rich.) Horchst, is a drought-tolerant and multipurpose fruit tree indigenous to Africa (Hall et al. 2002). The tree is widely distributed in African drylands and has been introduced outside its native range, including the Negev Desert in Israel (Hall et al. 2002, Nerd & Mizrahi 2000). The species has also been introduced in botanical gardens in the USA, India, Oman, and Australia (Hall et al. 2002), and in China for experimental trials as a commercial crop (Li et al. 2015). *S. birrea* has three distinct subspecies, namely, *S. birrea* subsp. *birrea*, *S. birrea* subsp. *caffra*, and *S. birrea* subsp. *multifoliata* (Hall et al. 2002), and all are found in Tanzania (Hall et al. 2002, Munna et al. 2023b). *S. birrea* is rarely planted by farmers; instead, it is retained in agricultural fields (Jama et al. 2008). The tree can be integrated into dryland agroforestry systems to maintain soil fertility and support human nutrition, health, and income security (Jama et al. 2008).

Sclerocarya birrea was named "arido-active" tree species due to its ability to continue metabolic activity, including sprouting leaves, during the dry season before rain onset (Seghieri et al. 1995). Moreover, *S. birrea* is a keystone tree species that supports a wide range of domestic and wild animal species, including elephants (Gadd 2002). In arid and semi-arid savannas where trees are scattered, birds and animals normally seek shelter and food under tree canopies, and consequently act as agents for importing nutrients (Vetaas 1992). Inorganic N, microbial biomass-C, and nitrogen mineralization of soils under *S. birrea* canopies were investigated by Diallo et al. (2017), who showed that concentrations of inorganic N and soil microbial biomass-C were generally higher under the canopies. However, the study was limited to the species level, with no disaggregation of subspecies potential and no information on the potential cycling of other nutrients. Disaggregation of subspecies' litter nutrient and carbon concentrations is important because the subspecies occur in different ecological regions in Tanzania (Munna et al. 2023b) and worldwide (Munna et al. 2023a). Thus, their potential to enhance soil fertility and carbon storage will likely vary.

Global drylands have the potential to store about 30% of the world's carbon stock (Hanan et al. 2021). Our previous work estimated suitable areas for *S. birrea* subspecies as between 3,751,057 km² and 24,632,452 km² of Earth's surface (Munna et al. 2023a). Additionally, *S. birrea* is known for its long lifespan, as evidenced by the subspecies *caffra*, which has lived for over 200 years (Hall et al. 2002). However, research on the potential of *S. birrea* subspecies' litterfall to improve soil organic carbon, fertility, and carbon storage in drylands remains limited. Thus, there is a need to understand *S. birrea* potential for agroforestry in drylands.

This study was conducted to (i) determine organic carbon and total nitrogen concentration in *Sclerocarya birrea* subspecies leaf and fruit litterfall, (ii) compare nutrient (macro- and micro-nutrients) concentration variations among *S. birrea* subspecies litterfall types, and (iii) determine the potential of *S. birrea* subspecies leaf and fruit litterfall in enhancing soil fertility and carbon storage in drylands of Tanzania. The study's findings will enhance our understanding of the potential of *Sclerocarya birrea* subspecies litterfall to improve soil fertility and combat global warming by storing carbon in drylands.

Materials and methods

Description of study areas

The study was conducted in three districts in Tanzania: (i) the Serengeti district in Mara region; (ii) the Iringa district in Iringa region; and (iii) the Morogoro municipal in Morogoro region (Fig. 1). The salient features and the locations of trees where leaf and fruit litterfall samples were collected are detailed in Tab. S1 (Supplementary material).

In the Serengeti district, litterfall was collected in Bonchugu village, located between 01° 30′ S and 02° 40′ S and 34° 15′ E and 35° 30′ E, at altitudes ranging from 1000 to 2300 m a.s.l. The Serengeti district shows a bimodal distribution of rainfall during the year: short rains from October to December and long rains from March to May. The total rainfall in the district ranges from 900 to 1000 mm per year. Temperatures in the Serengeti district range from 15 °C in April to 29 °C in July. The district harbors the *Sclerocarya birrea* subspecies *birrea*. The major soil types in the Serengeti district are Ferralic Cambisols and Eutric Planosols (Western Serengeti), Luvic Phaeozems (North-eastern Serengeti), and Luvic Phaeozems, Mollic Solonetzs, and Luvic Chernozems (East Serengeti – Masuki & Mbogoni 2003).

S. birrea subsp. *caffra* leaf and fruit litterfall samples were collected in Kiegea village, Morogoro municipal. Morogoro municipal lies between longitudes 37° 34′ 52″ E and 37° 45′ 25″ E and between latitudes 06° 38′ 56″ S and 06° 55′ 8″ S (Ernest et al. 2017). The annual rainfall ranges from 600 mm in the lowlands to 1200 mm in the highland plateau. Morogoro receives short, unreliable rainfall between September and

December, while long rains occur from February/March to April/May. The mean monthly temperature ranges from 17.48 °C in the mountains to 31.31 °C in river valleys, with an average temperature of 25 °C. The soil of Morogoro municipality originates from a Precambrian basement complex called the Usagaran unit, with high-grade metamorphic rocks including amphibolite, gneiss, and granulites, and a Neogene formation, known for its thick layer of red soil, heavy black clay "*mbuga*" soil, and alluvium (Mkumbo et al. 2022).

