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High rates of nitrogen fixation and transfer by pigeon pea (*Cajanus cajan*) to associated crops in a semi-arid agroforestry system

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Abstract The integration of pigeon pea as a leguminous shrub into agroforestry systems (AFS) is expected to enhance soil nitrogen and its availability for associated crops. This study aimed to estimate, over a three-month period, the atmospheric nitrogen fixation rate (%Ndfa) by two-year-old pigeon pea (*Cajanus cajan*) grown as a sole crop and in association with cassava (*Manihot esculenta*), and the transfer of N from pigeon pea to cassava (%Ndft) in the mixed pigeon pea-cassava plots. The ^{15}N isotope dilution method was used with six-month-old sole cassava crops as reference. Nine plots (three replicates per treatment) were randomly selected in farmers' fields. A 100 m^2 area was delimited in each plot for ^{15}N soil labeling using 98 atom% ^{15}N-NH_4 solution. Plant samples were collected from both species for isotopic analysis. Results showed that %Ndfa was 100% in both pigeon pea systems. Considering %Ndfa of 100% from planting date, the quantity of N fixed was twice as high in sole pigeon pea (19.7 kg N ha^{-1}) as in mixed pigeon pea-cassava (7.4 kg N ha^{-1}). This finding was consistent with the 2.8 times higher planting density in sole pigeon pea plots compared to mixed pigeon pea-cassava plots. Nitrogen transfer from pigeon pea to cassava was greater (73.9%) when the cassava plant was positioned between pigeon pea rows (in the middle) rather than adjacent to them (42.8%). Our results suggest that integrating pigeon pea into semi-arid AFS could enhance the nitrogen status of the associated crop, particularly in unfertilized AFS.

Keywords Leguminous shrubs · Cassava · Symbiotic N_2 fixation · N transfer

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Introduction

Agroforestry is described as a mixed cropping system that includes at least one perennial woody species and one species grown for forage or annual or perennial crop production (Somarriba 1992). Agroforestry systems (AFS) can sustain smallholder production and enhance social, economic and environmental benefits (Leakey 2017). These systems can require less tillage and provide more organic matter to the soil than annual cropping systems, thereby improving crop nutrition (Bekele-Tesemma 2007; Mafongoya et al. 2007; Sileshi et al. 2020). AFS often include nitrogen-fixing plant species (NFS), which help to improve soil fertility and crop nutrition (Rosenstock et al. 2014; Menge et al. 2014). NFS improve the availability of nitrogen (N) which is frequently deficient in semi-arid areas (Yahdjian et al. 2011), and help to create favorable micro-environments for crop development (Nair et al. 2021). This role is particularly important given the frequent problem of N losses in conventional cropping systems through export at harvest (Kim and Isaac 2022), ammonia (NH_3) volatilization, and nitrate (NO_3) and ammonium (NH_4^+) leaching (Cameron et al. 2013; Elrys et al. 2022; Kim and Isaac 2022). By contrast, N-fixing tree or shrub species can reduce N loss within AFS and supply N to the system through atmospheric dinitrogen (N_2) fixation (Kim & Isaac 2022; Nygren et al. 2012). This process of N_2 fixation is nonetheless influenced by environmental factors, including soil nutrients (Bordeleau and Prévost 1994) and seasonal variation (Paula et al. 2018; Dovrat and Sheffer 2019). N_2 fixation by soybean can decrease with drought stress (Serraj et al. 1999; Freitas et al. 2022) and low soil phosphorus (P) availability (Yao et al. 2022) can decrease N_2 fixation due to reduced photosynthesis and a lower supply of photosynthates to the nodules (Sheoran et al. 1988; Nandwal et al. 1991).

Crops associated with NFS can benefit from direct N transfer through root exudates and common mycorrhizal networks, or indirectly through litter mineralization, and fine root and nodule turnover (Nygren et al. 2012; Munroe and Isaac 2014; Paula et al. 2015; Thilakarathna et al. 2016). Previous studies in tropical environments suggested that N transfer may be stronger when the associated crop is grown close to the NFS (Paula et al. 2015). Based on a literature review of the N uptake pathway, Zayed et al. (2023) reported that in N-deficient soils, plants may activate physiological and molecular mechanisms to improve their N uptake efficiency. For example, *Eucalyptus* hybrids (*E. grandis* x *E. urophylla*) grown in association with *Acacia mangium* developed a more extensive root system and were likely to increase root exudation (Oliveira et al. 2021). These traits contribute to improved N transfer from NFS to the associated crop in mixtures (Oliveira et al. 2021).

Among the NFS used in AFS, pigeon pea (*Cajanus cajan* (L.) Millsp) is one of the species recommended for semi-arid areas (Daniel and Ong 1990; Mula and Saxena 2010; Saxena et al. 2019). This leguminous shrub is adapted to harsh climatic and environmental conditions such as low rainfall and nutrient-poor soil (Odeny 2007; Mula and Saxena 2010; Saxena et al. 2019). Pigeon pea efficiently fixes atmospheric N_2 (Kumar Rao and Dart 1987; Sameer Kumar et al. 2017; Bopape et al. 2022). For example, in semi-arid Kenya, the percentage of N derived from atmospheric fixation (%Ndfa) of five pigeon pea varieties was greater than 80% in the roots, leaves, stover, and grains (Kwena et al. 2019).

