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Successional agroforestry promotes biomass carbon storage in cocoa production systems: results from a long-term system comparison experiment on organic and conventional systems

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ABSTRACT

Agroforestry systems are perceived as an effective approach to store carbon in agroecosystems by building tree biomass and raising soil organic carbon (SOC) stocks. This is especially evident in the tropics, where the cultivation of cash crops such as cacao in agroforestry systems is increasingly used. Among agroforestry systems, organic management, which avoids synthetic inputs for crop protection and fertilization, and the concept of successional agroforestry (SA), which aims to increase carbon storage by using high initial tree densities and intensive pruning without external inputs, have gained interest as alternatives to monocultures with less environmental impact. To assess the temporal development of carbon storage of differently managed agroforestry systems, we revisited a 14-year field experiment located in the Alto Beni Region of Bolivia to quantify biomass and SOC stocks in five distinct cocoa production systems. The field experiment includes SA as well as organic and conventional monocultures (OM and CM) and agroforestry systems (OA and CA). We found that all agroforestry systems increased carbon stocks in the biomass and the soil, especially in the particulate organic matter fraction. No significant effect of organic management practices was observed. After 14 years, the highest biomass carbon was observed in the SA system and topsoil SOC stocks increased significantly in SA and CA. Our findings emphasize the potential to enhance carbon accumulation in agroforestry systems with high initial tree density and rigorous pruning, even without additional fertilizer or synthetic plant protection inputs.

1. Introduction

In the last century, intensification of agricultural management practices has put severe pressure on the environment through the loss of biodiversity (IPBES, 2019), emission of greenhouse gases (Crippa et al., 2021; IPCC, 2023), and acceleration of nutrient cycles (Peñuelas and Sardans, 2022). Land use is a major driver of soil organic carbon (SOC) losses (Kopittke et al., 2019; Sanderman et al., 2017), which is the most important indicator for soil quality (Bünemann et al., 2018) and intimately linked to the provision of soil ecosystem services (Adhikari and Hartemink, 2016). Still, agroecosystems have the potential of acting as carbon sinks through the capture and storage of substantial amounts of atmospheric carbon dioxide in above- and belowground biomass and soils. Therefore, the implementation of agricultural practices that enhance biomass and SOC stocks in agroecosystems is a critical challenge for the 21th century (Griscom et al., 2017; Lal, 2018; Smith, 2016).

Agroforestry systems, the combination of crops and trees, is perceived as sustainable approach for agricultural production that contributes to multiple sustainable development goals (SDG) such as

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reducing poverty and food security (SDG1 and 2) mitigating climate change (SDG13) and promoting biodiversity (SDG15) (Goparaju et al., 2020). The potential for storage of carbon in biomass and soils is a key benefit for agroforestry systems; however, this varies considerably between different systems and regions (Chatterjee et al., 2018; Lorenz and Lal, 2014; Nair et al., 2009; Rajab et al., 2016). Tree diversity and planting density, type of management and age of the trees, among others, influence the potential for carbon storage of agroforestry systems (Asigbaase et al., 2021; Saj et al., 2013).

Successional agroforestry systems (also known as dynamic or syntropic) combine high plant diversity and density with regular and rigorous pruning in a zero-input system and aim to maximize biomass growth and SOC storage. Inspired by the natural process of plant community's succession, these systems aim to ensure crop nutrient supply by maximizing pruning inputs and enhance soil organic matter mineralization (Schneider et al., 2017; Young, 2017). Successional agroforestry systems are not yet the focus of research, although they are perceived as an innovative approach to combine agricultural production with the regeneration of native ecosystems (Andrade et al., 2020; Jacobi et al., 2025). In line with this, a recent study showed that these systems can shape soil microbial communities in temperate systems, counteracting the homogenisation of the soil microbiome by arable farming (Vaupel et al., 2025).

Higher root density in agroforestry compared to monocrop systems (Niether et al., 2019) supports water and nutrient uptake, which in turn benefits plant biomass production (Liste and White, 2008). Lal, (2018) reports enhanced root structure in agroforestry systems protecting SOC from erosion. Moreover, root-derived carbon inputs are considered more effective in building belowground carbon pools compared to above ground carbon inputs, possibly due to higher humification potential (Kätterer et al., 2011). Long-term stabilization of SOC is governed by a complex interplay of biological activity and soil physicochemical properties (Lehmann and Kleber, 2015), which divides SOC into functionally and structurally different pools (Lavallee et al., 2020). A simple approach distinguishes between size-fractionated labile particulate organic matter (POM) and stable mineral-associated organic matter (MAOM) (Cotrufo et al., 2019). Differentiating these pools is of particular importance for agroforestry systems in tropical climates, where soil organic matter turnover rates are high and, thus, SOC stock changes can occur faster compared to temperate climates (Chenu et al., 2019).

Cacao (*Theobroma cacao*) is an important cash crop in the tropics, traditionally grown in the shade of partially cleared forests or in agroforestry systems together with other trees and crops (Rice and Greenberg, 2000). In recent decades, the development of cacao monocultures have increased yields at the cost of negative impacts on biodiversity and soil quality (Asigbaase et al., 2019; Tondoh et al., 2015). Cacao agroforestry is now recognized as a sustainable management of reforestation by restoring tree cover in monocultures, but also as a driver of deforestation in natural forests (Somarriba and Lopez, 2018; Zo-Bi and Hérault, 2023). A recent metanalysis showed no differences in SOC concentrations between cacao agroforestry systems and monocultures (Niether et al., 2020).

Organic cacao cultivation is another strategy, which can add to the reported reduction of environmental impacts in comparison to conventional management (Armengot et al., 2021). Mineral fertilizers and synthetic plant protection are prohibited in organic farming systems. Therefore, crop nutrient supply is based on the inclusion of legumes and organic inputs such as manure or compost, while plant protection measures are based on biological active substances, manual operations and indirect effects. To date, there has been only few studies on organic cocoa production systems and in general, there is a paucity of data pertaining to the temporal development of carbon stocks in agroforestry systems, particularly in the context of successional agroforestry systems.