In the Iringa district, leaf and fruit litterfall of *S. birrea* subsp. *multifoliata* were collected close to Maliganza village. The Iringa district lies between latitudes 07° 00′ and 08° 30′ S and longitudes 34° 00′ and 37° 00′ E, at an altitude of 800 to 1800 m a.s.l. The rainfall in the district has a unimodal distribution of 600-1000 mm annually, falling from November/December to April/May, and a mean temperature of 15-20 °C. In this district, soils in the lowlands zone are dominated by red/brown loam, which are moderately fertile; the midlands zone is characterized by intermediate clay soils, which are moderately drained and leached; while the highlands zone is characterized by red/yellow, well-drained, and highly weathered and leached clay soils (URT 2020).

Litterfall and soil sampling

Leaf and fruit litterfall samples were collected from nine randomly selected female trees for each *S. birrea* subspecies in each study site (Tab. S1 in Supplementary material). Leaf litterfall samples were collected using four traps (60 × 60 cm nets with 2 mm of mesh size) set in the four cardinal directions under the trees' canopies, which were placed 2 m above the ground. Leaf litterfall samples were collected from March to April for the subspecies *birrea* in Bonchugu village in Serengeti district, May to June for the subspecies *multifoliata* in Malinzanga village in Iringa district, and from May to July for the subspecies *caffra* in Kiegea village, Morogoro Municipal. The leaf litterfall samples from four traps per tree were thoroughly mixed, and a composite sample weighing at least 2 kg was collected and packed in zipped plastic bags.

Fruit samples were collected under the *S. birrea* subspecies canopies in a 2 × 2 m plot with a tree trunk in the middle. The fruit samples of subsp. *birrea* were collected in Bonchugu village in March 2020, subspecies *caffra* and *multifoliata* were collected in Kiegea and Malinzanga villages, respectively, both in April 2020. Fruit litterfall samples averaging 5 kg were collected from the traps and packed into clean woven polypropylene bags. Overall, a total of 54 fruit and leaf samples, 18 samples (9 fruits and 9 leaves) for each subspecies, were collected from 27 sampled trees of *S. birrea* subspecies in Tanzania.

Soil samples were collected under each sampled tree, including leaf and fruit samples. Soil samples were collected following a four-compass cardinal direction and composited to constitute one sample per tree. Soil samples were collected at 0-20 cm depth, under (about 1 m from the tree trunk) and away (about 40 m away from the canopy margin) from the tree canopy. Soil samples from each tree were thoroughly mixed, and composite samples weighing at least 0.5 kg were taken and packed in zipped plastic bags. The litterfall (leaf and fruit litterfall) and soil samples were transported and air-dried in a dust-free screen house at the Soil Science laboratory, Sokoine University of Agriculture, Morogoro, Tanzania.

Leaf and fruit litterfall, and soil samples preparation

Once at the screen house, the seeds were removed from the fruit samples. The leaf litterfall samples were sorted and sieved in a 5-mm sieve to remove unwanted materials. The leaf and fruit litterfall samples were separately oven-dried to a constant weight at 70 °C, and then weighed. Soil samples were air-dried in a screen house. Separately, leaves and fruit samples were ground to a fine powder using a plant grinder for chemical analyses. The soil samples were ground in a mortar on a clean, hard surface and passed through a 2-mm sieve for chemical analyses.

Laboratory analyses

Leaf and fruit litterfall samples were analyzed for Total Nitrogen (TN), organic carbon (OC), Phosphorus (P), Sulphur (S), Potassium (K), Calcium (Ca), Magnesium (Mg), and Sodium (Na), as well as for micronutrients (Copper - Cu, Iron - Fe, Zinc - Zn, Manganese - Mn) as follows. The TN was determined by using the micro-Kjeldahl digestion method in concentrated sulfuric acid and mixed catalysts, followed by distillation with 40% NaOH and titration with acid (Bremner & Mulvaney 1982). The OC was determined by using the Walkley and Black dichromate method (Nelson & Sommers 1982). The leaf and fruit litterfall samples were separately digested using the wet digestion method in a microwave digester (Multiwave Pro® 24HVT80, Anton Paar, Australia), and the digests were used to quantify total P, K, Na, Ca, Mg, Zn, Cu, Fe, and Mn. The Na and K concentrations in the digest were determined using a flame photometer (Banerjee & Prasad 2020). Total P was determined by UV Spectroscopy after blue color development with ammonium molybdate, as described by Murphy & Riley (1962). Sulphur concentration was determined by the turbidity method with $BaCl_2$ (Moberg 2001) and quantified using a UV-visible spectrophotometer (BioMate™ 6 model, Thermo Fisher, USA). The concentrations of Cu, Zn, Fe, Mg, and Mn were determined by an atomic absorption spectrometer (iCE3300, AA System model, UK – Lindsay & Norvell 1978).