The southern Androy region of Madagascar is characterized by a semi-arid climate, with frequent droughts, and severe wind erosion. These environmental constraints, combined with widespread poverty, led to deforestation, poor soil fertility and low agricultural productivity (Violas et al. 2020). To address this issue, a land-use strategy, locally referred to as "agroecological blocks", was implemented in 2014. These blocks cover a minimum area of 10 ha and include agroforestry zones (AFS-zones) where different vegetation strata, ranging from trees and shrubs to creeping plants, are combined (Violas et al. 2020). AFS-zones are expected to limit wind erosion and improve soil fertility by integrating ground cover species and NFS (Violas et al. 2020), strengthening the resilience of agroecosystems to drought while supporting food production (Fahad et al. 2022; Pancholi et al. 2023; Octavia et al. 2023).

Pigeon pea is one of the key species used in these AFS-zones, either as sole crop or as an associated crop with cassava, sorghum or maize. The limited access of farmers to fertilizers as observed in this region (Violas et al. 2020) likely leads to progressive soil nutrient depletion (Vanlauwe et al. 2023). The integration of pigeon pea into the AFS-zone is therefore expected to promote N input and improve the N

status of the soil and associated crops. The stress-gradient hypothesis suggests that facilitative interactions (as N_2 fixation and N transfer) increase under stressful environmental conditions such as those in the study area while competitive interactions decrease (Callaway and Walker 1997; Maestre et al. 2009; Holmgren and Scheffer 2010; Kikvidze et al. 2011). However, as far as we are aware, there is no information on the amount of N_2 fixation by AFS in semi-arid regions of Madagascar. Moreover, no work reports N transfer in AFS involving pigeon pea. The aim of our study was to assess the rates and amounts of N_2 fixation by pigeon pea and N transfer to the associated crop. We hypothesized that both processes would occur at high rates given the adverse conditions of the study area. We also hypothesized higher N transfer adjacent to pigeon pea rows than between the rows. The results should optimize the management of semi-arid AFS with pigeon pea as the tree component, by guiding their spatial configurations to enhance biological N input and improve soil fertility without external inputs.

Materials and methods

Study site

The study was carried out in the Karoke Mahandrorano AFS-zone (25°15'15"S, 46°1'21"E), located in the Androy region of South Madagascar near the city of Ambovombe, at 200 m above sea level. Established in 2013, this is one of the oldest AFS-zones in the region, and serves as a reference site for the other AFS-zones. The site is located in a coastal area, and the soil is a cambic arenosol according to the FAO classification (FAO 2014) which is underlain by a limestone formation, with bedrock outcrops at a depth of about 150 cm. The relief was characterized by gently undulating topography with slope < 5%. The soil texture was uniform below a depth of 30 cm with 79% sand, 18% clay and 3% silt (Razafimahatratra 2022). The soil pH_{H2O} ranged from 7.2 to 9.1 depending on the plots. Soil chemical analyses down to a depth of 0.30 m are given in Table 1.

The experimental area was characterized by low topsoil fertility (0–30 cm). According to Boyer (1982), the critical deficiency concentrations for plants grown on tropical soils are 0.5 g N kg^{-1} for total N and 3 mg P kg^{-1} for available P, while the deficiency thresholds are 1.5 g N kg^{-1} and 10 mg P kg^{-1}, respectively. Our soil analysis integrating three layers (depth 0–10, 10–20 and 20–30 cm, Table1) showed total N levels below both the critical level and the deficiency threshold, while available P levels were comparable to the critical level but still above the deficiency threshold.

Table 1 Main chemical soil attributes at three depths (0–10, 10–20, and 20–30 cm) in the plots without pigeon pea at the AFS-zone study area (mean values ± standard deviation; n = 4)

Soil depth (cm)	0–10	10–20	20–30
pH	8.92	8.62	8.70
Organic C (g kg^{-1})	2.83 ± 0.69	2.46 ± 0.58	1.95 ± 0.61
Total soil N (g kg^{-1})	0.29 ± 0.08	0.21 ± 0.06	0.20 ± 0.05
Available P (mg k^{-1})	5.07 ± 2.24	2.58 ± 1.32	2.88 ± 1.45
K ($cmol^{+}kg^{-1}$)	0.03 ± 0.01	0.02 ± 0.01	0.02 ± 0.02
Ca ($cmol^{+}$ kg^{-1})	1.65 ± 1.04	1.68 ± 1.03	1.70 ± 1.24
Na ($cmol^{+}$ kg^{-1})	0.01 ± 0	0.01 ± 0	0.02 ± 0