Therefore, the objective of this study was to quantify soil and biomass carbon pools in cacao production systems over the course of a long-term experiment in Bolivia that compares organic and conventional practices in monoculture and agroforestry systems and also includes a successional agroforestry system. We hypothesized that, i) agroforestry systems, raise biomass and SOC stocks due to higher tree density compared with monocultures, especially in highly diverse and dense systems; ii) organic management of cocoa production systems enhance SOC stocks and POM through organic fertilization of cacao trees.

2. Material and methods

2.1. Site description and experimental setup

The long-term trial is part of the program Farming Systems Comparison in the Tropics (SysCom, system-comparison.fibl.org), which aims to evaluate the performance of organic and conventional agriculture in the tropics. The field site is located in Sara Ana (Bolivia) in the Alto Beni region at the eastern foothills of the Bolivian Andes at an altitude of 380 m a.s.l. (15°27′36.60″S and 67°28′20.65″W). The climate is tropical humid with dry winters. Mean annual temperature is 26°C and mean annual precipitation is 1535 mm. The field site covers an area of around 9 ha with Lixisols and Luvisols as predominating soil types, according to the WRB classification. After clearing of a secondary forest in 2007, five cocoa production systems were implemented in a complete randomized block design with four repetitions. The cocoa production systems aim at mimicking regionally applied cocoa production and include two monoculture (M) and two agroforestry systems (A), under conventional (CM and CA) and organic (OM and OA) management, and a highly diverse successional agroforestry system (SA) without external inputs (Schneider et al., 2017). Conventional management uses mineral fertilization and synthetic plant protection, while organic management uses organic fertilizers and mechanical weeding. The main vegetation and management practices are summarized in Table 1. The plot size was 48 m × 48 m, with a net plot for data collection of 24 m × 24 m located in the center of each plot (Fig. 1). Cacao trees were planted in a 4 m × 4 m grid (625 trees ha^{-1}) in all systems. The cacao tree density was kept for the whole study period, i.e., death trees were replaced in all systems. Temporal development of AFS tree density is shown in Table 2.

2.2. Estimation of the carbon in the above- and belowground biomass

2.2.1. Cacao and agroforestry tree biomass

The aboveground tree biomass was estimated in the 24 m × 24 m net plot in 2011, 2015, 2019 and 2022 as described in Pearson et al. (2005). Briefly, all trees with a diameter larger than 5 cm at breast height (1.30 m) were measured, as well as bananas and coffee plants as described in Niether et al. (2019) and Schneidewind et al. (2019). Tree biomass was estimated on the base of stem diameter and/ or stem height using allometric equations. When available in the literature, a specific equation for a specific species was used; otherwise, a general equation for tropical trees was used. The allometric equations used for each species is detailed in Table S1. The root biomass of the cacao trees was estimated based on Norgrove and Hauser (2012), who reported that aboveground biomass contributed 87 % of the total plant biomass cacao trees. The root biomass of the agroforestry trees was estimated from the aboveground biomass, according to the equation developed by Cairns et al. (1997). Above- and belowground biomasses were converted into carbon stocks through multiplication by 0.5 (Pearson et al., 2005).

2.2.2. Transitional material

Biomass of the herb and shrub layer (diameter < 5 cm), as well as the litter layer (branches with diameter < 10 cm) and deadwood (with a diameter >10 cm) were recorded along a diagonal transect in the net plot in four 50 cm × 50 cm squares. Since these pools are prone to decomposition, they were aggregated as transitional material. All herbaceous plants were cut, and litter and branches were collected, dried at 70 °C until constant weight was reached, and weighed (Schneidewind

Table 1
Description of the vegetation and the main management practices of cocoa production systems.

	Vegetation and transmitted light*	Management
CM	Only herbaceous strata. Plantain (*Musa spp*) planted at a density of 625 trees ha^{-1} (4 ×4 m) from 2009 to 2011 to protect the cacao tree seedlings. Predominance of grass species and generalist species resistant to glyphosate (Marconi and Armengot, 2020). Bare soil. TL: 92 %	Chemical fertilizer (Blaukorn BASF, Germany, 12–8–16–3 N-P_2O_5-K_2O-MgO) at 112 kg ha^{-1} split in two doses applied in March and December to cacao trees. Weeding with brush cutters and herbicide applications, mainly Glyphosate 4–5 times per year. Annual cacao tree pruning. Pruning residues chopped and left around the trees.
OM	Only herbaceous strata. Plantain (*Musa spp*) planted at a density of 625 trees ha^{-1} (4 ×4 m) from 2009 to 2011 to protect the cacao tree seedlings. A perennial legume (*Neonotonia wightii*) was used as a cover crop and fully covered the soil during the first years. It slowly disappeared over the years while cacao tree cover increased (Marconi et al., 2022). About 10 % of soil covered by the cover crop at the end of the study. No bare soil. TL: 92 %	Locally made compost with crop and vegetation residues, hens' slurry and wood chips. Annual application started in 2010, at a dose of 17 l per cacao tree for 3 years and 21 l the following years. Weeding with brush cutters. Annual cacao tree pruning. Pruning residues left around the tree.
CA	Much less herbaceous strata compared with CM and OM. Plantain (*Musa spp*) planted at a density of 625 trees ha^{-1} (4 ×4 m) from 2009 to 2011 to protect the cacao tree seedlings. Banana (*Musa spp.*) were planted in the cacao tree inter-row space in 2011. Shade trees consisted mainly of legumes (8 × 8 m), such as pacay (*Inga ingoides* and *Inga expansa*) and ceibo (*Erythrina poeppigiana* and *Erythri*na fusca). With lower densities (16 × 8 m), fruit species, such as avocado (*Persea americana*), copoazú (*Theobroma grandiflorum*), rambutan (*Nephelium lappaceum*), and timber trees, such as mara (*Swetenia macrophylla*) or Quina quina (*Myroxylon balsamum*). In the low strata coffee (*Coffea arabica*) is planted in lines. Complete list of tree species in Table S1. TL: 39 %	Chemical fertilizer (Blaukorn BASF, Germany, 12–8–16–3 N-P_2O_5-K_2O-MgO) at 56 kg ha^{-1} split in two doses applied in March and December applied to cacao trees. Weeding with brush cutters and herbicide applications, mainly Glyphosate, but less times and less quantity required compared to CM. Annual cacao and shade tree pruning. Pruning residues left around the tree.
OA	Much less herbaceous strata compared with CM and OM. Plantain (*Musa spp*) planted at a density of 625 trees ha^{-1} (4 ×4 m) from 2009 to 2011 to protect the cacao tree seedlings. Banana (*Musa spp.*) were planted in the cacao tree inter-row space in 2011 Shade trees consisted mainly of legumes (8 × 8 m), such as pacay (*Inga ingoides* and *Inga expansa*) and ceibo (*Erythrina poeppigiana* and *Erythrina fusca*). With lower densities (16 × 8 m), fruit species, such as avocado (*Persea americana*), copoazú (*Theobroma grandiflorum*), rambutan (*Nephelium lappaceum*), and timber trees, such as mara (*Swetenia macrophylla*) or Quina quina (*Myroxylon balsamum*). In the low strata coffee (*Coffea arabica*) is planted in lines. Complete list of tree species in Table S1. A leguminous cover crop was planted at the beginning but it completely disappeared by the end of this study. TL: 39 %	Compost applied from 2010 to 2016 at half of the dose of OM. Weeding with brush cutters. Annual cacao and shade tree pruning. Pruning residues left around the tree.
SA:	Highly diverse and abundant herbaceous strata, characterized by native and endemic species (Marconi and Armengot, 2020). Plantain (*Musa spp*) planted at a density of 625 trees ha^{-1} (4 ×4 m) from 2009 to 2011 to protect the cacao tree seedlings. Additional crops in the low strata such as coffee, ginger and curcuma. The shade trees consist of similar design of the OA and CA, but with additional trees both coming from natural regeneration of the vegetation, planted or seeded, such as peach palm (*Bactris gasipaes*). Banana trees to replace plantain in much lower density TL: 26 %	No external inputs. Weeding with machetes and brush cutters. Cacao and shade tree pruning, at least once per year. Pruning residues chopped and left around the trees.

