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Is Soil Fertility the Cause or the Effect of Land Invasion by *Prosopis*?

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ABSTRACT

Background: For 20 years, *Prosopis juliflora* is aggressively spreading throughout the "Njemps Flats" in Kenya, where it changes vegetation cover and affects pastoral livelihoods. Its invasion dynamics is related to shallow groundwater tables (*Prosopis* being a phreatophyte), and it reportedly preferentially colonizes sites with favourable soil fertility attributes.

Aim: We contest this latter hypothesis, surmising that the N_2-fixing ability, the nutrient pumping by the deep root system, and year-round leaf litter fall will improve soil fertility attributes under *Prosopis*, irrespective of the initial soil status.

Methods: We assessed stand densities (number of individuals and their percentage cover) and selected soil attributes at 75 sites in the Njemps Flats. The stand densities of *Prosopis* were visualized by ground-truthed remote-sensed data, and subsequently related to soil fertility attributes. We further determined the isotope signatures ($\delta^{15}N$ and $\delta^{13}C$) of the prevailing (past) C4-dominated pasture and the (current) C3-*Prosopis* vegetation, as well as at three depths of the topsoil.

Results: The findings confirm favourable fertility attributes (low EC and high N, C, P, and K contents) being associated with dense *Prosopis* stands. However, the isotope analysis of the topsoil indicates typical signatures of C4 vegetation in non-invaded pastureland and typical signatures of N_2-fixing C3-plants in the top 5 cm (but not at deeper layers) of soils in *Prosopis* stands. *Prosopis* contributes about 16% of N derived from fixation, and significantly increases C, N, P, and Ca contents of the topsoil.

Conclusions: We conclude that high soil fertility is the result rather than the driver of *Prosopis* invasion.

1 | Introduction

Biological invasions have steadily increased over recent centuries (Pyšek et al. 2020), and the spread of invasive alien plant species is recognized to be a global problem (Seebens et al. 2021). It severely affects livelihoods and biodiversity (Shackleton et al. 2015), even in its native range of distribution (Kaur et al. 2012). In East Africa, *Prosopis juliflora* (Swartz) DC is listed among the most common alien invasive plant species (GISD 2017; Hussain et al. 2021). Due to its rapid spread, it affects agricultural and grazing lands in dryland areas of Ethiopia, Kenya, Somalia, Rwanda, Sudan, and Tanzania (reviewed by Kamiri, Choge, and Becker 2024). It reportedly reduces the diversity of native species (Wakie, Laituri, and Evangelista 2016) and affects agriculture-based livelihoods (Maundu et al. 2009; Mwangi and Swallow 2008).

Prosopis is an evergreen perennial shrub/tree native to dryland areas of America. It belongs to the Fabaceae family (sub-family of the Mimosoideae) and can fix atmospheric N_2 with rhizobia from the cowpea group (Kulkarni, Surange, and Shekhar-Nautiyal

2000). As a phreatophyte (plant requiring access for its roots to shallow groundwater tables; Dakhil et al. 2021), it populates mainly littoral zones of lakes, floodplain, and inland valley wetlands (Puppo and Felker 2022). Apart from the Njemps Flats (riparian floodplain of Lake Baringo in Kenya, main focal area of the present study), other wetland sites that recently started to be invaded include the Lorian and Lengurruahanga Swamps and the Tana River Delta in Kenya, the Afar region and the Awash River basin in Ethiopia, and the Tokar River and Gash River Deltas as well as the Kassala Plains in Sudan (Kamiri, Choge, and Becker 2024). At all these sites, *Prosopis* spread has resulted in a gradual displacement of the originally prevailing C4 grass-dominated vegetation, entailing an associated loss of pasture quality.

Besides favourable hydrological conditions with shallow groundwater tables or the presence of irrigation infrastructure, *Prosopis* invasion has often been associated with favourable edaphic conditions on highly fertile or potentially productive Gley-, Fluvi-, and Vertisols (Kamiri, Choge, and Becker 2024). Thus, a rapid invasive spread and high stand densities of *Prosopis* were shown to be associated with high available soil P (Masakha and Wegulo 2015) and high concentrations in the basic cations K, Ca, and Mg (Kaur et al. 2012). As a result, it has been hypothesized that the invasive spread of *Prosopis* occurs preferentially at sites with favourable hydro-edaphic conditions (Alvarez et al. 2019), and that the associated loss of prime land for crop or pasture production will negatively affect food security and rural livelihoods (Becker et al. 2016).