Soil samples were subjected to the following analyses. Soil pH was measured with a pH meter at a 1:2.5 soil:water ratio (McLean 1986). Available P was extracted by the Bray-1 method as described by Bray & Kurtz (1945) followed by blue color development using ammonium molybdate and quantified by using UV Visible Spectrophotometer method (Murphy & Riley 1962). TN was determined by the micro-Kjeldahl method (Bremner & Mulvaney 1982), and OC was assessed by the Walkley-Black dichromate method (Nelson & Sommers 1982). Exchangeable bases (Ca, Mg, K, Na) in soil samples were extracted using 1 N ammonium acetate (NH_4OAc) leaching solution, buffered at pH 7.0 (Thomas 1986), and quantified by AAS for Ca and Mg, flame photometer for K and Na, and CEC by distillation-titration method after displacement of NH_4^+ of NH_4OAc saturation with KCl (Okalebo et al. 2002). Monocalcium phosphate [$Ca(H_2PO_4)_2$] solution was used to extract S (Combs et al. 1998), while Zn, Cu, Fe, and Mn were extracted using diethylenetriaminepentaacetic acid (DTPA – Lindsay & Norvell 1978) and quantified by AAS.

Statistical analysis

Nutrient concentrations in soils, and *Sclerocarya birrea* subspecies leaf and fruit litterfall concentration data were subjected to one-way analysis of variance (ANOVA – α = 0.05) to determine the differences in nutrient concentrations between litterfall types (leaves *vs.* fruits) in each subspecies. When significant differences were found, means were separated by the Least Significant Difference (LSD) at $p \leq 0.05$. To determine the effect of litterfall on soil fertility, an independent-samples *t*-test was used to assess differences in soil fertility between soils under and away from the canopies of the three *S. birrea* subspecies. All statistical analyses were conducted using SAS software v. 9.4 (SAS Institute 2012).

Results

Organic carbon and total nitrogen concentration in the leaf and fruit litterfall

The results showed that the concentration of OC did not differ significantly between leaf and fruit litterfall, ranging from 41.16 ± 0.71% to 43.49 ± 0.61% in leaf litterfall and 42.82 ± 2.02% to 49.57 ± 5.23% in fruit litterfall (Tab. 1); whereas the TN differed significantly between leaf and fruit litterfall (p = 0.0001 to 0.0279 – Tab. 1). TN was higher in the leaf litterfall (1.01 ± 0.01% to 1.19 ± 0.06%) than in the fruit litterfall (0.57 ± 0.07% to 0.94 ± 0.07% – Fig. 2). The leaf litter TN in *S. birrea* subsp. *birrea* was 1.19 ± 0.06%, in the *caffra* subspecies was 1.01 ± 0.01% and in the *multifoliata* subspecies was 1.14 ± 0.04%. The TN in fruits was 0.94 ± 0.07%, 0.57 ± 0.07%, and 0.79 ± 0.05% for *birrea, caffra*, and *multifoliata* subspecies, respectively (Tab. 1). The C:N ratios in the leaf litterfall ranged from 34.58% to 41.66%,

Tab. 1 - The organic carbon and total nitrogen content and their ratios in leaf and fruit litterfall of *Sclerocarya birrea* subspecies in Tanzania. Mean and p-values from analysis of variance (ANOVA) are reported. (df): degree of freedom. Significant ($p<0.05$) effects are indicated by different letters.

Litterfall type	Subsp. *birrea*			Subsp. *caffra*			Subsp. *multifoliata*		
	OC	TN	C: N	OC	TN	C: N	OC	TN	C: N
Leaf	41.16 ± 0.71 [a]	1.19 ± 0.06 [a]	34.58	42.08 ± 0.89 [a]	1.01 ± 0.01 [a]	41.66	43.49 ± 0.61 [a]	1.14 ± 0.04 [a]	38.14
Fruit	49.57 ± 5.23 [a]	0.94 ± 0.07 [b]	52.73	42.82 ± 2.02 [a]	0.57 ± 0.07 [b]	75.12	44.87 ± 3.37 [a]	0.79 ± 0.05 [b]	56.79
p-value (df=1)	0.1309	0.0279	-	0.7425	<.0001	-	0.6936	<.0001	-

Tab. 2 - Summary of analysis of variance (ANOVA) to compare macronutrients and sodium concentration in leaf and fruit litterfall of three *Sclerocarya birrea* subspecies in Tanzania. *p*-values from ANOVA are reported. (df): degree of freedom.

Source of variation	df	Subspecies	TN	P	K	S	Ca	Mg	Na
Litterfall type (leaf & fruit)	1	*birrea*	0.0279	<0.0001	0.0143	0.3129	<0.0001	0.0007	0.0003
	1	*caffra*	<0.0001	<0.0001	0.4266	0.1944	<0.0001	<0.0001	<0.0001
	1	*multifoliata*	<0.0001	0.0002	0.8421	0.3895	<0.0001	<0.0001	<0.0001

and in fruit litterfall ranged from 52.73% to 75.12% (Tab. 1).

Nutrient concentration in the leaf and fruit litterfall

Macro- and secondary nutrients

We found significant differences in P, Ca, Mg, and Na concentration between leaf and fruit littefall across all subspecies (Tab. 2). K concentration in leaf and fruit litterfall differed in subsp. *birrea* only (Tab. 2). Additionally, P was significantly higher in the fruit litterfall (0.17%-0.20%) than in leaf litterfall (0.02%-0.04%) for all subspecies (Fig. 2). In subsp. *birrea*, K was higher in fruit (0.56 ± 0.03%) than in leaves (0.39 ± 0.04%) (Fig. 2). Leaf and fruit S concentrations did not differ significantly across subspecies (Tab. 2). Concentration of Na also followed the same trend, with a higher concentration in fruit litterfall (11.65%-19%) than in leaf (0.41%-0.65%) for all subspecies (Fig. 2). Concentrations of Ca and Mg were higher in leaf litterfall, ranging from 0.54 ± 0.08% to 0.89 ± 0.12% Ca and 0.19 ± 0.01% to 0.27 ± 0.03% Mg, than in fruit litterfall, which ranged from 0.08 ± 0.01% to 0.11 ± 0.01% Ca and 0.10 ± 0.01% Mg (Fig. 2).