The climate of the region is classified as BSh (semi-arid hot) according to the Köppen-Geiger classification (Beck et al. 2018), with a wet season from December to April and a dry season from May to November (Figure 1). The average annual temperature is 24.4 °C, with temperatures varying from 19 °C (minimum in June) to 40 °C (maximum in January). Annual rainfall ranges from less than 300 to 600 mm, occurring mainly during the wet season. Sporadic and limited rainfall may also occur in May and June. However, frequent droughts and irregular rainfall patterns can be observed. For instance, in 2020, no rainfall was recorded for 18 consecutive months, and in some other years, there were only three to four rainfall events per season (UNICEF 2024). Potential evapotranspiration is 518 mm $year^{-1}$, which generally exceeds rainfall throughout the year (JICA 2006). From August to October, strong soil-eroding winds occur (Morlat and Castellanet 2012; Violas et al. 2020).

The study was conducted over 90 days starting in January 2024 and ending in April 2024. During this period, the average air temperature was 22.5 °C and the cumulative rainfall was 224 mm (https://www.historique-meteo.net).

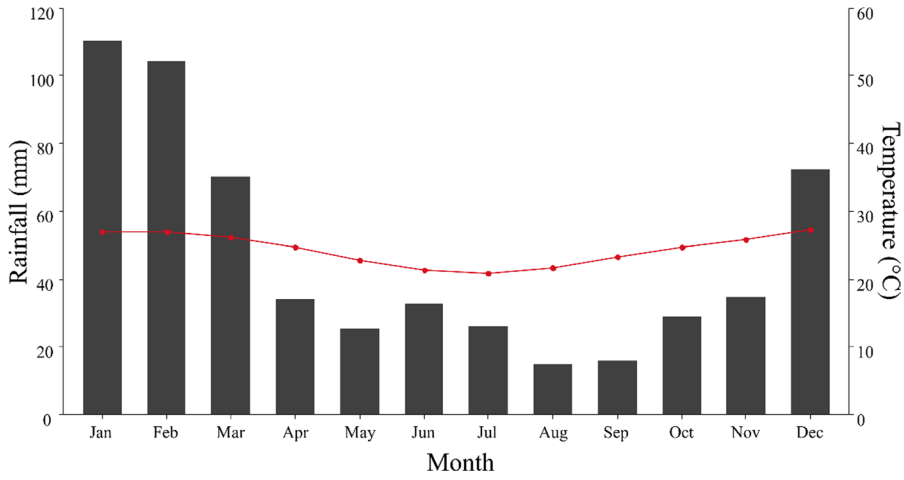


Fig. 1 Mean monthly rainfall (mm, bar graph) and mean monthly temperature (°C, line graph) in Ambovombe from 2014 to 2024 (data source https://www.historique-meteo.net)

Experimental design

The ^{15}N isotope dilution method was used to estimate the %Ndfa. The method was applied to sole pigeon pea, mixed pigeon pea-cassava (*Manihot esculenta* Crantz), and sole cassava systems. Nine farmers' fields were randomly selected within the AFS-zone for the soil labeling, corresponding to three treatments (herein referred to as cropping systems) with three replicates per cropping system: sole crop pigeon pea, mixed pigeon pea-cassava, and sole crop cassava. At the time of the experiment, all pigeon pea plants were two years old, and the cassava plants were six months old. Cassava, which is a non-N_2 fixing species, was chosen as the reference plant for %Ndfa estimation (Boddey et al. 1990). The cropping systems followed a pattern that was established by CTAS NGO, the "Centre Technique Agroécologique du Sud", the organization responsible for their management (Figure 2). Due to the highly limiting environmental conditions, there was little variation in management practices.