We contest this hypothesis and surmise that the presence of *Prosopis* will enhance soil fertility by its N_2-fixing ability, the nutrient pumping by the deep root system, and the year-round leaf litter fall, irrespective of the initial soil status. To test this, we first collected field data on *Prosopis* densities and cover and related those with selected soil fertility attributes. Subsequently, we analyzed topsoil samples from different depths for their isotope signatures in relation to the $\delta^{13}C$ and $\delta^{15}N$ contents of the previously dominating C4 pasture grasses and the presently prevailing C3 *Prosopis* vegetation. The analysis of such patterns will permit assessing if soils under C4 grass pasture were already fertile before, or if soil fertility improved because of *Prosopis* invasion. Such information is required for mapping/predicting areas at risk of future invasion (initial fertility scenario), or for assessing likely crop production potential after *Prosopis* clearing (induced fertility scenario).

2 | Material and Methods

2.1 | Study Site

The study was conducted in the Njemps Flats, South of Lake Baringo in Kenya at 0.4.70′55″°N and 35.97′92″°E. The site presents comparable land uses and climatic/hydro-edaphic conditions to other *Prosopis*-invaded sites in East Africa (i.e., Afar region in Ethiopia). The relatively flat lowland area is formed of tuffaceous sediments, resting on metamorphic basement complexes (Alvarez et al. 2017). The main soil classes comprise sodic Solonchaks in the South, well-drained Cambisol and Leptosol soils in the alluvial fans in the West, and poorly drained alluvial Fluvisol or Vertisol soils in the central floodplain (Snelder and Bryan 1995). The area experiences two rainy seasons with 650 mm of mean annual precipitation and a temperature range of 25–31°C. The agro-ecological zone is classified as a "dry savanna" with an average length of growing period of 95 days–Global Agro-Ecological Zones, GAEZ v4 of the Food and Agriculture Organization (FAO) of the United Nations. Agricultural land uses by grazed pastures or crop cultivation are constrained by severe hydric deficits from January to March and from June to September (Figure S1). The mean groundwater table during the dry season ranges from 1- to 4-m depth (data not shown) and is thus accessible for the deep roots of *Prosopis*.

2.2 | Invasion Mapping

To map *Prosopis* prevalence, we used LandSat pictures from the dry season of 2022, covering some 380 km^2 between the shores of Lake Baringo (North) and Lake Bogoria (South), and the footslopes of the adjacent Tugen Hills (West) and the Laikipa escarpment (East). During the dry season, evergreen *Prosopis* provides a dark blueish-green signal, while pasture vegetation has dried up (green-yellow colour), and farmlands are bare after the harvest of the wet season crop (brown colour). The map was overlaid with 750 grid cells of 500 × 500 m each. The grid cells were assigned mean greenness values using a supervised classification. Seventy-five grid cells (covering 10% of the total area) were assessed during field visits for the number of individuals per unit area, and the actual *Prosopis* cover percentage (share of area coverage by *Prosopis* relative to the total plant cover; Braun-Blanquet 1978): no invasion (0% *Prosopis*), low invasion (<20% *Prosopis* cover), medium invasion (20%–40% *Prosopis* cover), high invasion (40%–60% *Prosopis* cover), and very high invasion (>60% *Prosopis* cover). We applied these ground-truthed values of *Prosopis* cover to the remaining 90% of the grid cells (tiles), based on colour intensity (Figure 1).

2.3 | Sampling and Analysis

In each of the 75 sampling tiles, we collected composites of seven topsoil samples (0–15 cm), taken with a 5-cm-diameter auger along a diagonal across the tile. Before soil auger sampling, the over-laying mull layer of partially decomposed biomass on the soil surface was removed with a brush. The soil of each composite sample was oven-dried and sieved, in preparation for physico-chemical analyses at the laboratory of the Institute of Crop Science and Resource Conservation (INRES) of the University of Bonn, Germany.

In all tiles with the presence of *Prosopis*, we collected paired samples of the biomass of *Prosopis* leave and of directly adjacent *Acanthus* sp. (mainly *Acanthus polystachyus* Delile) as a non-fixing reference vegetation (composite sample from seven plants per tile). The C4 grass vegetation (composite sample from seven plants per tile) was sampled only in tiles without *Prosopis* and with a predominance of C4 pasture grasses (mainly *Cenchrus ciliaris* L. and *Cynodon dactylon* L. Pers.) but excluding tiles located on sodic Solonchak soil. All plant samples (*Prosopis*, *Acanthus*, and C4 grasses) were oven-dried, fine-ground, and analyzed for total nutrient concentrations. Soil pH was determined in water, using a 1:2.5 soil:water ratio. Total C and N in both soil and plant samples