Micronutrients

Significant differences in Cu, Zn, Fe, and Mn concentration were recorded between leaf and fruit litterfall in all subspecies (Tab. 3). The concentrations of Cu, Fe and Mn were significantly higher in fruit (11.71 ± 1.05, 262.72 ± 21.67 and 31.42 ± 5.49 mg kg^{-1} for *birrea*, respectively; 12.32 ± 1.22, 400.59 ± 62.65 and 54.77 ± 0.93 mg kg^{-1} for *caffra*; and 8.35 ± 0.44, 214.13 ± 27.69 and 51.90 ± 1.36 mg kg^{-1} for *multifoliata*) than in leaf (4.39 ± 0.64, 95.87 ± 8.90 and 18.97 ± 2.18 mg kg^{-1} for *birrea*, respectively; 3.41 ± 0.39, 64.10 ± 9.90 and 16.08 ± 0.89 mg kg^{-1} for *caffra*; and 3.32 ± 0.54, 107.70 ± 13.28 and

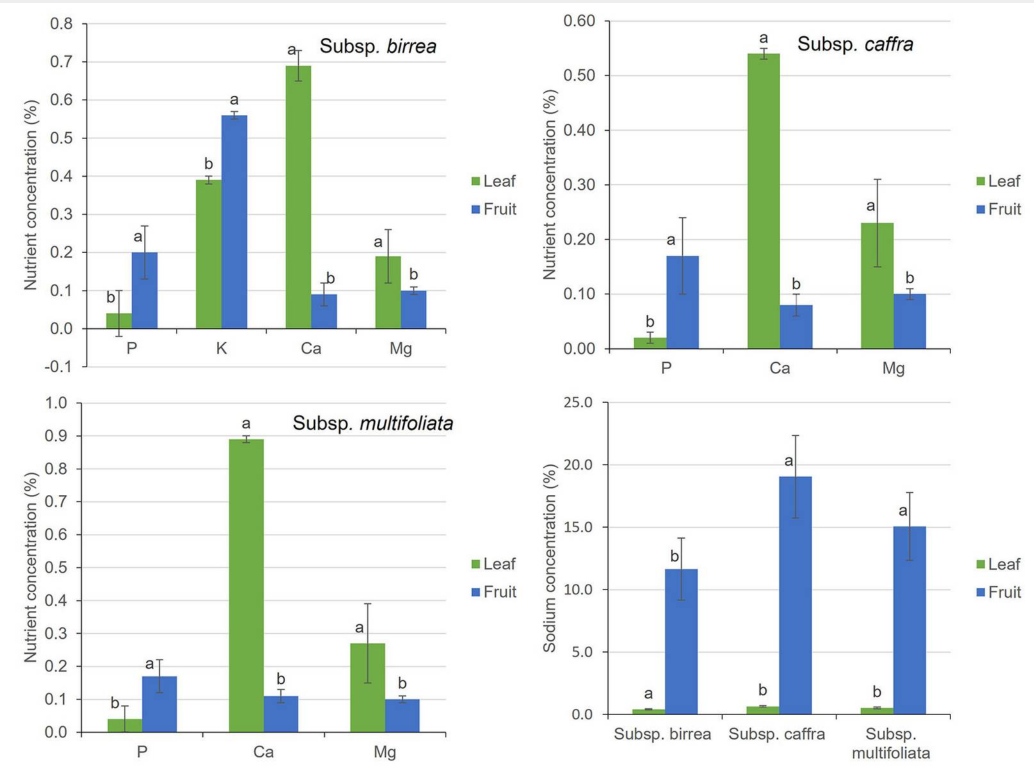

Fig. 2 - Mean concentration of macronutrients and sodium in the leaf and fruit litterfall of *Sclerocarya birrea* subspecies. Vertical bars show standard errors of the mean (n = 9). Bars within subspecies and nutrients with different letters are significantly different (α = 0.05).

18.04 ± 2.28 mg kg^{-1} for *multifoliata*) litterfall (Fig. 3). However, the concentration of Zn was 33 to 46 times higher in leaf (ranging from 412.97 ± 47.27 mg kg^{-1} in *multifoliata* to 499.78 ± 49.04 mg kg^{-1} in *caffra*) than in fruit litterfall (Fig. 3).

Contribution of litterfall in enhancing soil fertility in drylands of Tanzania

We found that only the OC and K concentrations in soil under the tree canopy were significantly ($p < 0.05$) higher (0.77 ± 0.25% and 0.40 ± 0.15 cmolc kg^{-1}) than in soil away from the canopy for subsp. *birrea* (0.46 ± 0.10% and 0.22 ± 0.07 cmolc kg^{-1}, respectively – Tab. 4). However, the soil OC was low in all the soils (<2.5%) as per Landon (1991). The soil pH, Cu, Zn, Mn, Fe, CEC, TN, Ca, Mg, Na, extractable P, and available S did not differ between soil under and away from the canopy of subsp. *birrea* (Tab. 4). For subsp. *caffra*, soil pH, Cu, Zn, Mn, Fe, CEC, TN, OC, Ca, Mg, Na, K, and extractable P did not significantly differ from those away from the canopies (Tab. 4).