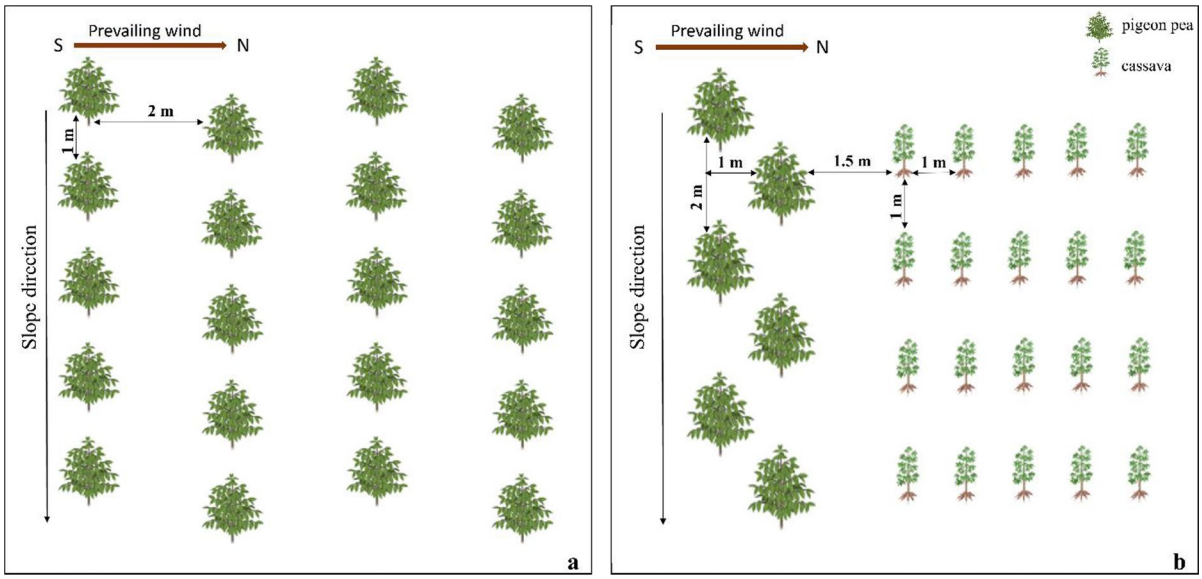


Fig. 2 Spatial arrangement and row direction of pigeon pea. **a)** Sole pigeon pea cropping system **b)** Mixed pigeon pea–cassava cropping system. For each field, the pigeon pea row is perpendicular to the prevailing wind

No organic or mineral fertilizers were applied in the AFS-zone.

^{15}N soil labeling

For each treatment and each field, an area of 100 m^2 was delimited for the ^{15}N soil labeling. Ammonium chloride (Cl-$^{15}NH_4$) with 98 atom% ^{15}N was applied in this area at a rate of 0.8 kg N ha^{-1} between 15 and 17 January 2024. The fertilizer was diluted in water and applied uniformly to the soil using a watering can. We assumed that the low amount of applied N did not affect the N_2 fixation of pigeon pea (Bouillet et al. 2008).

Plant sampling and analysis

In each sole and mixed cropping systems, pigeon pea plants were inventoried by counting individuals to determine mean planting density and plant height. The planting density of pigeon pea was higher in the sole crop system (3464 individuals ha^{-1}) than in the mixed pigeon pea-cassava system (1216 individuals ha^{-1}) where pigeon pea was planted only in rows spaced 6 to 8 m apart (Figure 3). Aboveground leaf biomass was estimated by randomly collecting leaves from 10 shrubs per plot, replicated four times (80 shrubs in total, Table 2). Both fresh and dry masses were recorded.

Leaf samples for N analysis were collected separately for each species at two dates: before soil labeling (January 2024) and 90 days after (April 2024). In the sole pigeon pea system, 20 leaves per shrub were sampled from five shrubs arranged in a cross pattern (Figure 3a). Leaves were collected from the upper crown on opposite branches (north–south and east–west) and pooled to make a composite sample representative of the system (Table 2). In the sole cassava system, four leaves per plant were collected from 10 plants using the same sampling design (Figure 3a). In the mixed pigeon pea-cassava system, pigeon pea leaves were collected from five shrubs in a row, with 20 leaves per shrub (Table 2), while cassava leaves were sampled at three distances from the pigeon pea row: adjacent, ¼ of the inter-row, and ½ of the inter-row (Figure 3b). The sampled leaves were dried to