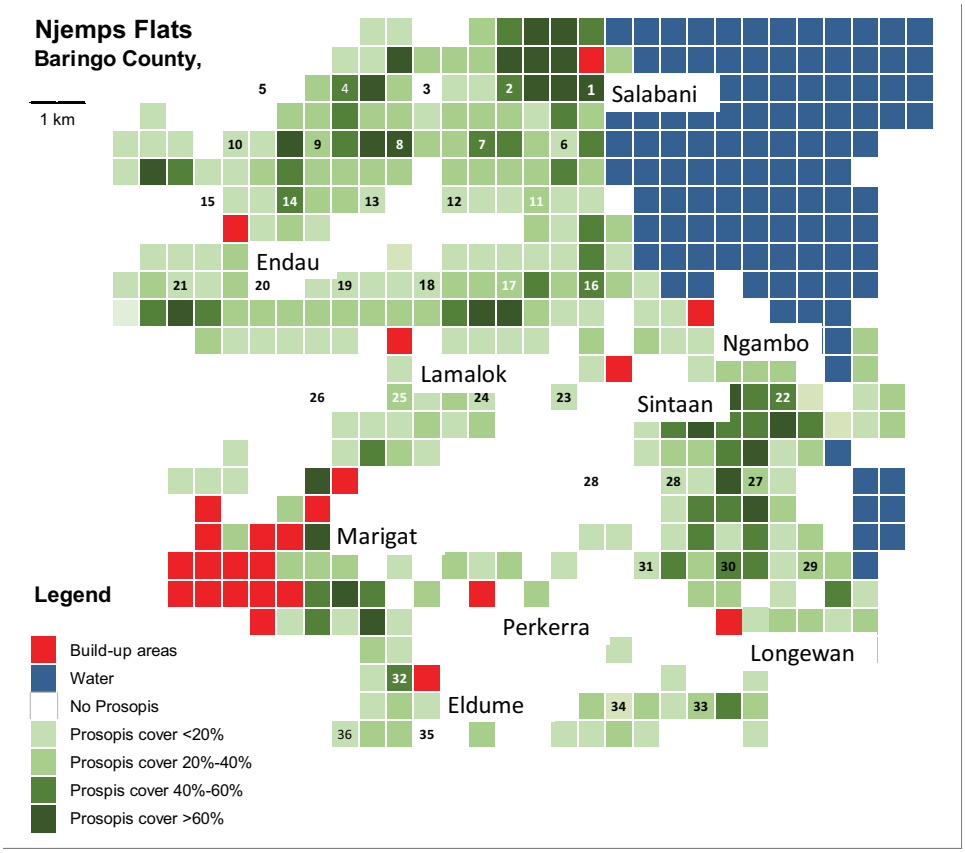

FIGURE 1 | Characterization of the *Prosopis* invasion in the Njemps Flats of Baringo County, Kenya. The area was subdivided into 750 tiles of 500 × 500 m; 75 tiles—10% of the area—were randomly selected; in each tile, observation plots of 10 × 10 m were used to assess *Prosopis* density (number of individuals m^{-2}) and *Prosopis* cover (%), and to collect soil (composites of seven individual samples).

were determined by C-N Elemental Analyser (EuroEA 3000 Series). Available P and extractable soil K were measured photometry, following the modified Olsen extraction. Soil samples were further analyzed for exchangeable Ca and Mg by flame photometry, following acetate-lactate extraction. Plant samples were analyzed for the same elements following pressure digestion.

For determining the staple isotope signatures of plants and soils in non *Prosopis*-invaded pastures, we selected only tiles with a prevalence of C4 grass vegetation on Cambisol or Fluvisol soils ($n = 8$), excluding all tiles in wet grasslands on sodic Solonchak soils. This was required, as for such sites, no Prosopis-infested site existed for pairwise comparisons. For the *Prosopis* sampling, we selected only tiles with >30% *Prosopis* cover on either Cambisol of Fluvisol soils, excluding the rocky foot slopes on Leptosol soils. Tiles with young *Prosopis* stands consisted of plants with a stem base diameter of <1 cm, assuming a plant age of <5 years (recent invasion; $n = 9$). Tiles with old *Prosopis* stands consisted of plants with a stem base diameter of >5 cm, assuming a plant age of >10 years (long-term invasion; $n = 27$). The soil samples taken under C4 grass pasture or under young and old *Prosopis* stands were stratified by dividing them into three layers of (1) 0–2.5 cm, (2) 2.5–5 cm, and (3) 5–15 cm. The isotope ratios of C (Staddon 2004) and N (Teixeira et al. 2006) in both plant and stratified soil samples were assessed by mass spectrometry using a coupled GC-MS (ANCA-SL 2020 mass spectrometer), and data were expressed as ‰ natural abundance of $\delta^{13}C$ and $\delta^{15}N$.