Available S was significantly ($p<0.05$) higher in the soils under canopies (1.70 ± 0.10 mg kg^{-1}) than those away from the canopies (1.57 ± 0.08 mg kg^{-1}) for subsp. *caffra* only (Tab. 4). The soil in Kiegea village, Morogoro municipal, where the subspecies *caffra* is found, had very low available S (< critical value of 9 mg S kg^{-1}), but S was sufficient in Bonchugu village, Serengeti district, and Malinzanga village, Iringa district, where subspecies *birrea* and *multifoliata* are found, respectively, as per Huda et al. (2004) and Landon (1991). For subsp. *multifoliata*, the concentration of Na in soils under the canopy was significantly ($p<0.05$) higher (0.29 ± 0.12 cmolc kg^{-1}) than that away from the canopy (0.19 ± 0.06 cmolc kg^{-1} – Tab. 4). However, all soils had deficient soil exchangeable K (< 0.41 to 1.2 cmolc kg^{-1}), except soils under the canopy of the subsp. *caffra* in Kiegea village as per Landon (1991). There were no significant differences in soil pH, Cu, Zn, Mn, Fe, CEC, TN, OC, Ca, Mg, and P in soils under and away from the canopies of the subsp. *multifoliata* (p <0.05 – Tab. 4). Generally, all soils studied had low Zn (< 1.0 mg kg^{-1}), low P (< 15 mg kg^{-1}), and low exchangeable Ca (< 5.1 to 10.0 cmolc kg^{-1} – Landon 1991).

Tab. 3 - Summary of analysis of variance (ANOVA) to compare micronutrient concentrations in the litterfall of three *Sclerocarya birrea* subspecies in Tanzania. *p*-values from ANOVA are reported. (df): degree of freedom.

Source of variation	df	Subspecies	Cu	Zn	Fe	Mn
Litterfall type (leaf & fruit)	1	*birrea*	<0.0001	0.0006	<0.0001	0.0515
	1	*caffra*	<0.0001	<0.0001	<0.0001	<0.0001
	1	*multifoliata*	<0.0001	<0.0001	0.0032	<0.0001

Discussion

This study provides a quantitative assessment of the potential of the litterfall of *Sclerocarya birrea* subspecies to enhance soil fertility in agroforestry systems. Notable differences in leaf and fruit litterfall may be related to the roles of the respective nutrients in plant growth. Higher concentrations of Cu, Fe, Mn, P, and Na in fruit litterfall than in leaf litterfall of subspecies (Tab. 2, Fig. 2, Fig. 3) are due to the deposition of these nutrients in reproductive parts of the plants, *i.e.*, fruit growth and seed development (Johnson & Mirza 2020). These results also show that when fruits are harvested, Cu, Fe, Mn, and P may not be recycled in agroforestry systems and may need to be supplemented from other sources. Lack of significant difference in OC and S in leaf and fruit litterfall indicates that both leaf and fruit litter have comparable potential addition of OC and S in the soil. The results in Tab. 1 show that litterfall can potentially supply about 411.6 and 495.7 kg OC from the accumulation of 1 ton of leaf and fruit, respectively.

The higher concentrations of Zn, TN, Ca, and Mg in leaf litterfall than in fruit litterfall across all subspecies are related to the significant role of these nutrients in leaf physiological functions in photosynthesis. Zinc plays a vital role in the catalytic reaction of the enzyme carbonic anhydrase, which occurs in chloroplasts and the cytoplasm, thereby enhancing photosynthesis and biomass production by increasing CO_2 absorption per unit leaf area (Marschner 1995). Calcium and Mg are positively correlated to photosynthesis (McLaughlin & Wimmer 1999), which mostly occurs in leaves. Based on the N, P, and K concentration in Fig. 2, one ton of leaf litterfall can supply approximately 10 to 12 kg N, 0.2 to 0.4 kg P, and 3.9 to 6.4 kg K, while fruit lit-