Mean cacao tree density is 625 trees per ha^{-1} for all systems.
*The fraction of transmitted light (TL) was measured below the canopy. It was measured by taking four hemispherical photographs of each plot between the cacao tree lines using a Nikon CoolPix5400 equipped with an FC-E8 converter lens with a 180° angle of view. LT can vary according to the pruning activities (Niether et al., 2018)
Modified from Durot et al. (2023).

et al., 2019). Downed deadwood was measured (length and diameter) and the biomass of standing biomass was calculated according to four decomposition classes as described in Pearson et al. (2005).

2.3. *Quantification of SOC stocks*

2.3.1. *Soil sampling*

Soil sampling was conducted in September 2010 and late October 2020. The obtained bulk soil samples of each sampling campaign were taken after the removal of coarse organic residues from the soil surface and represent a composite of 15–20 individual soil cores per field plot. In 2010, evenly-distributed grid sampling was applied across the net-plot (24 m × 24 m) and each soil core was separated in two soil depths (0–25 cm and 25–50 cm). To consider the spatially distinct soil management practice around cacao trees in organic and conventional cacao production systems, two sampling locations within each plot were distinguished, at 0.5 m and 2 m distance to the cacao tree trunks in 2020. Additionally, each soil core was separated in three soil depths (0–10 cm, 10–25 cm, and 25–50 cm) to account for the mean depth of the natural Ah-horizon of ~10 cm. Before their transport to Switzerland, all soil samples were air-dried and sieved to 2 mm. In both years, volumetric samples were collected at the given soil depth and sampling location using a 100 cm cylinder and reporting dried sample weight (105 °C for 24 h). ($n = 3$ in 2010 and $n = 4$ in 2020).

2.3.2. *Particle size fractionation and soil texture*

Following a modified fractionation scheme of Cotrufo et al. (2019), topsoil samples from 2020 were fractionated by size via wet-sieving into a coarse fraction (20 – 2000 μm) and a fine fraction (< 20 μm), which are referred to as POM (particulate organic matter) and MAOM (mineral-associated organic matter), respectively (Cotrufo et al., 2019, 2013; Lavallee et al., 2020). For this, 15 g of air-dried sample was shaken with glass beads and 0.5 % sodium hexametaphosphate ($(NaPO_3)_6$) for 18 h and wet- sieved using a 2000 μm and a 20 μm sieve. Thereafter, the obtained soil fractions were dried at 60 °C, weighed and ground for further elemental analysis. Soil texture was analyzed using PARIO Plus Soil Particle Analyzer (METER Group, Germany/USA) as described in Mayer et al. (2022).

Fig. 1. Drone image of the field site investigating cocoa production systems. CM - conventional monoculture; OM - organic monoculture; CA - conventional agroforestry; OA - organic agroforestry; SA- successional agroforestry.

Table 2
Development of mean shade tree and banana density in agroforestry systems.

System	2011 mean ± SD	2015 mean ± SD	2019 mean ± SD	2022 mean ± SD
Shade tree [stems ha−1]				
CA	165 ± 29 a	291 ± 19 a	330 ± 21 a	308 ± 50 a
OA	130 ± 19 a	299 ± 19 a	356 ± 9 a	321 ± 36 a
SA	1095 ± 21a	843 ± 106 b	894 ± 70 b	943 ± 95 b
Banana density [stems ha−1]				
CA	1097 ± 41 b	635 ± 41 b	749 ± 21 b	513 ± 51 b
OA	813 ± 232 b	638 ± 95 b	657 ± 77 b	437 ± 19 b
SA	284 ± 87 a	217 ± 19 a	242 ± 50 a	239 ± 48 a

The stem density is higher than the actual density of individual plants because for some species (e.g., *Musa* spp, *Euterpe oleracea*., *Bactris gasipaes*) more than one stem per tree can be present. Different Tukey post-hoc letters indicate significant differences between agroforestry systems at $p < 0.05$. CA - conventional agroforestry; OA - organic agroforestry; SA - successional agroforestry.