The share of nitrogen derived from the atmosphere (%Ndfa) in *Prosopis* (but also in organic matter at different soil depths) was calculated as:

$$\%\ \text{Ndfa} = \frac{\delta^{15}\text{N (reference)} - \delta^{15}\text{N (}Prosopis\text{)}}{\delta^{15}\text{N (reference)} - B\text{-value}} \times 100. \quad (1)$$

We used a "B-value" (natural isotopic discrimination) of *Prosopis* of −1.6‰ ^{15}N as suggested by Kurdali and Al-Shamma'a (2009) and later confirmed by Lebrazi and Fikri-Benbrahim (2022). We used *Acanthus polystachyus*, growing directly adjacent to the sampled *Prosopis* plants as a non-fixing reference vegetation ($\delta^{15}N$ reference).

2.4 | Data Analysis

Data were cleaned, and descriptive statistics (mean and standard errors of the mean as well as Pearson's linear regressions) were done in Excel. The abundance of plant species was recorded both as cover (percentage area share) and as density (expressed as number of individuals per 1 m^2). Due to their non-normal distribution, data on *Prosopis* cover were log-transformed before analysis of variance (ANOVA) and mean separation by Tukey test. The soil pH values were square root transformed to meet normality assumptions, while no transformation was necessary for the other soil variables before analysis. We applied princi-

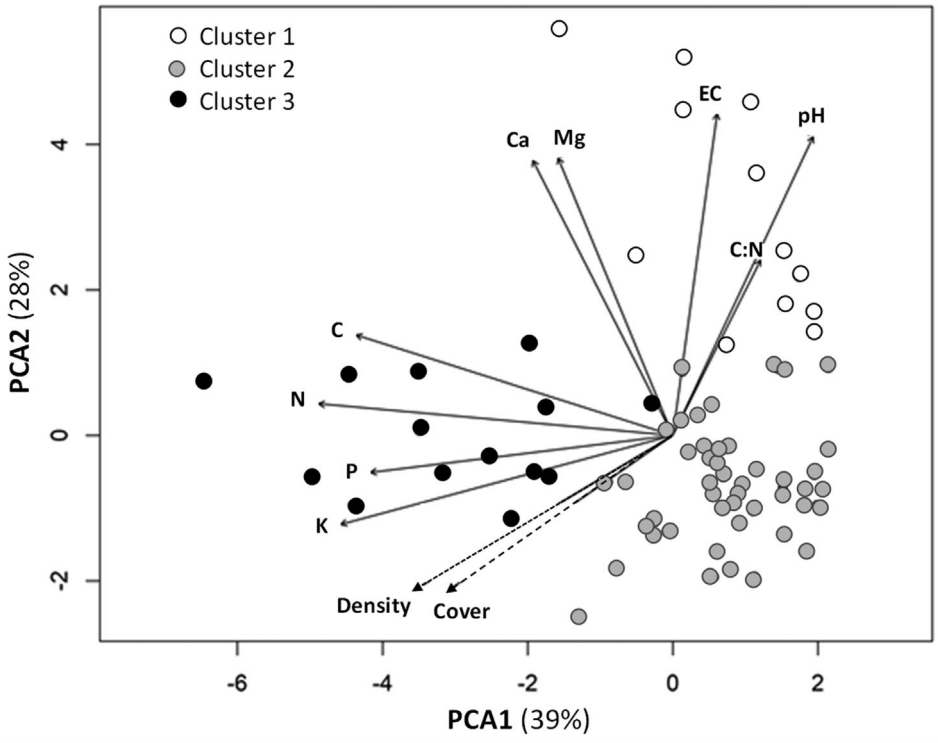

FIGURE 2 | Principal component analysis and k-means clustering of selected topsoil attributes with fitted *Prosopis* stand characteristics (density and cover) in Baringo County, Kenya.

pal component analysis for data ordination of normalized soil variables, complemented with k-means clustering forming three cluster groups, and fitted *Prosopis* stand attributes. The mean separation of soil attributes by cluster group was done by Dunn test with Holm correction ($p < 0.05$). These analyses were done using R 4.4.2 (R Core Team 2024).

3 | Results

3.1 | Variations in Prosopis Density and Soil Quality Attributes

We estimated the density and cover of *Prosopis* in the field, and the spatial distribution of land cover classes strongly varied across the Njemps Flats (Figure 1). There were distinct hotspots with high or very high densities of *Prosopis*, mainly around Salabani, North of Lamalok, East of Marigat, and South of Ngambo. On the other hand, *Prosopis* was largely absent on intensively cropped areas in the centre of the floodplain and within the Perkerra irrigation scheme, in pasture land on Vertisol areas, on the fringes of the floodplain with deep groundwater tables, as well as in wet grasslands on sodic Solonchak soil (data not shown).

Similarly, different soil fertility-related attributes varied strongly between the sampling points (tiles). The electrical conductivity (EC) was generally low but reached >2 dS m^{-1} on sodic soils (Solonchak) in the South of the Njemps Flats. The soil pH followed a similar pattern with values of >7.5 on sodic soils and near-neutral pH elsewhere (high significant correlation between EC and pH; Table S1). Soil C and N contents were generally low and were closely inter-correlated. While extractable K contents were mostly within the sufficiency range for crop production, available soil P varied between very low (<3 mg kg^{-1}) to high (>20 mg kg^{-1}). Exchangeable Ca and Mg contents showed little variation and were mostly within the sufficiency range.

