Perennial legume intercrops provide multiple belowground ecosystem services in smallholder farming systems

Laurie E. Drinkwater [a,*], Charles A.O. Midega [b,c,1], Rachel Awuor [b], Dickens Nyagol [b], Zeyaur R. Khan [b]

[a] Cornell University, School of Integrated Plant Science-Horticulture Section, Ithaca, NY 14853, USA
[b] International Centre of Insect Physiology and Ecology (icipe), PO Box 30772, Nairobi 00100, Kenya
[c] Unit for Environmental Sciences and Management, IPM Program, North-West University, Potchefstroom 2520, South Africa

ARTICLE INFO

ABSTRACT

Soil degradation is a major underlying cause of poverty and malnutrition in smallholder agrarian communities across the globe. Legume diversification, through polyculture or intercropping, is a strategy that increases yields and income while improving family nutrition. However, the potential for these legume-cereal intercrops to restore soil functions in smallholder fields remains uncertain, with many studies failing to detect increases in soil organic matter (SOM). In sub-Saharan Africa, smallholders typically grow maize either intercropped with short-lived annual food legumes or as a monoculture. Recently, a novel maize system which includes perennial legumes in the genus *Desmodium* as intercrops, known as "push-pull" (hereafter, PP) has been increasingly adopted by smallholders across the region. The yield, nutritional and economic benefits of the PP system are well-documented. We investigated the effects of PP maize intercropping on soil fertility compared to the predominant maize culture systems (hereafter, NPP) using soils from long-term experiments and smallholder fields in western Kenya. Maize-desmodium intercrops promoted SOM accrual and increased plant available phosphorus. In the long-term research station experiments soil organic N was 20% greater and labile organic N reserves were five-fold greater in PP compared to NPP soils. Despite equal P fertilizer application rates, extractable soil P was two-fold greater in PP compared to NPP soils. Soils under maize-food legume intercrops did not show any detectable accrual of SOM compared to maize monocultures. Soil benefits in smallholder PP fields tended to mirror those found in the controlled experiments. Taken together, our results demonstrate that the perennial legumes in PP system restore soil function and fertility. Developing additional well-designed intercropping systems that include perennial legumes could play a significant role in reversing the trajectory of soil degradation in smallholder farming systems while enhancing human well-being.

1. Introduction

Forty percent of the world's population lives in rural communities that rely on smallholder subsistence agriculture as their primary food source (Poole, 2017). Improving yields and sustainability in smallholder agriculture remains an elusive goal and the majority of these communities are chronically food insecure (Kates and Dasgupta, 2007; van Ittersum et al., 2016). Sub-Saharan Africa (SSA), where smallholders produce 80% of the food, is a case in point. Despite decades of efforts to improve food production in smallholder farms, yield gaps continue to plague the region. Average maize yields in SSA during 2003–2012 ranged from 1.2 to 2.2 t/ha, far below regional yield potentials and in some countries, average yields continue to trend downward (van Ittersum et al., 2016). Improving crop production while reversing environmental degradation and restoring ecosystem services continues to be the focus of poverty alleviation efforts in SSA (Khan et al., 2014; Droppelmann et al., 2017).

While a number of obstacles account for the persistence of poor yields, one of the major underlying causes is soil degradation (Romney et al., 2003). Soil degradation is widespread in SSA and 40% percent of

soils in the region exhibit nutrient depletion (Tittonell and Giller, 2013; Tully et al., 2015; Barbier and Hochard, 2018). Moreover, smallholder subsistence farmers frequently respond to the reduced crop yields resulting from poor soil by intensifying their farming systems in ways that accelerate soil erosion and deplete soil organic matter and nutrients, creating a vicious cycle that perpetuates food insecurity and poverty (Lal, 2009; Vanek and Drinkwater, 2013; Barbier and Hochard, 2018). The consequences of these declines in soil fertility and function have become even more severe as the changes in precipitation patterns driven by climate change have increased the frequency and severity of droughts in the region (Müller et al., 2011). Efforts to close yield gaps using high yielding varieties and fertilizer subsidies have met with limited success due to economic, social and environmental constraints (Barbier and Hochard, 2018). Clearly, there is a need for innovative approaches that can reverse the unsustainable trajectory of soil degradation and poverty endemic to SSA and are compatible with smallholder farming systems.

One approach that has been gaining traction is the use of diverse polycultures to support yields and restore a range of ecosystem functions (Snapp et al., 2010; Tittonell and Giller, 2013). Intercropping is a diversification strategy where farmers grow two or more crops simultaneously in the same field as a mixture. Resource-limited farmers in developing countries commonly use intercropping because it can increase yields and economic profitability, reduce risk, and provide other agronomic benefits (Malezieux et al., 2009; Martin-Guay et al., 2018). Cereal-legume intercrops are the most widely used mixtures, in part because of the importance of these crops as staples and also because legumes can produce protein-rich grain even in impoverished soils (Snapp et al., 2010). In SSA, smallholder farmers commonly plant annual food grain legumes such as common bean or chickpea between rows of maize and other staple crops (Ojiem et al., 2007; Snapp et al., 2010; Nyawade et al., 2019b). Compared to monocultures, legume-cereal grain intercrops produce greater yields more often than not across a variety of environments and crop species (Bedoussac et al., 2015; Yu et al., 2016).

An extensive literature documents the influence of plant species diversity on the ecological processes that contribute to overyielding in legume-cereal intercrops (Brooker et al., 2015a; Martin-Guay et al., 2018). Plant-plant interactions, including complementarity, resource partitioning and facilitation are well studied, and these mechanisms enable greater nutrient acquisition and improve fertilizer and water use efficiency (Iverson et al., 2014; Brooker et al., 2015b; Duchene et al., 2017). Species mixtures can also provide other ecosystem services including weed suppression (Silberg et al., 2019), control of pathogens (Boudreau, 2013) and reductions in arthropod pests (Iverson et al., 2014). The effects of intercropping on soil processes have received less attention and the findings are inconsistent. Most studies do not detect any differences in soil fertility or soil organic matter (hereafter SOM) between intercrops and monocultures (Snapp et al., 2010; Wang et al., 2015) while others report benefits such as moderate increases in labile SOM and reduced erosion (Beedy et al., 2010; Nyawade et al., 2019a, 2019b).