2.3.3. Calculations of SOC stocks

SOC contents of the bulk soil samples from 2010 (n = 40, 20 plots × 2 soil depths) and 2020 (n = 120, 20 plots × 2 locations × 3 soil depths), as well as the two soil fractions obtained by physical fractionation of topsoil (0–10 cm) samples of 2020 were measured in duplicates via dry combustion using a Vario Max cube analyzer (Elementar Analysensysteme GmbH, Hanau, Germany). Since the bulk soil samples were carbonate-free in previous studies (Lori et al., 2022), it was assumed that carbon concentrations obtained also corresponds to SOC. SOC stocks were calculated as follows:

$$SOC_{stocks} = SOC_{contents} * bulk\ density * soil\ depth * 0.1$$

With SOC_{stocks} in t ha^{-1}, $SOC_{contents}$ in kg t^{-1} soil, bulk density in t m^{-3} and soil depth in m. To verify the physical fractionation and subsequent C/N analyses, the mass (100.70 ± 0.16 %) and carbon recovery (97.62 ± 0.77 %) rates were calculated as the sums of the weights and carbon contents of all fractions per weight and carbon content of bulk soil sample.

To estimate plot-specific carbon stocks from samples taken in 2020, the managed area around the cacao trees was assumed to be up to 1 m from the cacao trunk, with a relative proportion of 19.6 % of the total plot area. This corresponds to soil samples taken at a distance of 0.5 m from the cacao trees. Samples taken at 2 m from the cacao trees correspond to the area between the rows of cacao trees and represented 80.4 % of the total plot area.

2.4. Statistical analyses

Statistical analyses were conducted in R version 4.2.2 and RStudio (R Core Team, 2023; RStudio, 2022). Mean annual changes in biomass carbon and SOC stocks (t ha^{-1} years^{-1}) was calculated as mean annual difference between 2011 and 2022 for biomass carbon and 2010 and 2020 for SOC. Two linear mixed effects models (lme) were applied to determine the effects of production systems and experimental factors on soil and biomass carbon stocks for each year, as well as annual carbon stock changes, using the lme function of the nlme package (Pinheiro et al., 2022) with plot nested in block as a random factor. Residuals were tested for normal distribution and homogeneity of variances was tested by Levene's test. Raw data were log or sqrt transformed when assumptions were not met.

The first lme assessed the effect of the production systems (CM, OM, CA, OA, SA) on biomass and soil organic carbon stocks using systems as random term. The anova.lme function was used to retrieve the statistical significance of production systems (sAOV) and Tukey post-hoc tests were applied (Russell et al., 2023). In a second lme, the effects of experimental factors, such as management (MA, organic vs. conventional) and crop diversity (D, agroforest vs. monoculture), as well as their interaction on biomass and SOC pools was assessed (fAOV). For this purpose, SA were excluded to maintain a full factorial and balanced design. To test the effect of production system on SOC stock differences between 2010 and 2020 a paired *t*-test was used using the t.test function of the stats package (R Core Team, 2023).

3. Results

3.1. Effect of cocoa production systems on biomass carbon stocks

Above- and belowground biomass carbon increased in all cocoa production systems from 2011 to 2022 (Fig. 2). In 2022, biomass carbon estimated in the agroforestry systems more than doubled those of the monocultures (Table 3). Transitional material was higher in the agroforestry systems from 2015 onwards and it accounted for the largest proportion of biomass carbon stocks at the beginning of the experiment (Tables S2–4). Biomass carbon from the cacao trees was around 72 % higher in the monocultures compared to the agroforestry systems. No significant differences were observed between conventional and organic management when comparing biomass carbon stocks within the same sampling year (Tables S2-4). By 2022, SA had developed the largest biomass carbon stocks (66.2 ± 3.1 t ha^{-1}), followed by OA (55.36 ± 2.15 t ha^{-1}) and CA (52.75 ± 3.38 t ha^{-1}), due to significantly higher biomass carbon of the agroforestry trees. At the same time, the lowest biomass carbon stocks were measured in CM (26.31 ± 2.36 t ha^{-1}) and OM (26.04 ± 3.47 t ha^{-1}). In 2022, carbon from transitional material was also highest in SA, followed by OA and CA, and smallest in the cacao monocultures.

3.2. Effect of cocoa production systems on SOC stocks

Overall, neither in 2010 nor in 2020 did total SOC stocks (0–50 cm) differ significantly between systems (Table 4, Table S5). In 2010 topsoil SOC stocks (0–25 cm) ranged from 27.27 ± 5.32 t ha^{-1} in CA to 42.89 ± 4.44 t ha^{-1} in OA, while subsoil SOC stocks (25–50 cm) ranged from 20.57 ± 7.04 t ha^{-1} in CM to 30.08 ± 5.44 t ha^{-1} in OM (Tables S5). In 2010, SOC stocks at 0–25 cm depth differed between systems, with the significantly lowest value in CA. SOC stock at 0–25 cm in 2010 were higher in the organic systems compared to the conventional ones and no differences in SOC stocks were observed at the 25–50 cm depth in 2010 (Table S5). In 2020, topsoil (0–10 cm) POM and MAOM in 0–10 cm followed the same trend with significantly highest POM and MAOM stocks in OA (8.50 ± 0.69 and 23.65 ± 2.22 t ha^{-1}) compared to CM (5.91 ± 0.58 and 17.74 ± 1.33 t ha^{-1}). However, no significant differences between systems were found for 10–25 cm nor for 25–50 cm. When excluding the SA from the analysis (fAOV), organic systems showed higher SOC stocks in the 0–10 cm and in the 25–50 cm depth. In addition, agroforestry systems had higher POM compared to monocultures and significantly higher SOC stocks in 2020 compared to 2010 were observed for CA and SA in 0–25 cm (Table 5).

3.3. Changes in total carbon stocks across production systems

In the latest samplings, combined biomass (in 2022) and SOC stocks (in 2020) were largest in SA with 135 t C ha^{-1}, followed by OA with 132 t C ha^{-1}, CA with 113 t C ha^{-1}, OM with 103 t C ha^{-1} and finally, CM with 83 t C ha^{-1} respectively. Over time, biomass carbon stocks increased, especially in agroforestry systems due to the high carbon accumulation in agroforestry trees (Fig. 3). But also mean annual changes in SOC in the 0–25 cm layer were positive in all production systems, with a significantly higher increase in CA compared to CM (Table S6, Fig. 3). In the deeper soil layer (25–50 cm), SOC decreased slightly and non-significantly in all production systems between 2010 and 2020 (Table 5). Also, bulk density remained similar between sampling dates. Overall, mean annual change in total carbon stocks was significantly higher in agroforestry systems compared to cacao monocultures but it did not significantly differ within agroforestry systems (Table S6, Fig. 3). Organic managements did not show any significant influence on development of biomass carbon nor SOC stocks compared to conventional farming.