3.2 | Relationships Between Fertility and Prosopis Density

In a subsequent step, we assessed associations of soil fertility attributes with *Prosopis* density and cover values. As already indicated, both densities and cover of *Prosopis* were negatively correlated with EC and pH, with complete absence of *Prosopis* on Solonchak soils. Only the *Prosopis* cover (not the plant densities) appears to be associated with high C and N, and with high available P and exchangeable Ca contents of the soil (Table S1). Absolute values and ranges of soil attributes were sub-divided by *Prosopis* density classes (low, medium, high; Table 2). The data confirm that high stand densities and cover values of *Prosopis* are associated with low EC and pH values and with the highest soil carbon (0.78%) and nutrient contents (56, 16, and 45 mg kg^{-1} of K, P, and Ca, respectively). Vice-versa, low *Prosopis* invasion classes show the lowest soil nutrient contents, mainly those for C, N, P, and K. In addition, principal component analysis and k-means clustering discriminated three distinct cluster groups of associations of *Prosopis* stand and soil fertility attributes (Figure 2) with explained variance of 39% for PCA–1 and 28% for PCA–2. The data from sampling tiles on sodic Solonchak soils (high pH and EC values) form a distinct cluster with a near-complete absence of *Prosopis*, marked in while colour (Cluster 1 in the ordination). This sodic cluster was distinct from the clusters of high soil fertility with high stand densities or high *Prosopis* cover

(black colour) and of low fertility and low stand densities (grey colour). High stand densities and cover values were associated with high C, N, P, and K contents, as well as with low pH and EC of the soil. Extractable Mg and Ca show an intermediate position with no clear associations with either cover or density of *Prosopis*. The detailed relationships of the cluster groups and selected soil attributes are presented in Figure S2. They highlight negative relationships between *Prosopis* density (upper left) and cover (upper right) with pH and EC (lower graphs), and positive relationships with soil C and N as well as with P and K contents (middle graphs). Consequently, our data confirm high *Prosopis* invasion to be associated with high soil fertility or with favourable soil attributes.

3.3 | Vegetation Attributes and Isotope Signatures

In a final step, we elucidated if high soil fertility (or the prevalence of favourable soil attributes) has been instrumental for the invasive spread of *Prosopis* (initial fertility scenario), or if soil fertility was rather improved under *Prosopis*, irrespective of the initial soil fertility status (induced fertility scenario). Accordingly, we analyzed the C and N isotope signatures of the C4 pasturelands that dominated the land use of the Njemps Flats until the early 2000s, and of areas that have more recently been invaded by *Prosopis* (<5 vs. >10-year-old stands).

The N content of *Prosopis* was 3.2% compared to 1.9% in pasture grasses (effect of biological N_2 fixation by *Prosopis*). The content of P in the dry biomass of *Prosopis* (0.24%) was higher than in C4 grasses (0.13%), and irrespective of available soil P content, suggesting likely mechanisms of soil P mobilization. In addition, the Ca contents in *Prosopis* of 0.48% varied little, irrespective of soil Ca contents of the topsoil, suggesting Ca pumping from the subsoil or from the groundwater.

We further analyzed the vegetation as well as the soil samples from different depths for $\delta^{15}N$ and $\delta^{13}C$, assuming subsoils showing the δ signatures of the initial pasture vegetation, while topsoils reflecting the prevailing current vegetation cover. Finally, we related isotope signatures to current soil C and N contents as proxy indicators for soil fertility. The analysis of plant samples reflected the nutrient contents expected for monocotyledonous (pasture grasses) and dicotyledonous plants (*Prosopis*) (Table 2). The carbon isotope signature of the pasture grasses was typical for C4 plants, with $\delta^{13}C$ contents of −14‰ to −17‰. *Prosopis* leaves, on the other hand, showed the $\delta^{13}C$ signature typically expected for C3 plants (−25‰ to −28‰). In addition, the N signatures of the grass vegetation reflected those of the soil (8.8‰ $\delta^{15}N$), while the ^{15}N content of *Prosopis* has been lowered (dilution by atmospheric N_2) to 6.5 $\delta^{15}N$ (range of 4.6‰–8.7‰). Accordingly, the average rate of biological N_2 fixation by *Prosopis* was determined as about 17% N derived from the atmosphere (Ndfa). This share of N_2 fixation (but also the N isotope signature of the soil) differed between locations and soil class (Table 3). The highest δ signatures of the soil (or the non-fixing *Acanthus polystachyus* reference vegetation) were observed in Vertisol (9%) and the lowest in Leptosol soils (7%). Accordingly, the shares of N_2 fixation by *Prosopis* varied between 10% in the alluvial fan (Leptosol soils) on the western side of the floodplain, 15%–17% on Vertisol and 22%–25% Ndfa on Fluvisol and Cambisol soils.