The innovative push-pull (PP) intercropping system developed in western Kenya is a legume-cereal intercropping system that is currently being implemented in SSA (Khan et al., 2014). This novel system uses plant biodiversity to solve the complex, interrelated problems that limit maize yields in the region (Khan et al., 2008b, 2010, 2011, 2014). In addition to planting food legumes as intercrops with maize, PP intercropping adds the perennial legume, *Desmodium* spp. (commonly referred to as desmodium) between maize rows and fields are surrounded by perennial grass borders. In western Kenya, maize yields under PP intercropping increase two- to three-fold compared to yields under the typical farmer practices of maize-food legume intercrops or maize monocultures (Khan et al., 2008b, 2014; Midega et al., 2015). Moreover, PP intercropping enables small-scale farmers to venture into dairy cattle and goat keeping, as both desmodium and the species used

as grass borders are excellent fodder crops (Khan et al., 2008c). Because of these striking improvements, adoption by farmers has grown tremendously to more than 150,000 farmers in Kenya, Uganda, Tanzania, and Ethiopia (Murage et al., 2012, 2015a; Khan et al., 2014).

The extensive research on the PP intercropping system has focused almost exclusively on pest control, yields, nutritional and economic outcomes, and the chemical ecology governing interactions among organisms. The goal of our research was to investigate the effects of desmodium in push-pull intercropping systems on SOM and soil fertility compared to the typical farmer practice of either maize monoculture or maize-food legume intercropping. To that end, we designate the monocultures and maize-food legume intercrops common to the region as non-push-pull (NPP) cropping systems and broadly compare these systems to PP intercropping. In addition, we compare the effects of maize monocultures and five distinct maize-food legume intercrops to a maize-desmodium intercrop. We characterized soil organic matter pools, including labile soil OM pools that provide essential ecosystem services and are sensitive to management as well as macro and micro-nutrient contents, pH and CEC. We conducted these measurements in three long-term, replicated research station experiments comparing PP and NPP treatments under well-documented management regimes. We also conducted on-farm research to assess the impact of PP intercropping in working farms where practices are more variable.

We hypothesized that inclusion of desmodium in PP systems would increase SOM accrual and soil fertility compared to NPP cropping systems. Specifically, we hypothesized that SOM and soil N would reflect the continuum of legume intensity being greatest in PP, intermediate in annual legume-maize intercrops and lowest in maize monocultures. We reasoned that the continuous presence of desmodium in PP would increase the legume-derived inputs of litter, root exudates and symbiotic N fixation compared to short-lived annual food legumes. In addition, we were interested in comparing belowground benefits on working farms, where farmers face real world constraints and harvesting pressure can be more intensive, to the benefits obtained under the favorable management conditions of the research station. Based on the literature comparing on-farm outcomes to those from research facilities, we expected the effects of PP to be highly variable in smallholder fields. While yield improvements in smallholder PP systems are consistently achieved, we wanted to determine whether soil benefits could be realized under the more varied management regimes of farmers.

2. Methods

2.1. Overview of push-pull intercropping systems

The PP intercropping system involves intercropping cereals such as maize and sorghum with a perennial legume, usually *Desmodium* sp., which repels insect pests (push) while simultaneously planting a trap crop that draws pests to the field boarder (pull). Specifically, Napier grass (*Pennisetum purpureum*) or brachiaria grass (*Brachiaria* sp., cv mulato II) is planted as a border crop around the maize-desmodium intercropped field. Volatiles released by desmodium repel stemborer moths (e.g. *Chilo partellus*) from maize crop and at the same time, these insects are attracted to the trap crop border, preventing damage on the cereal crop (Midega et al., 2010; Khan et al., 2014). In addition, this diversified plant community modifies arthropod community composition and trophic interactions, attracting natural enemies and vastly reducing herbivore pressure on maize (Khan et al., 2000; Midega et al., 2009). By a stroke of luck, desmodium also controls striga (*Striga hermonthica*), a parasitic weed endemic to the region that can reduce maize yields by as much as 80% (Khan et al., 2000, 2002). Desmodium root exudates induce abortive germination of Striga (Khan et al., 2000; Hamilton et al., 2012). This suicidal germination eventually leads to the elimination of striga from infested fields. Furthermore, desmodium also boosts maize yields by supplying N to the maize since it can grow vigorously and fix N, even as an understory plant (Kifuko-Koech et al.,

2012).

2.2. Experimental sites

The three long-term experiments were located in the western region of Kenya at the International Center for Insect Physiology and Ecology (*icipe*) research station, Thomas Odhiambo Campus, Mbita Point (Fig. S1). The smallholder fields we sampled were located nearby in the Vihiga and Kisumu districts 60–70 km northeast of the research station. This region has a tropical climate and a bimodal precipitation pattern with "long rains" March through July and "short rains" September to November. Annual rainfall is highly variable but, in general, Mbita Point has a drier climate with an average annual rainfall of 1100 mm compared to Vihiga where the average annual rainfall is 1388 mm. There is also a small difference in the elevation; Mbita Point is at a slightly lower elevation, (1140 m) compared to the farm sites (1430–1470 m).

2.2.1. Long-term experiments at the icipe research station

The three research station experiments were initiated during 1998–2003 and all included PP and NPP maize cropping system treatments. The experiments at the Thomas Odhiambo research station (0°25'57.31"S, 34°12'24.49"E) provided sites where detailed information about management history and yields were available. Soils on the research station are poorly drained clays, predominantly Chromic vertisols/Typic chromusterts, also known as "black cotton soils" (Ahn and Gieger, 1987). While some management details vary across the three experiments, all management practices, including tillage, hand weeding, maize variety, planting date, irrigation and fertility management are identical between the PP and NPP treatments in each experiment and the three experiments are in very close proximity to one another (Fig. S2). Here we provide brief descriptions of each experiment; however, detailed design and management information is available (Khan et al., 2002, Khan et al., 2007).

1) Push-pull and maize monoculture fields established in 1998 (hereafter PP-1998): The experiment consists of two adjacent fields, each approximately 30 × 30 m, designed to simulate field size and typical management regimes used in smallholder fields. The NPP field is a continuous maize monoculture while in the PP field the continuous maize is intercropped with silverleaf desmodium (*Desmodium uncinatum*) and surrounded by a Napier grass (*Pennisetum purpureum*) border. From 1998–2004 maize crops in both fields received diammonium phosphate (DAP, 60 kg ha^{-1}) and calcium ammonium nitrate (CAN, 30 kg ha^{-1}) giving application rates of 19 kg N ha^{-1} and 12 kg P ha^{-1}. Since 2005, both fields have received farmyard manure at 3.7 m^3/ha for each maize crop and chemical fertilizers have been discontinued. Preliminary assessment indicated that soils in these fields are homogeneous without any apparent variation in topography or drainage, so we divided the two 30 × 30 m unreplicated fields into four 15 × 15 m sections for sampling (Fig. S2).