At the earliest sampling campaigns (soil 2010; biomass 2011), SOC stock exceeded biomass carbon in all systems. However, at the latest

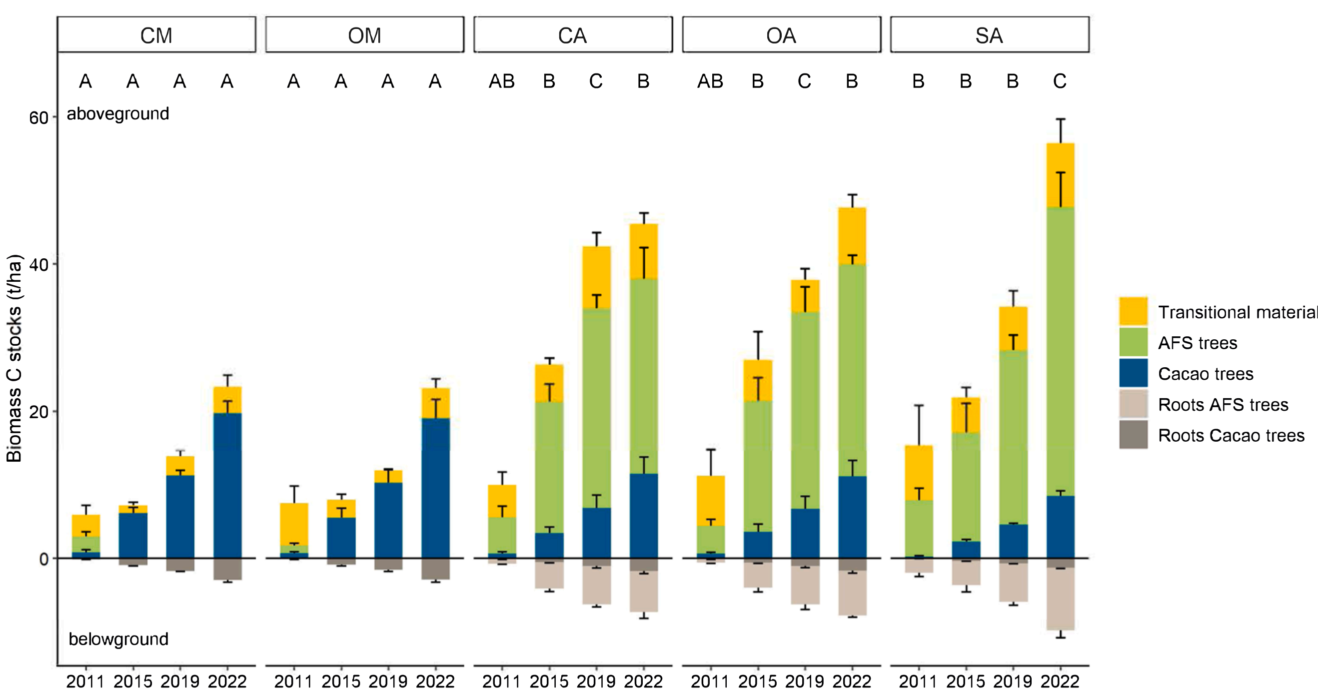

Fig. 2. Mean above- and belowground biomass carbon stocks (t^{-1}ha^{-1}) across four sampling years and five cacao production systems (n = 4). Biomass carbon pools are displayed in different colors. Agroforestry (AFS) trees appearing in CM and OM in 2011 represent plantain plants for temporal shade at the beginning of the experiment in 2008. Transitional material is defined as the sum of dead wood, litter and the herb layer. Capital post-hoc Tukey letters show differences across production systems within the same sampling year at $p < 0.05$. CM - conventional monoculture; OM - organic monoculture; CA - conventional agroforestry; OA - organic agroforestry; SA- successional agroforestry.

Table 3
Mean biomass carbon stocks (t ha^{-1}) in 2022 in five cocoa production systems and post-hoc Tukey letters. sAOV and fAOV are based on two different linear mixed effects models. sAOV tests for differences between production systems using systems as random effect. fAOV assesses the experimental factors management (MA, organic vs. conventional) and diversity (D, monoculture vs. agroforestry), by excluding the SA system.

			Total biomass		Cacao trees		Roots Cacao trees		Transitional material			AFS trees		Roots AFS trees	
	System		mean ± SD	Tukey	mean ± SD	Tukey	mean ± SD	Tukey	mean ± SD	Tukey		mean ± SD	Tukey	mean ± SD	Tukey
	CM		26.31 ± 2.36	a	19.77 ± 1.62	b	2.95 ± 0.24	b	3.58 ± 1.58	a		-	-	-	-
	OM		26.04 ± 3.47	a	19.06 ± 2.53	b	2.85 ± 0.38	b	4.13 ± 1.22	a		-	-	-	-
	CA		52.75 ± 3.38	b	11.51 ± 2.26	a	1.72 ± 0.34	a	7.51 ± 1.46	b		26.45 ± 4.24	a	5.57 ± 0.88	a
	OA		55.36 ± 2.15	b	11.17 ± 2.13	a	1.67 ± 0.32	a	7.69 ± 1.76	b		28.78 ± 1.19	a	6.05 ± 0.27	a
	SA		66.21 ± 3.14	c	8.49 ± 0.68	a	1.27 ± 0.10	a	8.72 ± 3.28	b		39.21 ± 4.72	b	8.52 ± 1.00	b
	ANOVA	dF	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	dF	F-value	p-value	F-value	p-value
sAOV	system	12	114.15	**<0.001*** **	31.87	**<0.001*** **	31.63	**<0.001*** **	4.02	**0.027***	6	12.14	**0.008****	14.92	**0.005****
fAOV	MA	9	0.49	0.502	0.30	0.597	0.31	0.591	0.17	0.687	3	0.95	0.401	0.98	0.394
	D	9	276.90	**<0.001*** **	71.35	**<0.001*** **	70.49	**<0.001*** **	18.27	**0.002****	3	-	-	-	-
	MA x D	9	0.74	0.412	0.04	0.849	0.04	0.839	0.04	0.838	3	-	-	-	-

Since no agroforestry trees grow in cacao monocultures, AFS tree C-pools were tested for management only. Transitional material is defined as the sum of dead wood, litter and the herb layer. P-values < 0.05 are expressed in bold and marked with * for p < 0.05, ** for p < 0.01 and *** for p < 0.001. CM - conventional monoculture; OM - organic monoculture; CA - conventional agroforestry; OA - organic agroforestry; SA- successional agroforestry.