Considering the distribution of both the C and the N staple isotope signatures along the soil profile can inform on past and present soil fertility attributes, and regarding the role of the prevailing vegetation cover. Table S2 presents the data on total soil C and N, the isotope signatures of $\delta^{13}C$ and $\delta^{15}N$, and the shares of N in soil organic matter derived from N_2 fixation in young (<5-year-old) and old (>10-year-old) *Prosopis*-invaded soil. While isotopic signatures of the top-most soil layer (0–2.5 cm) largely reflect those of the dominant vegetation (C4 grasses or *Prosopis*), such differences gradually disappeared with depth, reaching the values of the initially prevailing C4 grass vegetation of –23% $\delta^{13}C$, and intermediate values between C4 grasses and *Prosopis* with +7.5% $\delta^{15}N$ at depth of 5–15 cm (Figure 3). The differentiation from C4 grass-dominated soils was more pronounced under old (>10-year-old) than in young (<5-year-old) *Prosopis* stands. These patterns confirm the effects of the currently prevailing vegetation in the top-most soil layer, while largely reflecting the initially prevailing C4 vegetation at deeper soil layers, irrespective of soil fertility attributes.

4 | Discussion

Nearly the entire floodplain of the Njemps flats is affected by *Prosopis* invasion as reported before (Choge, Mbaabu, and Muturi 2022; Masakha and Wegulo 2015). Exceptions are the dry footslopes of the western escarpment (Leptosol) and the alkaline wet grasslands (Solonchak) in the South (Figure 1). However, *Prosopis* stand densities differ by land use (partial control in croplands) and soil type (low cover on Vertisol soils; Alvarez et al. 2019). The complete absence of *Prosopis* on the Solonchak soils with EC >2 dS m^{-1} and pH >7.5 in the present study contradicts previous observations from India (Bhojvaid and Timmer 1998), Egypt (Abbas et al. 2017), and Iran (Moradi et al. 2017), resulting in recommendations to use *Prosopis* for the afforestation and reclamation of saline and sodic soils (Singh 2022).

The present data (Table 1, Figure 2) suggest high stand densities of *Prosopis* being associated with favourable soil attributes, as also suggested by Kamiri, Choge, and Becker (2024). Similarly, in their native range of distribution in Venezuela and Peru, but also in India and the United States, encroaching or invading capacities of *Prosopis* (here several different species) appear to be associated with high soil C and N contents (Kaur et al. 2012). Other works (Becker et al. 2016; Eshete et al. 2020; Masakha and Wegulo 2015) have attributed a rapid invasive spread and high stand densities of *Prosopis* to high available soil P and high concentrations in the basic cations K, Ca, and Mg. As a result, spatial models for defining and mapping areas with high risk for future *Prosopis* invasion have been based (besides altitude) on hydro-edaphic conditions in Kenya (Alvarez et al. 2019) and elsewhere (Abbas et al. 2023; Dakhil et al. 2021; Rembold et al. 2015; Sintayehu, Egeru, and Ng 2020).

While most of these studies considered high soil fertility to be a prerequisite for *Prosopis* spread dynamics, others (i.e., Patnaik, Abbasi, and Abbas 2017) suggested soil fertility attributes to improve under *Prosopis* cover. Thus, the deep root system of *Prosopis* (and of other deep-rooting agroforestry species) has been shown to provide opportunities to capture deep soil nutrients (mainly K, Ca, and Mg). These elements accumulate in the