2) Mechanisms of striga suppression experiment established in 1999 (hereafter Str-1999): A randomized, complete block design with 6 × 6 m plots, three replications comparing continuous maize monocultures (NPP) to maize monocultures mulched with maize stover (NPP+mulch) and maize intercropped with *Desmodium uncinatum* (Khan et al., 2002; Midega et al., 2013). All three cropping systems have + /- N treatments: The +N plots receive 120 kg N/ha applied to each maize crop as CAN. In addition, all plots received phosphorus, in the form of DAP (60 kg/ha) for total application rates of 12 kg P ha^{-1} and either 27 kg N ha^{-1} or 147 kg N ha^{-1} in the –N and +N treatments, respectively. Maize yields in these plots have historically been more than three-fold greater in the PP compared to the NPP treatments (Midega et al., 2013; Table S1).

3) Food legume striga suppression experiment established in 2003 (hereafter F-Leg-2003): A randomized, complete block design with 6

× 6 m plots and four replications comparing maize monocultures to six different maize-legume intercrops that are harvested as a forage, leafy green vegetable or dry beans (Midega et al., 2014). The six species of legumes are as follows: Greenleaf desmodium [forage, *Desmodium intortum* (Mill.) Urb.] crotalaria (*Crotalaria ochroleuca* G. Don, leaves used as a vegetable), and four grain legumes: cowpea [*Vigna unguiculata* (L.) Walp. (Var.ICV2)], greengram [*Vigna radiata* (L.) Wilczek) (Var. Local), groundnut (*Arachis hypogaea L.*) (Var. Homabay), and common beans *(Phaseolus vulgaris* L.) (Var. Local 'Nyayo'). All treatments were fertilized at maize planting with CAN (60 kg ha^{-1}) and DAP (60 kg ha^{-1}) at application rates of 27 kg N ha^{-1} and 12 kg P ha^{-1}. At harvest, beans, maize and bean stover, and desmodium shoots were removed from the plots. Average historic grain yields have been about two-fold greater in the PP plots compared to the NPP treatments (Midega et al., 2014; Table S1).

2.2.2. Smallholder fields

Non-push-pull cropping systems are the dominant system for maize production in western Kenya and consist of either continuous maize monocultures or maize-food legume intercrops. The push-pull systems we sampled consisted of maize-desmodium intercrops-with and without intercropped food legumes. Borders of either Napier grass or *Brachiaria* sp. usually surround PP fields. Because the PP intercropped systems are less common than NPP maize, we started by identifying potential PP fields to serve as research sites.

To identify research sites, we first selected PP farmers who had previously cooperated with *icipe* research and extension projects and conducted interviews with 52 farmers in seven villages. PP farmers tend to be clustered in villages where one innovative farmer began working with *icipe* and then influenced other farmers in the village to adopt PP intercropping (Murage et al., 2011, 2012, 2015a, 2015b). To identify a subset of farms for sampling, we first selected a village where our interviews showed that the majority of PP fields had been under typical PP management for more than ten years. We found two groupings of PP farms that met these criteria. We then determined whether there were NPP fields in close proximity on the same soil and landscape position using conventional management practices typical for the region (Khan et al., 2008a, 2008b). Only one of these two groupings had NPP fields that were in close proximity with soils/landscape positions similar to the PP fields.

We selected nine smallholder farms in the villages of Ebukanga and Lela, all located within 14 km of 0° 5' 41.51" N, 34°35 '31.03" E and have fields that had been under typical PP intercropping for 9–14 years. Several PP farmers also had adjacent fields that were under NPP management so in these cases, we sampled pairs of PP-NPP fields managed by the same farmer. When PP farmers did not have a NPP field located on the same soil type and landscape position as their PP fields, we identified adjacent NPP fields farmed by neighbors to include in the study. There were two instances where NPP farmers had large fields that were adjacent to multiple PP fields, so we subdivided the larger fields in order to compare areas under PP and NPP management on the same soils with similar landscape positions (Fig. S3). We collected management information and soil samples from 18 fields within these farms. We used semi-structured interviews to collect overall management history and to construct a detailed chart of fertilizer and manure additions with farmers using either written records or memory of inputs purchased for at least three growing seasons. Before sampling, we recorded which crop species were growing in the field, measured the area of each field including the grass borders of PP fields, and divided the area under maize into three sub-plots (blocks) to collect replicated composite samples (Fig. S3).

The PP and NPP fields we sampled had considerable overlap in some management practices. All but three of the 18 fields we sampled included common bean *(Phaseolus vulgaris* L.) as an intercrop with maize. Push-pull farmers intercropped maize fields with either *D. uncinatum* or *D. intortum* (7 and 4 fields, respectively) and all but two

of the PP fields had common bean planted within the maize rows. Likewise, all but one of the NPP fields had common bean intercropped with maize. The fields ranged from 0.014 to 0.19 ha; and while the largest fields were all NPP, there was significant overlap in the sizes of PP and NPP fields (Table S3).

2.3. Soil sampling and analyses

We sampled soils in two campaigns, with all research station experiments and most of the farms sampled during November-December 2015. We collected samples from the remaining farm sites in a second round of sampling in June 2016. In all experimental sites, we collected composite soil samples (8–12 cores/plot, depending on plot size), using a 2.5 cm diameter corer, to 20 cm depth.

In the factorial research station experiments, we collected one composite sample from each plot as follows: Str-1999: 6 soil samples (2 treatments x 3 blocks) and F-Leg-2003: 24 soil samples (6 treatments x 4 blocks). For the PP-1998 field experiment, which was designed to mimic smallholder fields, each of the two fields (PP and NPP) was sub-divided into four quadrants giving a total of eight samples from this experiment (4 quadrants x 2 fields; Fig. S2). To minimize the impact of varying amounts of roots from non-legumes and legumes in fields with intercropped desmodium, we collected soil cores in maize monocultures and intercropped maize at a constant distance from maize plants (17 cm). This avoided sampling in maize rows where fertilizer was applied while also avoiding soil samples dominated by legume roots in the intercropped treatments. We also collected cores of a known volume for bulk density measurements in the experimental plots (Blake and Hartge, 1986).

In the farmer fields, composite soil samples were collected in a stratified, randomized pattern. Fields were divided into three sub-plots based on landscape position (Fig. S3) and soil cores were collected from three random locations representing one third of the plot resulting in three composite samples from each field. We followed the strategy described above for locating cores to avoid fertilizer and minimize roots in the samples.