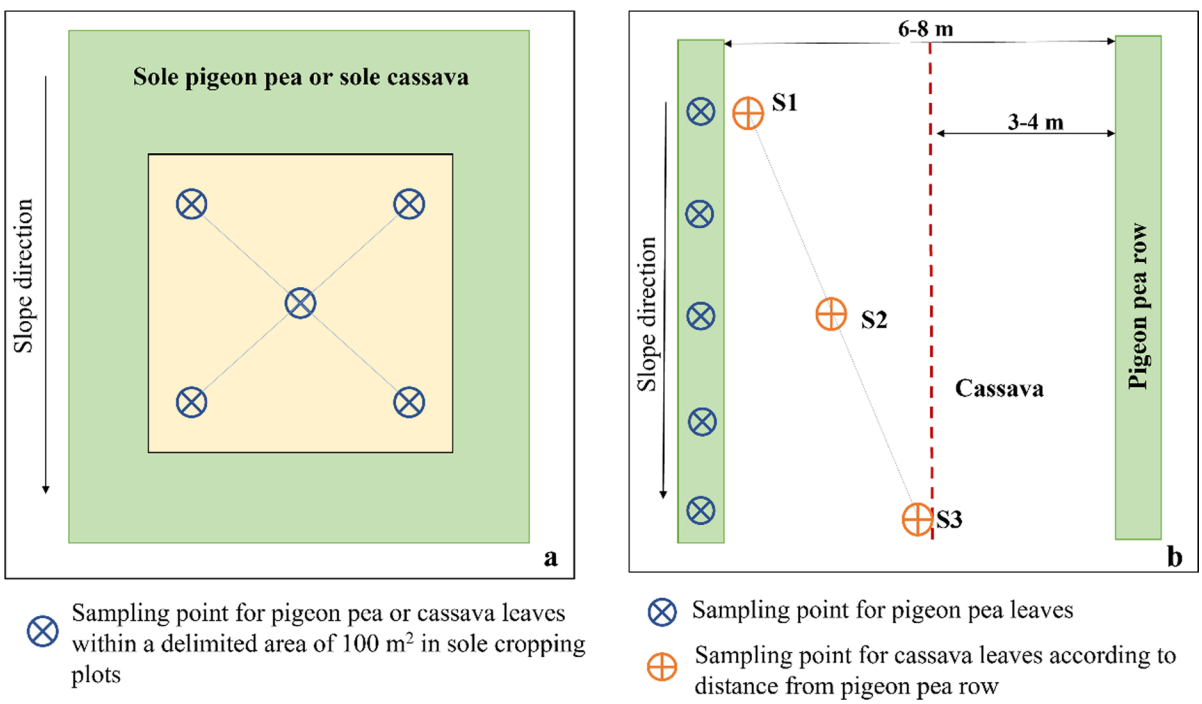


Fig. 3 Leaf sampling method in plots for nitrogen analysis. **a)** Sampling points for leaves in the sole pigeon pea or in sole cassava plots. **b)** Sampling points for leaves in the mixed pigeon pea-cassava plots. S1: adjacent to pigeon pea, S2: ¼ of the inter-row, and S3: ½ of the inter-row

Table 2 Number of pigeon pea plants sampled for leaf biomass and leaf samples for nitrogen analysis in sole and in mixed cropping systems

		Pigeon pea plants sampled for leaf biomass	Sampled leaves for N analyses
Sole crop	Pigeon pea	10	100
	Cassava	–	40
Mixed crop	Pigeon pea	10	100
	Cassava	–	30
	Replicates	4	3
	Total	80	810

constant weight at 60 °C and ground to 0.5 mm using a disc mill, and sent to the SILVATECH Laboratory (https://www6.nancy.inrae.fr/silva/Plateformes/Silva Tech) for ^{15}N and N analysis. For this purpose, subsamples of 10 mg were placed in tin capsules. Total N concentrations and $\delta^{15}N$ of the leaves were determined using an elemental analyzer (vario ISOTOPE cube, Elementar, Langenselbold, Germany) coupled, via a gas box interface, to a continuous flow isotope ratio mass spectrometer (Isoprime100, IRMS, Elementar UK, Cheadle, United Kingdom). The precision of $\delta^{15}N$ measurement was 0.5‰.

Nitrogen derived from atmospheric fixation (%Ndfa) and N transfer (%Ndft)

The percentage of N derived from N_2 fixation (%Ndfa) for each plot during the experiment was estimated by using ^{15}N Atom Excess (AE) with the following equation (Bouillet et al. 2008):

$$\%Ndfa = 100\left(1 - \frac{\frac{(N_{Ffinal}AE_{Ffinal} - N_{Finitial}AE_{Finitial})}{(N_{Ffinal} - N_{Finitial})}}{\frac{(N_{REFfinal}AE_{REFfinal} - N_{REFinitial}AE_{REFinitial})}{(N_{REFfinal} - N_{REFinitial})}}\right) \quad (1)$$

where: AE = ^{15}N atom% - 0.3663, AE_{Ffinal}, $AE_{Finitial}$, $AE_{REFfinal}$, and $AE_{REFinitial}$ are the percentage atom excess of pigeon pea 90 days after soil labeling, the percentage atom excess of pigeon pea at soil labeling, the percentage atom excess of cassava 90 days after soil labeling, and the percentage atom excess of cassava at soil labeling, respectively. N_{Ffinal}, $N_{Finitial}$, $N_{REFfinal}$, and $N_{REFinitial}$ are the N content of pigeon pea 90 days after soil labeling, the N content of pigeon pea at soil labeling, the N content of cassava 90 days after soil labeling, and the N content of cassava at soil labeling, respectively; 0.3663 ^{15}N atom% is the standard atmospheric ^{15}N abundance (Mariotti 1983).

The proportion of cassava N derived from transfer (%Ndft) from pigeon pea during the experimental period was estimated using equation 2 (Snoeck et al. 2000):

$$\%Ndft = 100 \times \frac{\delta^{15}N_{REF} - \delta^{15}N_{REFasso}}{\delta^{15}N_{REF} - \delta^{15}N_{F}} \quad (2)$$

where: $\delta^{15}N_{REF}$ is the $\delta^{15}N$ value of cassava leaves in sole crop after 90 days ^{15}N labeling, $\delta^{15}N_{REFasso}$ is the $\delta^{15}N$ of cassava leaves in mixed crop after 90 days ^{15}N labeling, and $\delta^{15}N_F$ is the $\delta^{15}N$ of pigeon pea leaves in sole crop after 90 days ^{15}N labeling.