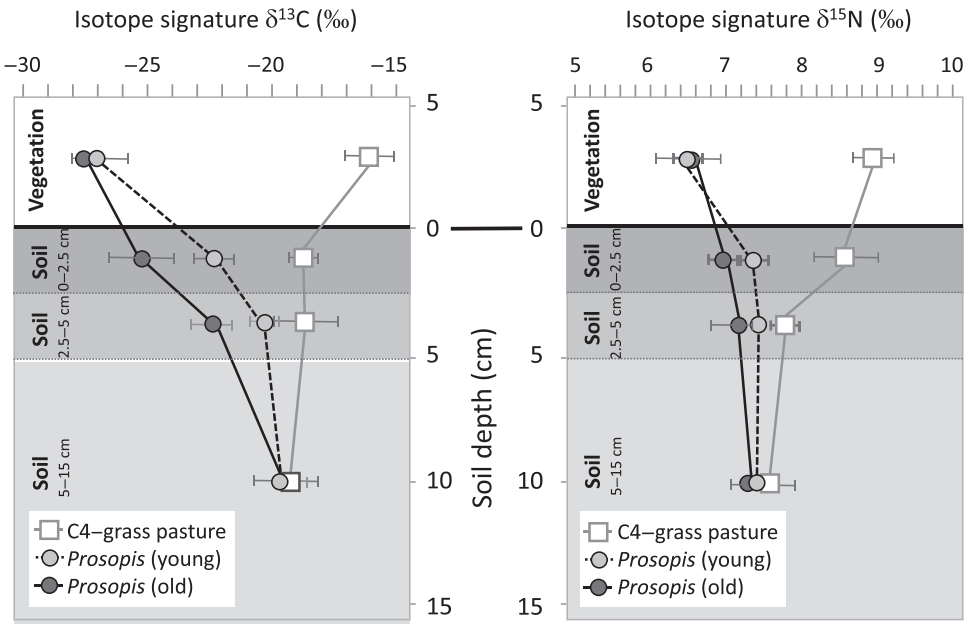

FIGURE 3 | Isotope signatures (δ^{13}C and δ^{15}N) at different depths of the topsoil, comparing of C4 grass-dominated pastures and C3 *Prosopis*-invaded land in Baringo County, Kenya. Young *Prosopis:* <5 years, stem base diameter <1 cm; old *Prosopis:* >10 years, stem base diameter >5 cm. Bars present standard errors of the mean ($n = 8$–27).

TABLE 1 | Topsoil fertility attributes associated with high, medium, and low *Prosopis* invasion (Baringo County, Kenya).

***Prosopis* invasion attributes**		**EC (dS m^{-1})**	**pH value (H_2O)**	**Total C (%)**	**Total N (%)**	**Extr. K (mg kg^{-1})**	**Avail. P (mg kg^{-1})**	**Exch. Ca (mg kg^{-1})**	**Exch. Mg (mg kg^{-1})**
High	Mean	1.11	6.60	0.79	0.08	55.9	15.9	44.7	19.0
(>3 individuals, >35% cover)	SE	0.06	0.09	0.07	0.01	6.1	1.9	4.0	2.6
Medium	Mean	1.49	6.97	0.71	0.07	40.2	14.8	30.1	13.4
(1–3 individuals, <35% cover)	SE	0.18	0.08	0.08	0.01	6.3	2.4	3.7	1.3
Low	Mean	2.03	7.13	0.69	0.07	37.0	9.5	35.2	19.1
(no *Prosopis* present)	SE	0.27	0.09	0.05	0.00	3.9	1.3	6.6	4.5

Note: SE: Standard error of the mean ($n = 14$–26). Available P and exchangeable K, Ca, and Mg were determined after soil extraction by the modified Olsen method.

topsoil, following leaf litter fall (Buresh et al. 2004), in addition to the associated enrichment in soil carbon (Moradi et al. 2017), and generally increased nutrient cycling (Mohanraj, Akil-Prasath, and Rajasekaran 2022). Similarly, the ability of *Prosopis* to fix atmospheric N_2 will enrich the topsoil in N (Pierret et al. 2016; Soper and Sparks 2017). Finally, the abandonment of crop cultivation provides extended periods of rest to the soil, reducing tillage-induced mineralization of soil organic matter. This contributed to a gradual increase in soil C (Haddaway et al. 2017) and the restoration of degraded land in the Njeps Flats (Kahi et al. 2009; Masakha and Wegulo 2015), but also in India (Bhojvaid and Timmer 1998), Iran (Imani, Moradi, and Basiri 2016), and elsewhere (Edrisi et al. 2020).

In the present study, we tried to elucidate this apparent contradiction (initial vs. induced soil fertility scenarios with *Prosopis*). We assumed that the initial soil attributes in the Njemps Flats have been shaped by the prevalence of C4 grass-dominated pastures in the past, while induced soil attribute changes may relate to the invasive spread of the N_2-fixing C3 *Prosopis*. Thus, C4 plants show a typical signature in the natural abundance of the carbon isotope δ^{13}C of −9 to −12‰, while C3 vegetation has typically isotope discrimination values of −20 to −26‰ δ^{13}C (Staddon 2004). On the other hand, the tissue N analysis of non-fixing grasses (here C4-dominated pasture) reflects the natural enrichment of the soil by the staple isotope ^{15}N, while N_2-fixing plants (here *Prosopis*) dilute the increased concentration of the heavy N isotope in the soil by biological fixation from the atmosphere, containing only 0.3663% ^{15}N (Knowles and Blackburn 1993; Unkovich et al. 2008). Combining the δC and δN signatures of both vegetation and soils will thus help defining if *Prosopis* is preferentially invading fertile soils (initial fertility scenario), or if *Prosopis* invasion is rather the driver soil fertility improvement (induced fertility scenario). Tables 2 and 3 show that deeper soil layers had the isotope signatures of the initially prevailing C4 grass-dominated pastures, irrespective of the current soil fertility status. In addition, topsoil

TABLE 2 | Nutrient content (C, N, P, Ca, and Mg), isotope signatures ($\delta^{13}C$ and $\delta^{15}N$), and the share of N derived from biological N_2 fixation (%Ndfa) of C4 grasses and *Prosopis* in Baringo County, Kenya.