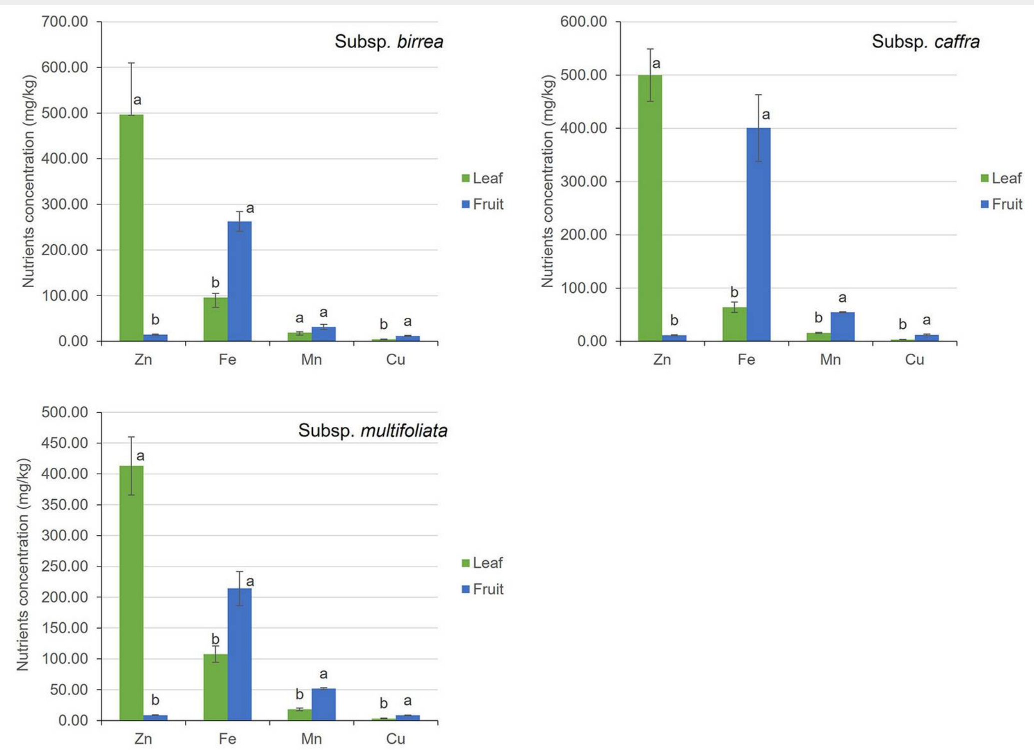

Fig. 3 - Mean concentration of micronutrients in the leaf and fruit litterfall of *Sclerocarya birrea* subspecies. Vertical bars show standard errors of the mean (n = 9). Bars within subspecies and nutrients with different letters significantly differ at α = 0.05.

Tab. 4 - Mean values (± standard error, n = 9) of selected soil properties under and away from the canopies of *Sclerocarya birrea* subspecies in Tanzania. (*): $p < 0.05$; (**): $p < 0.01$.

Soil properties	Subsp. *birrea*			Subsp. *caffra*			Subsp. *multifoliata*		
	Under canopy	Away from canopy	Pr > |t|	Under canopy	Away from canopy	Pr > |t|	Under canopy	Away from canopy	Pr > |t|
pH (in H_2O)	6.37 ± 0.27	6.16 ± 0.28	0.1189	6.59 ± 0.25	6.57 ± 0.23	0.9014	6.65 ± 0.60	6.50 ± 0.65	0.6265
Cu (mg kg^{-1})	0.46 ± 0.20	0.44 ± 0.22	0.8279	0.95 ± 0.65	1.14 ± 0.61	0.5446	2.51 ± 3.66	0.95 ± 0.39	0.2375
Zn (mg kg^{-1})	0.92 ± 0.31	0.78 ± 0.49	0.5119	0.77 ± 0.28	0.99 ± 0.62	0.3626	0.47 ± 0.34	0.43 ± 0.37	0.8169
Mn (mg kg^{-1})	43.85 ± 7.76	39.94 ± 15.94	0.5178	36.35 ± 17.70	33.99 ± 13.11	0.7521	13.55 ± 4.10	13.52 ± 4.34	0.9882
Fe (mg kg^{-1})	40.49 ± 17.34	67.43 ± 44.20	0.1081	19.36 ± 11.31	22.10 ± 13.44	0.6459	17.88 ± 15.55	23.84 ± 21.91	0.5154
S (mg kg^{-1})	26.08 ± 32.76	15.21 ± 10.5	0.3573	1.70 ± 0.10	1.57 ± 0.08	0.0108*	67.85 ± 18.13	91.51 ± 54.25	0.2436
CEC (cmolc kg^{-1})	5.07 ± 0.96	4.36 ± 0.36	0.0655	3.55 ± 0.34	3.77 ± 0.33	0.1855	3.75 ± 1.56	3.23 ± 1.47	0.4764
TN (%)	0.09 ± 0.01	0.07 ± 0.05	0.1515	0.09 ± 0.01	0.07 ± 0.01	0.0616	0.08 ± 0.05	0.09 ± 0.03	0.6296
OC (%)	0.77 ± 0.25	0.46 ± 0.10	0.0066**	1.21 ± 0.25	1.04 ± 0.31	0.2155	0.86 ± 0.37	0.67 ± 0.33	0.2605
Avail. P (mg kg^{-1})	5.44 ± 4.20	6.67 ± 9.38	0.7244	9.70 ± 15.00	3.99 ± 3.23	0.2935	8.38 ± 5.45	8.19 ± 8.97	0.9572
Ca (cmolc kg^{-1})	2.89 ± 0.49	2.71 ± 0.38	0.3980	1.29 ± 0.33	1.19 ± 0.33	0.5455	1.57 ± 0.97	1.18 ± 0.63	0.3286
Mg (cmolc kg^{-1})	1.07 ± 0.73	0.75 ± 0.40	0.2825	1.57 ± 0.46	1.47 ± 0.46	0.6492	0.90 ± 0.45	0.89 ± 0.31	0.9668
Na (cmolc kg^{-1})	0.20 ± 0.08	0.14 ± 0.06	0.1519	0.12 ± 0.02	0.13 ± 0.02	0.7408	0.29 ± 0.12	0.19 ± 0.06	0.0472*
K (cmolc kg^{-1})	0.40 ± 0.15	0.22 ± 0.07	0.0068**	1.02 ± 0.54	0.64 ± 0.38	0.1079	0.30 ± 0.13	0.19 ± 0.06	0.0516

terfall can supply 5.7 to 9.4 kg N, 1.7 to 2.0 kg P, and 6.4 kg K. The amount of N, P, and K supplied through litterfall is lower than the recommended rates for crop production. Therefore, high levels of litterfall are needed to meet crop production macronutrient requirements. Leaf and fruit litter can supply substantial amounts of OC in the soil.