Soils were air-dried and a 300 g subsample was sieved to 2 mm for analysis of soil texture, total N and organic C and soil chemical properties. We determined soil texture using the hydrometer method (Gee and Bauder, 1979). To quantify management effects on labile SOM pools we measured free and occluded particulate organic matter C and N (hereafter fPOM and oPOM, respectively) using unsieved soils (Marriott and Wander, 2006b). Briefly, this method combines density separation of free and occluded POM with wet sieving at 53 μm to extract two distinct POM fractions (Christensen, 2001; Marriott and Wander, 2006a). We analyzed total soil C and N and oPOM C and N using a LECO TruMac CN Macro Determinator (Lansing, MI) and for C and N content of the smaller fPOM fractions, we used a Vario-EL-III CN analyzer (Elementar, Hanau, Germany). Sieved soil samples were submitted for determination of chemical properties including soil pH, CEC and Mehlich 3 extractable P, K, Ca, Mg, Zn, Cu, S, CEC and percent saturation of the CEC by K, Mg, and Ca (Penn State Plant and Soils Analytical Laboratory, State College, PA).

2.4. Calculations and statistical analysis

All statistical analyses were performed using JMP (JMP Pro 13, SAS Institute Inc., Cary, NC, USA). We designed our statistical analyses to reflect the divergent requirements for analyzing data from the research station experiments and farmer fields.

Long-term experiments at the *icipe* research station: To test the effects of NPP versus PP management histories on soil properties, we used ANOVA and generalized linear mixed models. In models analyzing all three research station experiments, experiment was included as a random effect and experiment and cropping system effects were tested as well as possible interactions. Response variables were all the soil properties measured. When treatment effects in a single experiment (STR-1999 or F-LEG-2003) were analyzed, block was included as a random effect. In instances where we found significant differences across experiments in oPOM, we used regression analysis and Spearman's correlation to investigate the importance of clay content, since % clay is a known driver of oPOM accrual (Lavallee et al., 2020). Post-hoc analyses were conducted using Tukey-Kramer HSD.

To estimate treatment effects on soil N and P reserves on an area basis, we calculated kg ha^{-1} of SON, fPOM N, oPOM N and P in the top 20 cm using bulk density and concentrations of N and P. We also analyzed the distribution of N among SON pools by subtracting total POM N (fPOM N + oPOM N) from SON to estimate mineral associated OM (MAOM). This fraction accounts for the majority of SON and has a longer residence time compared to POM (Lavallee et al., 2020).

Smallholder fields: To document management practices used in PP and NPP fields we used interview data in conjunction with our measurements of field areas to calculate N, P and K application rates from chemical fertilizers. We estimated manure application rates based on the farmer reported unit of wheelbarrow loads multiplied by the typical volume of the wheelbarrows commonly used in the region (0.085 m^3).

For analysis of cropping system effects in farmer's fields, ANOVA and generalized linear mixed models included cropping system nested within farm pairs or cluster. While these methods are useful as a preliminary evaluation of the differences between adjacent PP and NPP fields, they cannot account for the multiple factors that vary across farmers' fields. We used principal components analysis (PCA) on the correlation matrix to generate independent variables that represented soil characteristics to examine management effects on soil characteristics in smallholder fields (Drinkwater et al., 1995, Schipanski and Drinkwater, 2011). The variables included in the PCA were selected to represent soil texture (% Clay) and soil characteristics that showed significant cropping system effects in the research station experiments including SOM quantity and quality (SON, fPOM C, fPOM C:N, oPOM N, oPOM C:N), soil nutrient content (extractable P, K and Zn) and pH. When two variables had a Pearson's correlation of > 0.8, only one of these variables was included in the PCA analysis (Pituch and Stevens, 2016). Principal components with eigenvalues greater than one and accounting for more than 10% of the variability in the data and eigenvectors > 0.3 were retained (Pituch and Stevens, 2016). We used ANOVA to test for differences in the distribution of PP and NPP fields along significant principal components.

3. Results

3.1. PP intercrops compared to maize monocultures in long-term experimental plots

For the most part, inherent soil properties were similar across the three long-term experiments, although there were some small differences in soil texture and chemical properties (Table S2). For example, while all three experiments were located on the same vertisol, the F-Leg-2003 experiment had a slightly greater clay content compared to the other two experiments (average clay content=51%, 44% and 45% for F-Leg-2003, PP-1998 and Str-1999, respectively; p < 0.05). There were no significant differences in texture between PP and NPP plots within experiments.

In contrast, management-induced differences resulting from the inclusion of desmodium intercrops with maize in PP systems for 12–17 years were highly significant across the three experiments. These effects of PP systems on soils were most evident for properties related to soil organic matter and included limited effects on soil chemical properties and micronutrients. Desmodium intercrops in the PP systems resulted in striking increases in SON (Fig. 1a) and SOC (similar results, Table S2) compared to NPP plots across all three long-term experiments. Extractable P was significantly greater in PP soils despite the long history of identical fertilizer additions to PP and NPP plots (Fig. 1b). Soil
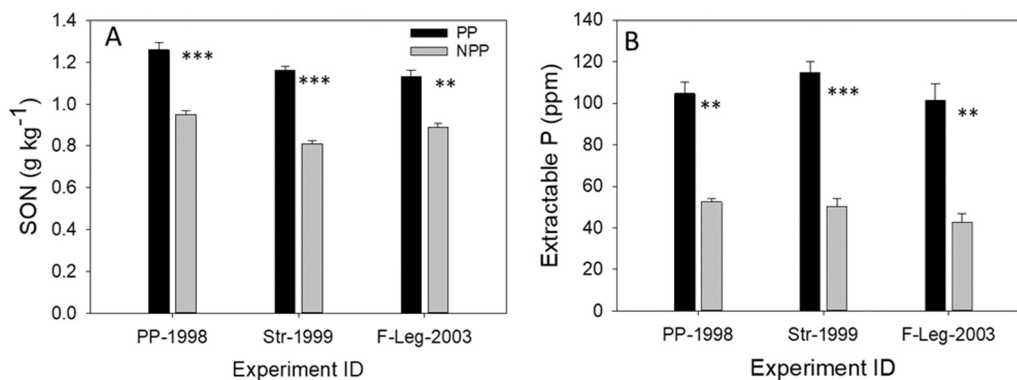
Fig. 1. Soil organic N (A) and extractable P (B) compared across the three experiments for PP and NPP plots. Means and SEs are shown, ANOVA, $p < 0.0001 =$ ***, $p < 0.001 =$ **.

extractable K showed a small but significant increase in PP compared to NPP soils (Table S2; ANOVA, $p < 0.05$) and extractable Zn was nearly two-fold greater in PP compared to NPP soils (ANOVA, $p < 0.0001$).