Statistical analyses

One-way analysis of variance (ANOVA) was conducted to compare total N content, $\delta^{15}N$ and AE between the two pigeon pea crop systems, with crop system as fixed factor. For %Ndft in the mixed pigeon pea-cassava system, ANOVA was performed with distance from pigeon pea as fixed factor. Tukey's post-hoc test was used to examine pairwise differences. Assumptions of normality and homoscedasticity of residuals were tested using Shapiro-Wilk and Bartlett tests, respectively. The values were log-transformed when variances were unequal. Statistical analyses were performed using R 4.0.3 and RStudio 4.1.1, with a significance level α of 0.05.

Results

.^{15}N values and percentage of N derived from atmospheric fixation (%Ndfa)

At the start of the experiment, atom excess (AE) mean values differed significantly among the crop systems (*p-value* = 0.009), with higher values in sole cassava leaves (0.007 atom%) than in pigeon pea leaves in sole (0.003 atom%) and mixed crops (0.002 atom%) (Table 3). After 90 days, AE values remained significantly higher in cassava leaves grown as sole crop than in pigeon pea leaves, both in sole and mixed crops (*p-value* < 0.001). On the other hand, the initial N content in pigeon pea leaves in sole and mixed crops (4.20 and 4.82 g N plant^{-1} respectively) was significantly higher (*p-value* < 0.001) than in cassava leaves (0.19 g N plant^{-1}). After 90 days, the N content in pigeon pea leaves remained significantly higher in sole (4.87 g N plant^{-1}) and mixed crops (5.41 g N plant^{-1}), compared to sole cassava (0.19 g N plant^{-1}). The %Ndfa was estimated to be 100% during the 90 days experiment both in the sole pigeon pea and in mixed pigeon pea-cassava systems.

Table 3 N content (g N plant^{-1}), ^{15}N atom excess of leaf samples (AE) in pigeon pea and cassava (^{15}N (atom%)), and %Ndfa of pigeon pea (mean values ± standard deviation, n = 3)

Systems	Leaf samples	Observed parameters*				
		$N_{initial}$	$AE_{initial}$	N_{final}	AE_{final}	%Ndfa
Sole cassava	Cassava	0.19 ± 0.02^{b}	0.007 ± 0.002^{a}	0.19 ± 0.15^{b}	0.083 ± 0.014^{a}	
Sole pigeon pea	Pigeon pea	4.20 ± 0.17^{a}	0.003 ± 0.000^{b}	4.87 ± 0.15^{a}	0.022 ± 0.010^{b}	100^{a}
Mixed pigeon pea-cassava	Pigeon pea	4.82 ± 0.44^{a}	0.002 ± 0.000^{b}	5.41 ± 0.46^{a}	0.011 ± 0.002^{b}	100^{a}

*$N_{initial}$ and N_{final} are the N content of leaf samples on soil labeling and after 90 days, respectively. $AE_{initial}$ and AE_{final} are the values of ^{15}N percentage atom excess at soil labeling and after 90 days, respectively. %Ndfa is the percentage of nitrogen derived from atmospheric N_2 fixation. Different letters (a—b) indicate significant differences ($p < 0.05$) between systems

Table 4 Aboveground pigeon pea growth parameters and nitrogen supply from N_2 fixation %Ndfa in 2-year-old pigeon pea plants, in sole crop and mixed pigeon pea systems (mean values ± standard error, n = 4)

Similar letters indicate no significant differences between systems ($p < 0.05$)

Variables	Sole pigeon pea	Mixed pigeon pea–cassava
Planting density (individuals ha^{-1})	3464 ± 946^{a}	1216 ± 377^{a}
Height (cm)	196.5 ± 8.0^{a}	188.3 ± 18.0^{a}
Leaf biomass (kg)	0.13 ± 0.05^{a}	0.17 ± 0.04^{a}
%Ndfa (%)	100^{a}	100^{a}
N input from N_2 fixation (g N plant^{-1})	5.70 ± 2.37^{a}	7.31 ± 1.74^{a}
N input from N_2 fixation (kg N ha^{-1})	19.76 ± 12.06^{a}	7.40 ± 1.21^{a}

Table 5 Mean ^{15}N values of leaf samples in the three cropping systems and %Ndft in the mixed system in relation to the distance between the non-leguminous crop (cassava) and the leguminous crop (pigeon pea) (mean values ± standard deviation, n = 3)

System	Leaf samples	Distance from pigeon pea	$\delta^{15}N_{final}$ (‰)*	%Ndft*
Sole pigeon pea	Pigeon pea	–	59.8 ± 26.1^{d}	–
Sole cassava	Cassava	–	227.1 ± 37.9^{a}	–
Mixed pigeon pea-cassava	Pigeon pea	–	28.4 ± 5.21^{d}	–
Mixed pigeon pea-cassava	Cassava	adjacent (S1)	124.2 ± 9.8^{bc}	52.4 ± 3.6^{b}
Mixed pigeon pea-cassava	Cassava	¼ inter-row (S2)	142.8 ± 14.8^{b}	42.9 ± 6.8^{b}
Mixed pigeon pea-cassava	Cassava	½ inter-row (S3)	82.1 ± 8.6^{cd}	73.9 ± 4.8^{a}