Soil fertility status under and away from the canopy reflects litterfall nutrient and OC concentrations. Significant higher soil exchangeable K and OC under the canopy of the subspecies *birrea*, S under the subspecies *caffra*, and Na under the subspecies *multifoliata* (Tab. 4), can be linked to the contribution of litterfall to enhance these aspects of soil fertility. The results are consistent with the highest OC, K, and S for specific subspecies. These findings are in line with the existing consensus that trees improve soil nutrient status and that agroforestry, in general, replenishes soil fertility (Garrity et al. 2010). Soil Cu, Zn, Mn, S, CEC, TN, Ca, Mg, and Na were higher (though not significantly different) under the canopies of subsp. *birrea* as compared to that away from canopies. The significantly higher OC (0.77%) and K (0.40 cmolc kg^{-1}) under the canopy than away from the canopy OC (0.46%) and K (0.22 cmolc kg^{-1}) of subspecies *birrea* in Bonchungu, Serengeti (Tab. 4) may be linked to litter residue management. Similarly, soil OC was reported to be higher under the canopy of *Prosopis juliflora* and *Acacia nilotica* in rangeland and agroforestry systems (Sadeq et al. 2020). Another study reported higher soil K concentrations under the canopies of *Acacia albida* and *Kigelia africana* than away from the canopies (Dunham 1991).

Generally, the soil pH and concentration of Mn, S, TN, OC, Ca, Mg, and K were higher (by 0.3%, 7%, 8%, 22%, 14%, 59%, 8%, and 37%, respectively) under the canopies of subsp. *caffra* than away from them, and this is probably due to litterfall accumulation. On the contrary, higher Zn, Mn, Fe, Na (by 20%, 29%, 14%, 6%, and 8%, respectively) in soils away from the canopies of this subspecies than in soils under the canopies indicates the possibility of greater absorption of these nutrients by trees than replenishment through litterfall. Only soil S concentration under the canopies of subsp. *caffra* differed significantly from that outside the canopies (Tab. 4), consistent with Pérez-Suárez et al. (2008). The higher S under the canopy (1.70 mg kg^{-1}) than away from the canopy (1.57 mg kg^{-1}) can be linked to the addition of S from litterfall in highly S-deficient soil.

For *S. birrea* subsp. *multifoliata*, the soil pH, Cu, Zn, Mn, CEC, OC, P, Ca, Mg, Na, and K were 2%, 62%, 9%, 0.2%, 14%, 22%, 2%, 25, 1%, 35% and 37% higher under the canopies compared to those away from canopies. However, the concentration of soil Fe, S, and TN was 33%, 35%, and 12% higher in soils away from tree canopies than that under the canopies. Na was the only soil nutrient that significantly differed from that away from the canopies (Tab. 4). Similarly, Comole et al. (2021) reported higher soil Na under the canopy of *Prosopis velutina* than that away from the canopies.

Soils under the canopies of all *Sclerocarya birrea* subspecies had higher OC, Mn, K, Ca, and Mg concentrations than those in open fields (Tab. 4). This could be due to the increased litterfall from trees and a higher biological activity, including litterfall decomposition (Belsky et al. 1989). Differences in nutrient concentration under the canopies among the subspecies can be related to differences in the soils where the subspecies studied were found. Higher nutrient concentrations under tree canopies may also be attributed to factors such as high concentrations of bird droppings, animal excrement, and urine, which can contribute to high soil nutrient concentrations over time (Vetaas 1992). This is because trees in drylands are often scattered, and provide shelter and food for birds and animals. The breakdown and mineralization of plant residues probably contributed to higher carbon and nutrient contents in the soils under the canopies of all *S. birrea* subspecies.

Sclerocarya birrea is a dryland tree species that inhabits soils with low fertility and receives little rainfall (Hall et al. 2002). Additionally, the subsp. *multifoliata* is more dominant in drier areas, followed by the subspecies *birrea* and *caffra* (Hall et al. 2002, Munna et al. 2023a, 2023b). Plants adapted to dry and infertile soil exhibit slow growth rates, long leaf longevity, low nutrient concentrations, and high concentrations of secondary chemical compounds such as lignin, which tend to immobilize nutrients in green tissues and increase the C:N ratio, thereby affecting nutrient cycling (Dent et al. 2006). As a result, plants at nutrient-limited sites produce small amounts of low-quality litterfall, which decomposes slowly and adds limited nutrients to the soils (Vitousek 1984). Additionally, the leaves and fruits of *S. birrea* subspecies are used as fodder by both wild and domestic animals (Hall et al. 2002), which may be attributed to slight differences in nutrient concentrations in soils under and away from the canopies.