The effects of desmodium on SOM accrual and composition were even more striking in labile SOC/SON pools. Across the experiments, fPOM and oPOM N reserves were 3-fold to 5-fold greater in PP compared
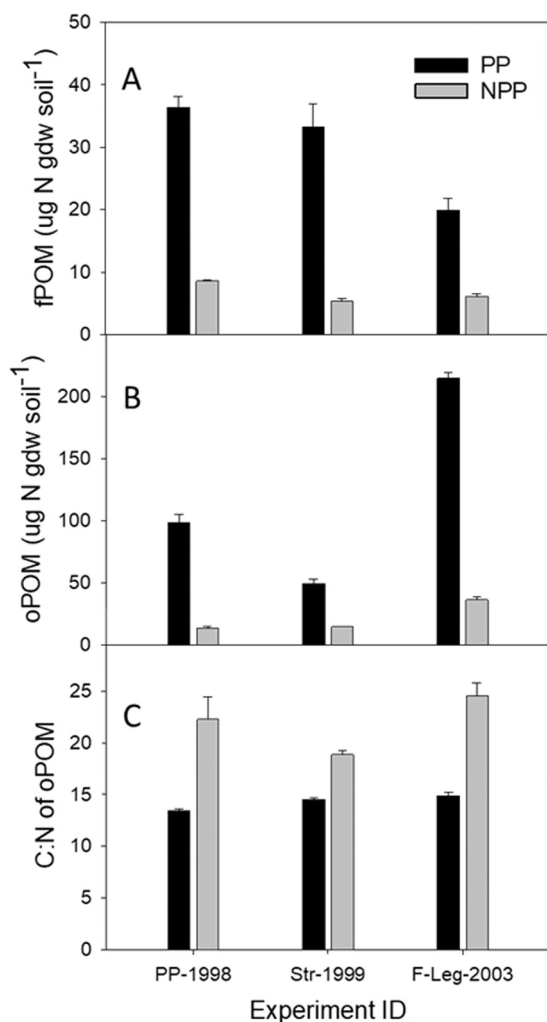

Fig. 2. A) fPOM (free particulate organic matter), B) oPOM (occluded particulate organic matter), and C) C:N ratio of oPOM in PP and NPP soils. All pairwise comparisons, PP vs NPP are highly significant (ANOVA, $p < 0.0001$) within each experiment. Means and SEs are shown.

to NPP soils (Fig. 2a and b). In general, under PP management, gains in oPOM were greater than increases in fPOM. Free POM and oPOM N pools were positively correlated across all three experiments. Occluded POM also differed qualitatively with average C:N ratios of 14 in PP compared to 21 in NPP plots (Fig. 2c).

Using bulk density measurements to estimate N and extractable P in the top 20 cm of soil showed that the scale of management-induced increases in soil fertility was agronomically significant. Bulk density in the top 20 cm of the soil profile was not significantly different across the three experiments (ANOVA, $p > 0.5$), averaging 1.22 and 1.37 g cm^3 in PP and NPP plots, respectively. Total N per ha In the top 20 cm of soil under PP and NPP management averaged 2900 and 2420 kg ha^{-1}, respectively. The substantial gains in total SON under PP intercropping were divided between MAOM and oPOM pools, and averaged 180 and 300 kg ha^{-1}, respectively. Only a small proportion of SON resided in fPOM, accounting for an average of 0.8% in NPP and 2.3% in PP of total SON. Extractable P was two-fold greater per ha in PP compared to NPP plots (260 versus 130 kg ha^{-1}, respectively).

3.2. Effects of different intercropped legume species on SOM

In addition to the maize monoculture and maize-desmodium intercrop treatments, the F-Leg-2003 experiment included NPP treatments consisting of maize intercropped with annual food legume species. Contrary to our expectations, we did not detect soil improvements under short-lived food legume-maize intercrops. Greenleaf desmodium (*D. intortum*) in the PP intercropping plots of this experiment increased SON (Tukey-Kramer HSD, $p < 0.02$) and oPOM N (Tukey-Kramer HSD, $p < 0.0001$); however, there were no detectable differences in either SON or oPOM N between maize intercropped with annual legumes and maize monocultures (Fig. 3). Occluded POM C showed a similar pattern in terms of PP compared to NPP treatments; however, three food legume intercrops (crotalaria, common bean, and green gram) had lower oPOM C compared to the maize monoculture (Fig. S4a, Tukey-Kramer HSD, $p < 0.03$) indicating small but significant differences in oPOM formation among these annual legume species. We did not detect any significant differences in extractable soil P under food legume-maize intercrops compared to maize monocultures (Fig. S4b, Tukey-Kramer HSD, $p > 0.05$).

These experiments were not designed to directly compare desmodium species; however, we noticed a striking difference in the magnitude of oPOM formation that corresponded with desmodium species rather than the longevity of the experiment. Compared to the other two experiments where PP treatments are intercropped with *D. uncinatum*, oPOM was significantly greater in the F-Leg-2003 experiment where *D. intortum* is used for the PP treatment (Fig. 2). In the two older experiments with *D. uncinatum* (PP-1998 and Str-1999), oPOM was three-fold greater in PP compared to the NPP plots whereas in F-Leg-2003

Fig. 3. Effects of desmodium and food grain legume intercrops and maize monocultures on soil organic matter after 12 years. Lower case letters indicate differences among treatments. Treatments are as follows: Mz-DG=maize/greenleaf desmodium, MzM=maize monoculture, Mz-CP=maize cowpea, Mz-CR=maize/crotalaria, Mz-CB=maize/common bean, Mz-GN=maize green gram. The perennial, greenleaf desmodium (D.intortum), used in the PP intercropping plots (Mz-DG) increased SON (A, Tukey-Kramer HSD, $p < 0.02$) and oPOM N (B, Tukey-Kramer HSD, $p < 0.0001$) compared to maize intercrops with food grain annuals and maize monocultures.

where maize was intercropped with *D. intortum* oPOM pools were six-fold greater in PP compared to the NPP maize monocultures (Fig. 2).

One explanation for the greater accrual of oPOM in the F-Leg-2003 experiment is the higher clay content in the F-Leg-2003 soil; however, % clay was only nominally related to oPOM content (adjusted $R^2 = 0.17$, $p < 0.1$ and Spearman $\rho = 0.40$, $p < 0.1$) and this weak correlation was largely driven by the four data points from the *D. intortum* plots which are far outside the 95% confidence interval (Fig. S5a). In contrast, oPOM was significantly correlated with fPOM (Fig. S5b, adjusted $R^2 = 0.34$, $p < 0.005$) and this relationship was even stronger when the *D. intortum* data points were removed (adjusted $R^2 = 0.71$, $p < 0.0001$). Furthermore, while there were no significant differences in fPOM C in PP plots across the three experiments, so the ratio of oPOM to fPOM is much greater in the maize *D. intortum* plots. Take together these results suggest that plant derived inputs may be a significant driver of these differences in oPOM accrual.