Table 4
Mean SOC stocks (t ha^{-1}) in 2020 in five cocoa production systems and post-hoc Tukey letters. sAOV and fAOV are based on two different linear mixed effects models. sAOV tests for differences between production systems using systems as random effect. fAOV assesses the experimental factors management (MA, organic vs. conventional) and diversity (D, monoculture vs. agroforestry), by excluding the SA system.

			Soil 0–50 cm		POM 0–10 cm		MAOM 0–10 cm		Soil 10–25 cm		Soil 25–50 cm	
	System		mean ± SD	Tukey	mean ± SD	Tukey	mean ± SD	Tukey	mean ± SD	Tukey	mean ± SD	Tukey
	CM		56.67 ± 9.23	a	5.91 ± 0.58	a	17.74 ± 1.33	a	15.19 ± 2.22	a	17.82 ± 6.51	a
	OM		76.57 ± 10.87	a	7.15 ± 1.38	ab	22.28 ± 2.83	ab	18.94 ± 2.84	a	28.21 ± 5.47	a
	CA		60.48 ± 14.77	a	7.09 ± 0.71	ab	20.42 ± 3.06	ab	15.77 ± 4.66	a	17.20 ± 7.58	a
	OA		76.59 ± 15.03	a	8.50 ± 0.69	b	23.65 ± 2.22	b	20.48 ± 4.46	a	23.95 ± 9.62	a
	SA		71.40 ± 9.72	a	7.60 ± 0.66	ab	22.11 ± 1.52	ab	19.64 ± 3.50	a	22.04 ± 5.39	a
	ANOVA	dF	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
sAOV	system	12	2.21	0.129	4.72	**0.016***	4.24	**0.023***	1.46	0.274	1.62	0.234
fAOV	MA	9	9.17	**0.014***	8.81	**0.016***	13.65	**0.005****	4.79	0.056	5.71	**0.041***
	D	9	0.10	0.755	8.09	**0.019***	3.70	0.087	0.30	0.596	0.46	0.514
	MA x D	9	0.10	0.757	0.04	0.845	0.39	0.549	0.06	0.809	0.26	0.624

P-values < 0.05 are expressed in bold and marked with * for p < 0.05, ** for p < 0.01 and *** for p < 0.001.
CM - conventional monoculture; OM - organic monoculture; CA - conventional agroforestry; OA - organic agroforestry; SA- successional agroforestry.

Table 5
T-values and p-values assessing the differences in soil organic carbon (SOC) stocks between 2010 and 2020 for each production system.

	Soil 0–50 cm		Soil 0–25 cm		Soil 25–50 cm	
System	t-value	p-value	t-value	p-value	t-value	p-value
CM	−1.44	0.889	−1.32	0.217	0.49	0.637
OM	−0.63	0.552	−1.42	0.221	0.42	0.688
CA	−0.91	0.399	−3.02	**0.026***	0.57	0.590
OA	−0.84	0.434	−2.31	0.062	0.08	0.932
SA	−1.17	0.284	−2.55	**0.045***	0.31	0.769

P-values < 0.05 are expressed in bold and marked with * for p < 0.05, ** for p < 0.01 and *** for p < 0.001.
CM - conventional monoculture; OM - organic monoculture; CA - conventional agroforestry; OA - organic agroforestry; SA- successional agroforestry.

sampling campaigns (soil 2020; biomass 2022) biomass carbon stocks in the agroforestry systems were almost as large as SOC stocks, while in both monocultures, SOC stocks were still at least four times greater than biomass carbon stocks (Figure S1).

4. Discussion

4.1. Agroforestry enhances biomass and SOC stocks

Our results show elevated carbon stocks in agroforestry systems already six years after establishment and thus confirm the huge potential of agroforestry systems to accumulate carbon compared to monocultures (Niether et al., 2020). The biomass carbon increased up to 3–4 t ha^{-1} yr^{-1} in the agroforestry systems, indicating that the storage of carbon in the form of biomass can be rapid and substantial. The studied agroforestry systems still have the potential to store more carbon in the biomass, given that 14-year-old agroforestry systems can be considered relatively young (Asigbaase et al., 2021). However, tree density in the agroforestry systems of this field experiment is above average (Niether et al., 2020) and especially in the SA system tree density is highly dynamic due to natural succession and removal of shade trees. Therefore, limits of biomass carbon storage in these agroforestry systems might not have been reached, but remain critical to be estimated. Relatively small gain in biomass carbon for CA and OA from 2019 to 2022 and large increases in biomass carbon for SA in the same period highlight distinct carbon accumulation potentials in shade and accompanying trees also