The leaf and fruit litterfall of *S. birrea* subspecies had high C:N ratios (Tab. 1), which suggests that organic carbon and nutrients are immobilized at initial stages of decomposition and will slowly be released to become available for use by crops. However, fruit and leaf litterfall of the subsp. *birrea* had high TN and lower C:N ratios compared to subspecies *multifoliata* and *caffra* (Tab. 1). The low C:N ratio of *S. birrea* subsp. *birrea* compared to that of subspecies *caffra* and *multifoliata*, suggests that the litterfall of the subspecies *birrea* can decompose in a short time and release nutrients into the soil for crop uptake (Liu & Sun 2013, Valente et al. 2023). Litterfall N is the primary nutrient that determines the decomposition of litterfall during the early stages of the litterfall decomposition process. In contrast, lignin is the major litterfall component that influences its decomposition at later stages (Liu et al. 2007). This suggests that *S. birrea* subspecies are among the dryland trees with the potential to improve soil fertility and boost agricultural productivity in drylands if adopted for agroforestry and their litterfall is used to amend soil fertility. However, more information is needed on their potential effects on dryland crops before promoting and adopting them in agroforestry.

Enhancing C storage in drylands with high C:N ratio litterfall through agroforestry is critical for increasing C sequestration in agricultural soils with relatively low soil vegetation cover. Our results show that the C:N ratios are higher in *S. birrea* subspecies fruit than leaf litterfall (Tab. 1). The findings of this study concur with McGroddy et al. (2004) and Dent et al. (2006), who reported that the C:N ratios in forest litterfall range from 35:1 to 88:1. Microbial decomposers such as bacteria, fungi, and actinomycetes, which have lower C:N ratios than most litterfall types, mainly decompose litterfall (Liu & Sun 2013). In general, the ideal litter C:N ratio for microbial activity is 20-30 (Liu & Sun 2013). Mineralization is expected when the litter C:N ratio is less than 20:1 during litter decomposition, and immobilization is likely when the ratio exceeds 30:1 (Liu & Sun 2013). Therefore, higher C:N ratios in the litterfall of all *S. birrea* subspecies imply that most nutrients are immobilized and decomposition is slow, allowing them to store carbon in their biomass for long time. The degree of C storage may vary among *S. birrea* subspecies due to slight differences in C:N ratio, as subspecies *birrea* had a relatively low C:N ratio, but still fall within C:N >1:30 (Tab. 1). Thus, *S. birrea* subspecies are potential candidate trees for use in drylands restoration to counteract global warming through carbon storage in drylands.

Early stages of plants' litterfall decomposition are often governed by the availability of limiting elements, such as litter N and C:N ratios, and late stages of litterfall decomposition have been linked to the elements needed to decompose recalcitrant secondary compounds, such as lignin, that accumulate in the remaining litterfall (Berg et al. 2010). The other main predictors of litterfall decomposition rate, in addition to N and C:N ratios, are P and C:P, lignin and lignin/N, and cellulose (Krishna & Mohan 2017). Thus, there is a need for further research to explore litterfall production and its decomposition rate. Moreover, further studies are needed to determine secondary chemical compounds in leaf and fruit litterfall and in other litterfall types, such as twigs and branches, as well as to improve our understanding of litterfall decomposition rate for *Sclerocarya birrea* subspecies, releasing nutrients for crop use and storing C. Twigs and branches of trees/plants normally contain proportionally higher lignin concentrations hence, higher lignin/N ratios than leaves and fruits (Valente et al. 2023). Thus, the high C:N ratios in the leaf and fruit litterfall of *S. birrea* subspecies (C:N > 30) suggest that these trees can immobilize carbon for a considerable period, making them suitable for mitigating global warming by storing carbon in their biomass. Furthermore, research to study total carbon stored in the biomass of the *Sclerocarya birrea* subspecies is recommended to better understand their contribution and potential to combat global warming.

Conclusions

The leaf and fruit litterfall of the *Sclerocarya birrea* subspecies has the potential to improve soil fertility and store carbon in dryland soils, though their potential varies across subspecies. The fruit litterfall generally had higher organic carbon and nutrient concentrations than leaf litterfall. As the fruits have economic potential, it will be necessary to supplement nutrients and apply organic carbon amendments. Soil pH and CEC under the canopy of *Sclerocarya birrea* subspecies and in open fields were generally similar, both being slightly acidic and exhibiting very low CEC values. Soils under the canopies were generally enriched with most nutrients compared to those in open fields, except for Fe.

Leaf and fruit litterfall of *Sclerocarya birrea* subspecies has the potential to enhance soil fertility but requires supplementation with other nutrient sources, as it showed high C:N ratio. This suggests that litterfall cannot be easily decomposed and mineralized, and that nutrients are immobilized and not readily available for crop uptake due to slow decomposition. From a climate change mitigation perspective, higher C:N ratios imply that *Sclerocarya birrea* subspecies can store carbon in their biomass for a long time, thus are potential tree species for combating global warming.

Author's Contributions

Munna AH: conceived the study, methodology, data curation and analysis, interpretation of results, writing the first draft, reviewing and editing of the manuscript, and project administration; Amuri NA: methodology, software, data curation and analysis, validation, and interpretation of results; reviewing and editing of the manuscript; Hieronimo P: reviewing and editing of the manuscript and Woiso DA: reviewing and editing of the manuscript. All authors endorsed the publication of the manuscript.

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Supplementary Material

Tab. S1 - Description of study sites where leaf and fruit litterfall samples were collected.

Link: Munna_4478@suppl001.pdf