*δ15Nfinal is the value of δ15N (expressed in ‰) of leaf samples after 90 days ^{15}N labeling. %Ndft is the proportion of N derived from transfer. Different letters (a–d) indicate significant differences between systems ($p < 0.05$)

Nitrogen input from N_2 fixation

Despite the marked variation in planting density of pigeon pea between sole and mixed crop systems, the average height of pigeon pea shrubs was similar in both systems (180–190 cm), suggesting comparable vertical growth regardless of planting arrangement (Table 4). More N was fixed by individual plants in the mixed pigeon pea-cassava system (7.31 g N plant^{-1}) than in the sole pigeon pea crop (5.70 g N plant^{-1}), reflecting the higher leaf biomass per plant in the mixed plot. However, when accounting for planting density, total N input over two years was twice as high in the sole pigeon pea crop (19.76 kg N ha^{-1}) than in the mixed pigeon pea-cassava system (7.40 kg N ha^{-1}) (Table 4).

Nitrogen transferred from pigeon pea to cassava (%Ndft)

After 90 days, the mean values of $\delta^{15}N_{final}$ differed significantly among the three cropping systems (Table 5). The highest $\delta^{15}N_{final}$ was recorded in cassava leaves from the sole crop (227.1‰), while the lowest value was observed in pigeon pea leaves from the mixed pigeon pea-cassava (28.4‰). Cassava-pigeon pea distance (adjacent, ¼ inter-row, and ½ inter-row) had no significant effect on $\delta^{15}N_{final}$ in cassava leaves , with values of 124.2‰, 142.8‰ and 85.0‰, respectively (Table 5). However, the %Ndft varied significantly with increasing distance from the pigeon pea plants (*p-value* < 0.001), with higher transfer in the ½ inter-row (73.9%) compared to those positioned adjacent to pigeon pea (52.4%) and in the ¼ inter-row (42.9%).

Discussion

High N_2 fixation efficiency of pigeon pea

Our hypothesis of high N_2 fixation rates by pigeon pea was verified with values of 100% in both sole and mixed cropping systems over the 90-day experimental period. The significantly lower initial values of AE for pigeon pea leaves in sole and mixed cropping systems than in sole cassava likely indicate that N_2 fixation already occurred before soil labeling. These findings suggest that, during the 90-day experimental period, all N in pigeon pea leaves originated from N_2 fixation regardless of the cropping system. Similar high levels of %Ndfa have been reported in other semi-arid regions: Rao et al. (1987) recorded %Ndfa values of 88% in sole pigeon pea and 96% in mixed pigeon pea-sorghum systems in India. Kwena et al. (2019) found %Ndfa values exceeding 80% in mixed pigeon pea-maize systems in Kenya without rhizobia inoculation. Adu-Gyamfi et al. (2007) found %Ndfa ranging from 93.8 to 99.9% in Malawi, and from 65.6 to 99.3% in Tanzania under mixed pigeon pea-maize crops. Mhango et al. (2017) reported %Ndfa of about 76% with no significant difference between sole pigeon pea and mixed pigeon pea-maize cropping systems.

These high N_2 fixation rates reflect the strong ability of pigeon pea to develop effective nodule symbiosis with native rhizobia, even under adverse climatic conditions and in nutrient-poor soils (Kumar Rao and Dart 1987; Bopape et al. 2022). N_2 fixation can be promoted by soil N deficiency (Dovrat et al. 2018; Figueiredo et al. 2025), but requires sufficient soil P availability (Alon et al. 2021). In our study, although close to the critical

level (Boyer 1982), soil P availability was sufficient to support the energy costs for the N_2 fixation. This availability of P may also have promoted effective nodulation. Such conditions may reflect efficient carbon allocation to nodules, supporting the high energy demand of the nitrogenase enzyme (Schwember et al. 2019). In contrast, Singh et al. (2026) reported that P starvation impairs nodule formation of *Phaseolus vulgaris*. This aligns with findings that low P availability combined with high soil N can suppress N_2 fixation in NFS within tropical rainforest ecosystems (Pons et al. 2007).

A potential limitation of our study that can explain the high N_2 fixation rates of pigeon pea is that the experiment was conducted only during the rainy season. In the dry Mediterranean region of Israel, Dovrat and Sheffer (2019) reported that biological N_2 fixation is generally optimal during the wet season. However, a short rainfall season with low precipitation, as in our experiment, limits biomass production and thus N content derived from N_2 fixation (Zhang et al. 2020; Lumactud et al. 2023). Paula et al. (2018) showed variability in N_2 fixation rates between seasons in mixed eucalyptus-acacia cropping systems in Brazil. Water availability is a key factor in N_2 fixation of *Lens culinaris* across Mediterranean agroecosystems, by improving carbon use efficiency and then increasing nodule biomass and activity (Parvin et al. 2018). However, pigeon pea is adapted to arid and semi-arid environments, owing to its deep root system and high transpiration efficiency (Jorrin et al. 2021; Berriel et al. 2022). Its high water-use efficiency likely allows sustained N_2 fixation, even under tropical dryland conditions (Berriel and Perdomo 2023).