3.3. Land use and soil fertility management in PP and NPP fields

The average area planted with maize was 2-fold greater in NPP fields, but this difference was not statistically significant due to the large variation in field sizes within each management system. However, there was a significant difference in the percentage of the field allocated to maize; PP farmers allocated 10–49% of their field area to perennial grass borders, and the area used for grass borders did not reflect field size (Fig. 4a). Field borders were most commonly planted with Napier grass; while two fields had borders of Brachiaria grass and two NPP fields included grass borders without using desmodium intercrops (Table S3).

There were similarities in fertilizer management practices among PP and NPP farmers, although patterns of fertilizer versus manure inputs differed between management groups (Fig. 4b). Fertilizer N and P additions consisted largely of CAN and DAP and application rates to each maize crop were highly variable, ranging from 41 to 185 kg N ha⁻¹ and 2–17 P kg ha⁻¹, respectively. Animal manure additions varied nearly ten-fold, ranging from 2.7 to 20.7 m³ ha⁻¹. Across PP fields, N fertilization rates for maize varied from 41 to 135 suggesting that some PP farmers were likely over applying N fertilizer and incurring unnecessary input costs.

Reliance on fertilizers versus manure varied with cropping system type. In general, for NPP farms, fertilizer and manure rates were inversely related (Pearson correlation, $r = -0.76$, $p < 0.05$) while there was no consist pattern in the relationship between reliance on these two inputs in the PP fields ($p = 0.91$). Some farmers applied greater rates of soil amendments to maize grown during the long rains reflecting their expectation for greater yields compared to the short rains.

In addition to the tremendous disparity in fertilizer and animal manure additions across fields, we noticed a great deal of variation in desmodium harvesting practices across smallholder farms (Fig. S6). In some fields, the desmodium stands were sparse, likely due to over-harvesting and, resource-limited farmers who were more aggressively harvesting desmodium were tended to have poorer soil fertility. For example, in the PP Field of pair #7 (Fig. S6d), virtually all desmodium biomass was harvested compared to other fields where desmodium was allowed to grow under maturing maize (Fig. S6a-c).

Fig. 4. Land use patterns and fertility management in PP and NPP fields. A) The area allocated to grass borders versus field size. Points along the zero line indicate NPP fields where the entire field is planted to maize. B) Application rates for manure and phosphorus in PP and NPP fields.

3.4. Soil properties in smallholder PP and NPP fields

Inherent soil properties such as texture, micronutrient profiles and CEC were very similar between adjacent PP and NPP fields. For the most part, soil textural classification was similar across field pairs/clusters; however, there was one case where both the PP and NPP fields had a clay loam texture (Cluster 7). All other fields were within the clay textural classification, with the majority having clay contents of 46–59% (Fig. 5a).

Although the effects of PP intercropping systems on soil organic matter and nutrient reserves were more variable, management-induced differences between PP and NPP fields paralleled those found in the research station experiments. Soil organic N (Fig. 5b) and SOC were generally greater in PP fields compared to adjacent NPP fields and this increase in SON reserves was most apparent in labile pools such as oPOM N (Fig. 5c). While there was tremendous variation in DAP and manure additions within both management types, extractable P was greater in PP soils compared to adjacent NPP soils and these differences between adjacent fields did not correspond with differences in P additions (Fig. 5d). The relationship between DAP rates and soil P differed between management types. In NPP fields, extractable soil P was positively correlated with fertilizer P additions ($r^2 = 0.28$, $p < 0.005$); however, in PP fields there was no significant relationship between soil P and either fertilizer P or manure additions. Only one instance of greater soil P in NPP compared to the adjacent PP field occurred, probably due to the greater DAP application rates in the NPP field (Fig. 5d, Table S2).

The PCA analysis yielded evidence for both inherent soil type variation and management history as drivers for differences in soil properties across fields and sites. The first four principal components were significant and comprised of 76.2% of the variance (Bartlett's test, $p < 0.0001$). Push-pull and NPP fields were significantly different along the PC1 axis (ANOVA, $p < 0.0001$) where labile OM pools had the greatest eigenvector loadings followed by extractable P and pH (Table 1 and Fig. 6). Coordinates of PP and NPP fields were also significantly different for PC2 (ANOVA, $p = 0.01$) where total SON, extractable P and Zn accounted for 79% of the variance contained in PC2. There were a couple of notable exceptions where adjacent PP and NPP fields did not differ along PC1 but instead separated along PC2 (Fig. 6) suggesting that compared to labile OM pools, stable SON, P and Zn played a larger role

Table 1

Matrix loadings for principal components 1–3. Variables included in this PCA were all those that were significantly affected by cropping system in the long-term experiments at the research station plus % clay which was included to benchmark soil textural variation. Abbreviations: SON-soil organic N, fPOM C-free particulate organic matter carbon, fPOM C:N-free particulate organic matter carbon to nitrogen ratio, oPOM N-occluded particulate organic matter nitrogen, oPOM C:N-occluded particulate organic matter carbon to nitrogen ratio.

| Variable	Prin1	Prin2	Prin3
% Clay	0.133	0.240	-0.200
SON	0.225	**0.756**	0.380
fPOM C	**0.467**	-0.095	**0.661**
fPOM C:N	**-0.728**	0.049	0.236
oPOM N	**0.865**	-0.278	0.115
oPOM C:N	**-0.711**	**0.434**	0.271
pH	**-0.569**	-0.010	**0.557**
Extractable P	**0.505**	**0.694**	-0.060
Extractable K	0.379	-0.311	**0.660**
Extractable Zn	0.242	**0.780**	-0.028

in distinguishing management regime effects in these cases.

4. Discussion

Our results provide evidence that soil fertility restoration is an additional mechanism contributing to the yield, nutritional and economic benefits that have been documented in smallholder farms using PP intercropping (Midega et al., 2013; Khan et al., 2014; Kebede et al., 2018). Our study is the first to demonstrate substantial SOM accrual and soil fertility benefits under maize-legume intercropping in both research station experiments and smallholder fields. The new insights gained are pertinent to the ongoing efforts to reverse soil degradation and poverty trajectories in SSA as well as smallholder, subsistence communities worldwide.