Vegetation	C (%)	N (%)	P (%)	Ca (%)	Mg (%)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Ndfa (%)
C4 grass								
Mean	35.9a	1.92b	0.13	0.43	1.12	−16.5b	8.8a	0
SE ($n = 8$)	4.9	0.43	nd	nd	nd	0.3	2.6	
Prosopis (young)								
Mean	37.9a	3.22a	0.25	0.47	0.69	−26.2a	6.42b	15.6
SE ($n = 9$)	2.1	0.20	nd	nd	nd	0.4	2.9	1.5
Prosopis (old)								
Mean	38.1a	3.16a	0.24	0.48	1.42	−27.2a	6.5b	16.7
SE ($n = 27$)	3.2	0.12	nd	nd	nd	1.4	3.0	1.9

Note: Young *Prosopis:* <5 years, stem base diameter <1 cm; old *Prosopis:* >10 years, stem base diameter >5 cm. C4 grass: location-dependent either *Cenchrus ciliaris* or *Cynodon dactylon*. Column data followed by different letters indicate significant differences ($p < 0.05$) by Tukey test.
Abbreviations: B-value: –1.6‰; Ndfa: Percentage share of N derived from the atmosphere; non-fixing reference plant: *Acanthus polystachyus*. nd: not determined as only one single composite plant sample was available.

TABLE 3 | Differentiation of N isotope signatures ($\delta^{15}N$) of non-fixing reference plant and *Prosopis* by soil type.

Location	C4 grass	*Prosopis* (young)		*Prosopis* (old)	
(soil type)	$\delta^{15}N$ (‰)	$\delta^{15}N$ (‰)	Ndfa (%)	$\delta^{15}N$ (‰)	Ndfa (%)
Alluvial fan (Leptosol)					
Mean	7.06	6.28	8.9	6.30	9.9
SE ($n = 10$)	0.49	0.25	1.2	0.21	1.2
Cropland (Vertisol)					
Mean	8.95	7.75	14.7	7.31	16.9
SE ($n = 8$)	0.10	0.27	1.5	0.26	1.5
Pastureland (Fluvisiol)					
Mean	8.68	7.93	24.7	8.70	21.7
SE ($n = 47$)	0.15	0.12	2.7	0.15	2.4

Note: Young *Prosopis:* <5 years, stem base diameter <1 cm; old *Prosopis:* >10 years, stem base diameter >5 cm. Correspondence of soil types with tile numbers (Figure 2). Leptosol: 10,15,20,21; Vertisol: 22,27,28,30; Fluvisol: other tiles. C4 grass: *Cenchrus ciliaris* or *Cynodon dactylon* depending on availability at specific locations. Non-fixing reference for Ndfa calculation: *Acanthus polystachyus*.
Abbreviations: B-value = –1.6‰; Ndfa = Nitrogen derived from the atmosphere; non-fixing reference: *Acanthus polystachyus*.

attributes significantly improved under dense *Prosopis* stands, or when comparing soils under old (>10 years) and young (<5 years) *Prosopis* stands (Table 1, Figure 3). In consequence, we reject the "initial fertility scenario" and confirm the improvement of soil attributes by *Prosopis* (induced fertility scenario), irrespective of the initial soil attributes. Thus, the invasive spread of *Prosopis* is mainly the result of shallow ground water tables and the seed distribution and scarification by endozoochory (Alvarez et al. 2017; Becker et al. 2016).

The widely reported negative effects of *Prosopis* invasion on biodiversity and rural livelihoods (Kamiri, Choge, and Becker 2024) may thus be partially counteracted by an improvement in soil fertility attributes. The recent trend in the Njemps Flats of clearing *Prosopis* stands for the commercial production of hybrid maize and forage grass seeds and of high-value vegetables was the result of infrastructure development (roads and irrigation canals) and of new marketing opportunities for high-value products (Sainepo, Behn, and Becker 2024). This agricultural intensification can thus take advantage of favourable soil conditions in former *Prosopis* stands. It may benefit future rural livelihoods and accelerate and improve the control of the invasive spread of *Prosopis* by mechanical land clearing and commercial crop production in the Njemps Flats of Baringo County and in similar *Prosopis* infested sites beyond.

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Data Availability Statement

The datasets generated during the current study are stored in the Bonn University Data Server (Campus Cloud—Sciebo) and will be made available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.