Nitrogen transfer dynamics in mixed cropping systems

In agreement with the hypothesis of high rates of N transfer from pigeon pea to the associated crop, we observed that 42% to 72% of N was transferred from pigeon pea to cassava, leading to a better N status of cassava. This finding is in line with Monroe and Isaac (2014) who showed that N from NFS can be an easily available source of N for associated crops through fine root decomposition and nodule turnover. Another contributing factor could be that an increase in legume root density leads to greater N release through rhizodeposition (Thilakarathna et al. 2016). Ingleby et al. (2007) and Oliveira et al. (2021) further hypothesized that N could also be transferred from NFS to associated crops through common mycorrhizal networks.

We found that N-transfer dynamics between pigeon pea and cassava were influenced by the spatial arrangement of cassava in the mixed cropping system, with higher %Ndft observed at greater distances from the pigeon pea row. This invalidates our hypothesis of higher %Ndft adjacent to pigeon pea, as previously observed for *Acacia mangium* and *Eucalyptus grandis* in mixed-species plantations (Paula et al. 2015). Thus, short distances between cassava and pigeon pea do not necessarily lead to higher %Ndft in cassava. This pattern could be due to the spatiotemporal dynamics of pigeon pea root systems. Schenk and Jackson (2002) reported that shrubs often exhibit wide lateral root spread, which can favor topsoil exploitation and physiological interactions with neighboring crops. Consistently, Sheldrake and Narayanan (1979) found that around 75% of the root mass of five-month-old pigeon pea growing in 150 cm deep brick chambers was located within the top 30 cm. We observed that pigeon pea lateral roots can reach up to 4 m from pigeon pea stems (data not shown). Our results therefore confirm that the 6 to 8 m spacing between pigeon pea rows, as adopted by farmers in the AFS-zones, allows effective N transfer from pigeon pea to cassava.

Nitrogen input to the cropping system

Two years after planting, N input to the cropping system through N_2 fixation reached 19.7 kg N ha^{-1} in sole pigeon pea and 7.4 kg N ha^{-1} in mixed pigeon pea-cassava systems, which is consistent with the 2.8 times higher planting density in the sole crop. Njira et al. (2017) also found higher N inputs through N_2 fixation in sole cropping systems (85.7 kg N ha^{-1}) than in mixed pigeon pea-cowpea systems (57.4 kg N ha^{-1}) after one growing season in Central Malawi. Similarly, Mhango et al. (2017) reported greater N_2 fixation in sole pigeon pea (32 kg N ha^{-1}) than in mixed pigeon pea-groundnut crop (15 kg N ha^{-1}) during a dry year in Northern Malawi, when rainfall was insufficient during the

pigeon pea vegetative phase. Other studies reported N inputs ranging from 75.0 to 44.2 kg N ha^{-1} in mixed pigeon pea-maize systems in Malawi and Tanzania, respectively (Adu-Gyamfi et al. 2007). N inputs can reach up to 253 kg N ha^{-1} for pigeon pea used as a cover crop in Uruguay (Berriel and Perdomo 2023). The lower N inputs through N_2 fixation observed in our study can be due to the harsh ecological conditions the Androy region. However, the N contribution of pigeon pea to the cropping system in this region is non-negligeable given that no fertilizers are applied by the farmers (Violas et al. 2020), especially when considering the long-term cumulative effects of NFS on the N balance in low-input agroecosystems (Mapfumo et al. 1999). The positive residual effects of sole pigeon pea cultivation on subsequent crops were observed in Central and Northen Malawi (Njira et al. 2017; Mhango et al. 2017; Mugi-Ngenga et al. 2022). Then moderate biological N inputs could help to maintain soil fertility and crop productivity, particularly when combined with organic recycling and residue retention (Vanlauwe et al. 2023).

Conclusions

Our study provides key insights into N fixation by pigeon pea, as well as into the dynamics of N transfer to the associated crop. We found that two-year-old pigeon pea largely relied on biological N fixation, regardless of the cropping system, which is of great importance in soils with high N deficiency. The high %Ndfa observed aligns with previous findings in semi-arid regions. These findings highlight the potential of AFS using pigeon pea to maintain N supply to the associated crop, thereby contributing to the sustainability of low-input cropping systems. However, further studies are needed to assess seasonal variations in N_2 fixation and the long-term effects on soil fertility and crop productivity. In addition, research should focus on identifying pigeon pea varieties best suited to semi-arid regions with sandy soils, and on the use of phosphorus fertilizers to improve the N_2 fixation efficiency of this NFS in P-depleted soils.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests. The contents are the sole responsibility of the authors and do not necessarily reflect the views of the GIZ, EU or BMZ.

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