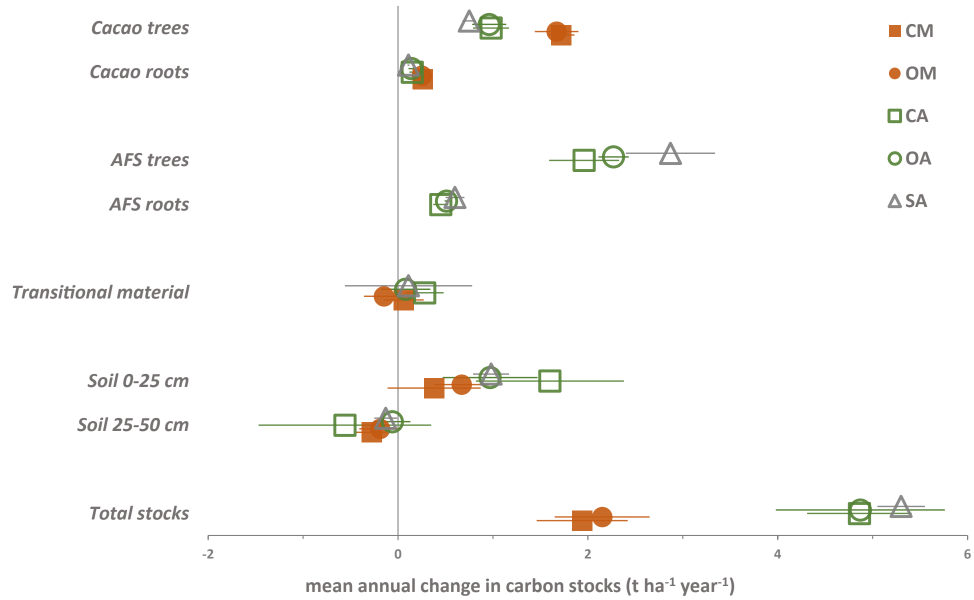

Fig. 3. Mean annual changes in biomass and soil carbon stocks (t ha^{-1} year^{-1}) across five cacao production systems (n = 4). Mean annual changes in biomass carbon stocks were estimated between 2011 and 2022. Mean annual changes in soil organic carbon stocks were calculated between 2010 and 2020. Detailed statistical analysis can be retrieved from Table S6. Transitional material is defined as the sum of dead wood, litter and the herb layer. CM - conventional monoculture; OM - organic monoculture; CA - conventional agroforestry; OA - organic agroforestry; SA- successional agroforestry.

within agroforestry systems. The higher biomass carbon from cacao trees in monocultures may be attributed to full sun exposure and reduced competition for space and nutrients. Conversely, the lower biomass carbon from cacao trees in agroforestry systems was compensated for by the biomass carbon storage in agroforestry trees, which contributed 60 %, 62 % and 72 % of biomass carbon in CA, OA and SA, respectively.

Total carbon storage in biomass and soil were at comparable levels with regional farmer plot implementing comparable systems at similar ages, with 143 C ha^{-1} for SA, 128 C ha^{-1} for agroforestry system and 86 C ha^{-1} for conventional monocultures (Jacobi et al., 2014). This study also included fallow plots (125 C ha^{-1}), with naturally regenerating pioneer vegetation and secondary forest, as integral part of local land use cycles and found similar biomass storage in agroforestry system compared to fallow plots (Jacobi et al., 2014). However, as in our study, SA systems further enhanced biomass and carbon stocks exceeding carbon storage even in fallow plots. The potential of agroforestry systems, to act as carbon sink or source, depending on the previous land use type (Somarriba and Lopez, 2018), also underscores the possibility of balancing the trade-off between crop production and carbon storage through the knowledge-intensive management of agroforestry systems (Esche et al., 2023).

However, it needs to be noticed that biomass carbon quantification in agroforestry systems remains challenging and traditionally, allometric equations have been employed to quantify tree biomass that derive from biomass assessments conducted in forest ecosystems, which might not fully encompass the biomass of indigenous tree species (Asigbaase et al., 2023; Nair et al., 2009). Furthermore, abiotic conditions, such as light and space, and management practices, such as pruning and fertilization, impact tree structure and can, therefore, alter allometric relationships, resulting in inaccuracies in biomass quantification (Feldpausch et al., 2011; Pretzsch, 2014). Nevertheless, a recent study compared the allometric relationship between stem diameter, height and crown area in cacao-based agroforestry systems and found that the allometric formulae were consistent with metabolic scaling theory despite different crown structures (Asigbaase et al., 2023). Furthermore, the study demonstrated that soil properties and nutrient availability influence shade tree crown structures, emphasizing the necessity for combined soil and biomass analyses to accurately assess the carbon storage potential of agroforestry systems.

In agricultural systems, SOC evolves at a slow rate, making precise quantification challenging. This is particularly the case in perennial systems, where spatial heterogeneities present a significant obstacle (De Stefano and Jacobson, 2018). A study of 229 sample plots in cacao-based agroforestry systems in Central America revealed a mean SOC stock of 51 t ha^{-1} (Somarriba et al., 2013). In comparison, our study observed greater SOC stocks in agroforestry systems, with values ranging from 60 to 76 t ha^{-1}. This discrepancy is likely attributable to the enhanced sampling depth of 50 cm employed in our study, whereas the topsoil carbon stocks up to 10 cm soil depth exhibited comparable levels. These findings underscore the necessity for carbon assessment to extend to deeper soil layers, ideally encompassing the depth of tree rooting (De Stefano and Jacobson, 2018).

Tree biomass and SOC stocks are typically the largest contributors to carbon stocks in agroforestry systems (Borden et al., 2019; Jacobi et al., 2014; Somarriba et al., 2013), other pools such as litter, dead wood, and herbs, also contribute to biomass carbon stocks. These pools were aggregated as transitional material and are important indicators of SOC and nutrient cycling, such as rhizodeposition and organic matter decomposition (Saj et al., 2021). Transitional material was higher in agroforestry systems from 2015 onwards (see Table 3, Tables S2-4), which indicates a constantly enhanced carbon influx to the soil in these systems. Among the carbon inputs to soil, pruning residues can make up a significant fraction and contribute twice as much to soil carbon inputs than litterfall (Schneidewind et al., 2019). Indeed, correlation of mean annual inputs via transitional materials like dead wood, litter and herbs in our study show significant correlation with POM and changes in topsoil SOC stocks, while fertilization inputs via compost did not correlate with changes in carbon stocks (Table S6 and 7). Consequently, higher carbon influx from transitional material to soils seem to be a major factor for enhanced topsoil carbon gains in agroforestry systems. Changes in SOC stocks accounted for 32 %, 19 % and 18 % of total carbon stock changes in CA, OA and SA, respectively.

In addition, rhizodeposition in agroforestry systems, might have added additional carbon to the soil and plays a crucial role in organic matter accumulation and stabilization (Villarino et al., 2021). However, only the POM fraction (0–10 cm) was significantly increased in agroforestry systems in 2020, while there was no significant trend for the MAOM fraction ($p = 0.087$). This highlights that agroforestry systems had a stronger impact on rather labile SOC fractions and increases of SOC stocks rely on constantly prevailing carbon influx to soil.