4.1. Push-pull intercropping and provision of ecosystem services

Compared to the common farmer practices of planting maize monocultures or maize-annual legume intercrops, maize-desmodium intercrops promoted SOC/SON accrual, altered the composition of
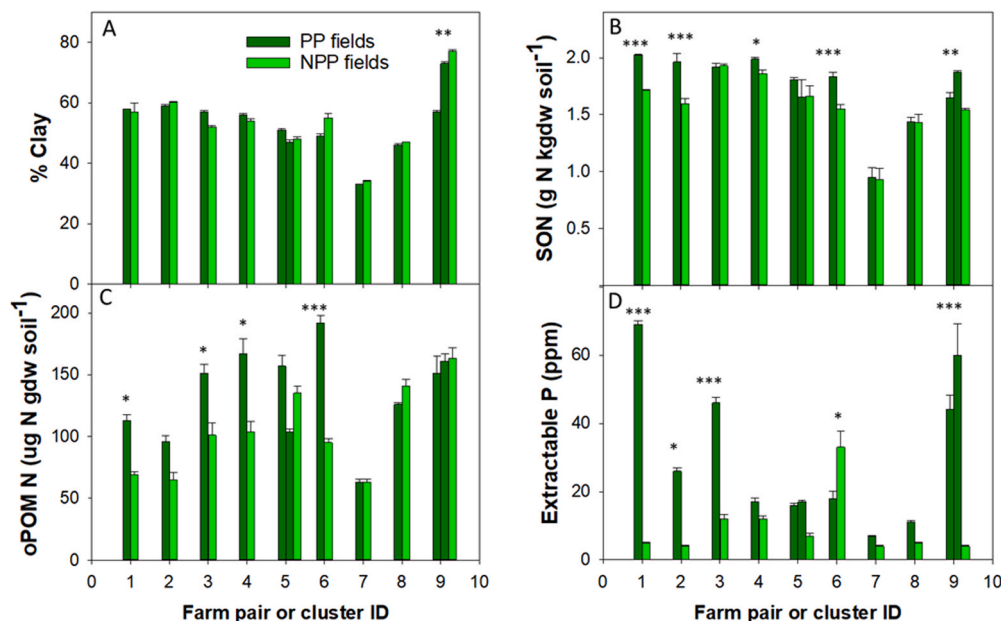
Fig. 5. Selected soil properties in adjacent PP and NPP fields. Mean + SE are shown for A) clay content, B) SON, C) oPOM N and D) extractable P. Cropping system effects were analyzed in a nested ANOVA and significant is between fields within each pair/cluster is indicated as follows: No significant difference = no symbols, $< 0.05*$, $< 0.001**$, $< 0.0001***$.
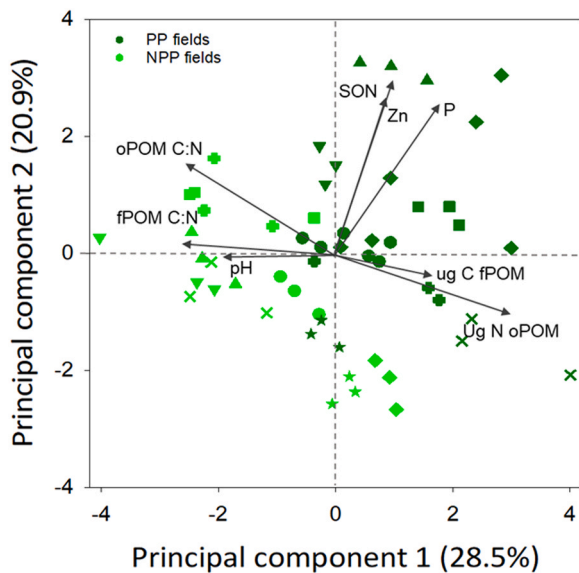
Fig. 6. Plot of the first and second principal components. PC1 and PC2 account for 29.5% and 20.9% of the variance, respectively. PC1 separates PP and NPP fields and represents management-induced differences. It has significant loadings for labile SOC and nutrient reserves and pH as indicated by the variables listed adjacent to the axis. Variables with significant loadings on PC2 include total soil N, Zn and extractable P, which are all positively correlated with PC2. Symbols with the same shape are adjacent fields.

SOM, and increased the capacity of soils to supply N and P to crops. In the long-term research station experiments average SON was 20% greater and oPOM N reserves were five-fold greater in PP compared to NPP treatments. Extractable soil P was two-fold greater in PP compared to NPP plots despite equal P fertilizer application rates to both treatments. Variation in practices used by farmers in managing PP and NPP maize crops influenced soil properties and interacted with cropping system effects in smallholder fields. As a result, the magnitude of management-induced differences varied across the paired PP-NPP fields and differences between PP and NPP fields were less consistent. Nevertheless, soil benefits in smallholder PP fields tended to mirror those found in the controlled experiments.

The greater gains in soil POM stocks compared to total SOM under PP intercropping follow a pattern commonly seen in other studies comparing management effects on SOM accrual (Puget and Drinkwater, 2001; Beedy et al., 2010; Schipanski and Drinkwater, 2011; Blesh and Ying, 2020). Labile pools with shorter turnover times such as fPOM and oPOM account for only 5–20% of SON reserves and are highly sensitive to management practices that alter SOM dynamics (Wander et al., 1994; John et al., 2005; Marschner et al., 2008; Jilling et al., 2020). Because net accrual or depletion of POM is more readily detected compared to changes in the larger stabilized SOM reserves, changes in POM can serve as an early indicator of the trajectory of soil fertility (Wander et al., 1994; von Lutzow et al., 2006; Schmidt et al., 2011). The stabilized, mineral-associated OM (MAOM) that dominates SOM reserves has a residence time ranging from 100 to > 1000 years and accounts for 70–80% of the total SON reserves making it difficult to detect small changes (Jilling et al., 2020; Lavallee et al., 2020).

Soil OM reserves play a crucial role in the provision of essential soil ecosystem services that support crop yields. First, both MAOM and occluded POM are major sources of mineralizable N and soils with greater N reserves in these two pools have corresponding increases in N mineralization potential and plant N acquisition (Bu et al., 2015; Blesh and Ying, 2020; Jilling et al., 2020). It is likely that the 5-fold increase in oPOM N in conjunction with the narrower C:N ratio of oPOM reserves significantly increases the supply of plant available N in PP soils (Berthrong et al., 2013).

Furthermore, oPOM plays a significant role in aggregate formation which in turn contributes to soil functions such as water storage, aeration, and water infiltration (Oades, 1984; von Lutzow et al., 2006; Marschner et al., 2008; Conceicao et al., 2013). This suite of more complex ecosystem services is essential for maintaining crop production in the face of rising temperatures and the greater frequency and severity of drought brought on by climate change (Li et al., 2009; Müller et al., 2011). Restoring soil properties that improve plant-soil-water relations may play a key role in climate change mitigation since other efforts to maintain yields through adoption of drought toleration crop varieties have met with mixed success in the region (Holden and Fisher, 2015).

Finally, the striking increases in plant available P in soils under PP management could also play a crucial role in supporting crop productivity in smallholder farms across SSA. This effect of PP intercropping was unexpected, particularly in the field station experiments where both the PP and NPP plots received the same applications of P fertilizers, and P removal through crop harvest was consistently greater in PP plots. Phosphorus limitation is widespread throughout SSA (Sanchez, 2002; Tully et al., 2015) and P limiting conditions contribute to low yields and malnutrition in this region (Lal, 2009). Our data corroborate this trend; 60% of the NPP farmer fields we sampled had extractable P levels < 10 PPM while only one PP field had extractable P this low.