A recent study on the same trial on fine root distribution, measured in in-growth cylinders to a depth of 50 cm, found 80 % of fine roots within the first 25 cm and 4 times enhanced fine roots in agroforestry system compared to conventional monoculture (Niether et al., 2019). Since this study used a strictly allometric approach to quantify root carbon we might have overestimated root biomass carbon especially in the conventional monoculture. While allometric quantification of aboveground biomass might well reflect actual carbon storage (Asigbaase et al., 2023), these observations highlight the uncertainties when it comes to quantification of root carbon in agroecosystem, that call for further method development to achieve accurate carbon storage potential especially in complex and diverse agroforestry systems.

4.2. The impact of organic management on soil and biomass carbon stocks

Because of their focus on soil fertility and the absence of synthetic pesticides and mineral fertilizers, organic systems typically produce lower yields (Seufert et al., 2012). However, in this long-term trial, no differences in yields were observed between conventional and organic agroforestry systems and significant differences in the monocultures were only observed during the first years of the experiment (Armengot et al., 2023, 2016; Niether et al., 2019). A comparison of 42 organic and conventional agroforestry systems across different trial age groups showed significantly enhanced biomass carbon under organic management, which we could not confirm (Asigbaase et al., 2021). In this field experiment, the impact of agroforestry on SOC stocks was markedly pronounced, whereas organic and conventional management exhibited no discernible effect. Nevertheless, the application of compost to OM and OA led to a notable elevation in SOC contents in the vicinity of cacao stems, particularly in the OM treatment (Lori et al., 2022). Yet, these locally augmented SOC contents did not translate to significant SOC stock increases across the whole experimental area. The fact that higher SOC stocks were observed in organic systems rather seems to be rooted in initial soil heterogeneities, and highest SOC stocks in OM were already observed in 2010 (Table S5) and in previous studies (Alfaro-Flores et al., 2015; Schneidewind et al., 2022). Spatial variabilities in soil texture and types also include in-plot variabilities (Niether et al., 2017) and complicate the identification of system effects on SOC. However, clay, silt and sand content did not differ significantly between systems (Figure S2, Table S7 and S8) but CM and CA showed a trend towards lower clay content which are assumed to be a major driver of long-term carbon storage due to the formation of organo-mineral complexes (Lehmann and Kleber, 2015). The fact that SOC changes in CM were negligible, while CA exhibited greatest increases in SOC stocks further highlights the benefits of agroforestry system on soil health and its potential to restore degraded soils (Lorenz and Lal, 2014).

4.3. Carbon management in successional agroforestry systems

The SA system is distinguished by its independence from external inputs, high initial tree density and regular shade tree management, including thinning, stratification and removal of trees as the system matures. Of particular importance is shade tree pruning, which is essential for maintaining the productivity of the system in terms of cacao yields (Esche et al., 2023). Following a system comparison approach, the combined effect of high tree density, pruning and thinning in SA cannot be fully disentangled, but resulted in a positive impact on biomass carbon in our study. Highest biomass carbon in SA was not observed from the start of the experiment and for the sampling campaigns in 2011, 2015 and 2019 SA did not exceed CA and OA in terms of biomass carbon storage. Intensive pruning events, which involved drastically cutting branches and reducing tree density were carried out in 2012 and 2017, which possibly reduced the potential carbon storage potential in the biomass for some years. Yet, with increasing age, biomass carbon storage in SA outcompeted the other agroforestry systems, as observed in 2022. This highlights the temporal scale of SA management, in which growth potential in an agroforestry system with high tree density is built up over several years by keeping trees in a premature growth stage (Young, 2017). However, pruning and thinning of trees to maintain cacao tree productivity is part of the SA management strategy and might limit carbon storage potential of tree biomass on the long run. Still, intensive pruning events add organic matter to soils, which acts as energy source for microbial activity. Indeed, distinct bacterial and fungal communities were observed for all systems of this field experiment, and in line with highest inputs via pruning residues highest capacity for organic matter decomposition, and thus carbon turnover, was observed in the SA systems (Lori et al., 2022). Overall our results show that within agroforestry systems there is potential to optimize carbon storage by following systemic management approaches that consider planting density and species selection to enable strata exploitation throughout maturing of the system.

5. Conclusion

The findings of our study demonstrate the significant advantages of agroforestry systems in addressing carbon storage when compared to cacao monocultures. After a period of 14 years, the biomass of the agroforestry systems had accumulated as much carbon as was present in the soil up to a depth of 50 cm. In the soil, there was an increase in labile carbon fractions in the topsoil in agroforestry systems, which highlights the importance of maintaining a continuous carbon input to soil within the system e.g. through pruning and crop residues. Organic management did not result in elevated biomass or SOC stock changes, but agroforestry systems demonstrated a capacity to store biomass carbon at a rate that was more than twofold that observed in monoculture systems. This was particularly evident in the context of highly dense and diverse successional agroforestry systems. This shows that high initial tree density and regular pruning and thinning is a promising approach to enhance biomass growth, even in the absence of additional inputs via mineral nutrients or synthetic plant protection.

CRediT authorship contribution statement

Marc Cotter: Writing – review & editing, Project administration, Funding acquisition. **Wiebke Niether:** Writing – review & editing, Methodology, Investigation. **Johanna Rüegg:** Writing – review & editing, Project administration, Investigation. **Sina Lory:** Writing – review & editing, Methodology. **Johannes Milz:** Writing – review & editing, Investigation. **Hans-Martin Krause:** Writing – original draft, Formal analysis, Conceptualization. **Georg Cadisch:** Writing – review & editing, Supervision. **Stephane Saj:** Writing – review & editing, Project administration. **Laura Armengot:** Writing – review & editing, Funding acquisition, Formal analysis, Conceptualization. **Ulf Schneidewind:** Writing – review & editing, Methodology, Conceptualization. **Monika Schneider:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Marc Cotter reports financial support was provided by Biovision Foundation for Ecological Development. Marc Cotter reports financial support was provided by Coop Sustainability Fund. Marc Cotter reports financial support was provided by Liechtenstein Development Service (LED). Marc Cotter reports financial support was provided by Swiss Agency for Development and Cooperation. If there are other authors,

they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109820.

Data availability

Data will be made available on request.

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