Plant species vary widely in their capacity to access sparingly soluble inorganic P and organic P reserves. Compared to monocultures, phosphorus acquisition often increases in grass-legume intercrops (Cu et al., 2005; Li et al., 2007, 2014). Investigations of the underlying mechanisms reveal that legumes facilitate cereal P uptake by mobilizing sparingly soluble P stocks which would otherwise be unavailable to these crops (Li et al., 2007). However, increases in extractable soil P have not previously been detected in either cereal-legume intercrops or mixed grasslands that include legumes (Oelmann et al., 2007; Beedy et al., 2010). Several mechanisms could contribute to the increased extractable P, including greater accrual of added P fertilizer into SOM pools (Garland et al., 2018).

4.2. Plant functional traits are more important than species richness

Contrary to our original hypothesis, significant increases in SOM stocks and greater levels of plant available soil N and P were specific for the two desmodium species and did not occur under maize intercropped annual food grain legumes indicating that functional distinctions among legume species were more important that simply increasing species richness. This finding is in keeping with the biodiversity-ecosystem function literature for unmanaged ecosystems. While species richness frequently corresponds with ecosystem functions such as primary productivity, plant nutrient acquisition and decomposition rate, functional diversity can sometimes be a more reliable predictor of enhanced ecosystem processes, particularly when species richness is low (Cadotte et al., 2011, 2012; Cardinale et al., 2011).

Species richness in agricultural systems tends to be low and the potential for single species additions to have a significant effect on ecosystem processes is great (Cadotte et al., 2011; Storkey et al., 2015). Intercrop diversification schemes tend to focus on plant-plant interactions that can improve yields. Cereal/legume intercrops are a prime example where the positive interactions between functionally distinct plant species are well understood. The most widely planted grass-/legume intercrops are composed of annual species, and niche complementarity and facilitation are the dominant mechanisms leading to greater yields (Yu et al., 2016; Duchene et al., 2017).

Thinking beyond the plant-plant interactions that directly affect crop yield, species diversity also drives community-level attributes, including the composition and array of species niches as well as multitrophic interactions, which act in concert to shape ecosystem functions that can also support yields (Diaz and Cabido, 2001; Castro-Diez et al., 2014; Soliveres et al., 2016; Laforest-Lapointe et al., 2017). Provision of complex ecosystem services that can restore soil functions requires

consideration of a wide range of plant functional traits (Finney and Kaye, 2017; Funk et al., 2017; Le Bagousse-Pinguet et al., 2019). Differences in plant species effects on soil biogeochemical processes can be harnessed to target desired agroecosystem functions such as stabilization of soil OM through aggregate formation, C and N accrual, and net reductions in N losses and P immobilization (Drinkwater and Snapp, 2007; Li et al., 2014; Poirier et al., 2018).

Several lines of evidence indicate that, compared to annuals, perennials have a greater capacity to restore soil functions and SOM reserves (DeLuca and Zabinski, 2011; O'Brien and Jastrow, 2013; Crews et al., 2016; Crews and Rumsey, 2017). In temperate grain systems, inclusion of perennial legume forages in rotation increases SOM and oPOM compared to simple rotations of corn-soybeans or continuous small grains (Schipanski and Drinkwater, 2012; Berthrong et al., 2013; Maillard et al., 2016). An experiment comparing perennial grasses, legumes, and grass/legume mixtures found increases in oPOM averaged 9%, 35%, and 49%, respectively, after only two growing seasons (Gan and Drinkwater, in prep.).

In addition to these stark differences between annual and perennial legumes, we found that the two perennial legume species may differ in their capacity to build oPOM stocks. Plant-microbial interactions in the rhizosphere govern countless processes in soils, including aggregate formation, N mineralization, SOC/SON accrual, and other biogeochemical cycling processes, and effects on these processes vary with plant species (Reynolds et al., 2003; Castro-Diez et al., 2014; Li et al., 2014; Emmett et al., 2017). Plant species effects on N cycling processes have received the most attention and are governed by direct, plant-induced mechanisms (litter quality, suppressive root exudates), and indirect, microbially-mediated mechanisms resulting from plant-microbial interactions in the rhizosphere (inorganic N concentrations, composition/activity of nitrifier communities) (Briones et al., 2003; Hawkes et al., 2005; Subbarao et al., 2007; Philippot et al., 2013). Plant species effects on aggregate formation and other soil OM stabilizing mechanisms that support SOC/SON accrual are less understood; however, it is interesting to note that compared to *D. uncinatum*, *D. intortum*, the species with the greatest capacity to promote aggregate and oPOM formation, is also more drought tolerant (Khan et al., 2014; Midega et al., 2015). An increased capacity to withstand drought has been linked to greater polysaccharide production and aggregate formation in the rhizosphere (Alami et al., 2000; Poirier et al., 2018). The wide variation in belowground functional traits across plant species suggests that further investigations of plant-rhizobiome interactions and their impact on soil function will greatly advance the strategic use of plant species to restore desired soil functions.

4.3. Prospects for reversing soil degradation trends in smallholder systems

The preceding discussion makes it clear that plant species diversity can be harnessed to restore SOM and fertility in smallholder, subsistence farms and that perennial legumes are more likely to provide these benefits within a meaningful timeframe. However, inclusion of perennial legumes in conjunction with food grain production presents challenges (Snapp et al., 1998). To meet the needs of smallholder farmers, intercropping systems must deliver the provisioning ecosystem services that support human well-being in the short-term while also improving soil functions that underlie soil fertility and health (Snapp et al., 1998; King and Blesh, 2018).

To effectively target the desired belowground ecosystem functions requires greater knowledge of plant functional traits (Cardinale et al., 2012; Bommarco et al., 2013; Brooker et al., 2015b). Looking back on development of the PP intercropping system, it is clear that the remarkable array of ecosystem services provided by the companion plants can be traced back to screening efforts that first evaluated a large number of candidate species for functional traits that either repel (push) or attract (pull) the primary herbivores causing yield reductions (Khan et al., 1997, 2001). This strategy of setting criteria for desired plant

functional traits and then screening many potential species, proved to be extremely effective and provides a way forward to successfully use of plant species diversity for sustainable food production. Further studies of plant functional traits and their connection to rhizosphere processes could yield valuable understanding of linkages between easily measured plant traits and desired outcomes that can regenerate soil OM, restore soil ecosystem services, and contribute to sustainable agroecosystems (Haynes and Beare, 1997; Garland et al., 2018; Emmett et al., 2020). For example, plant traits related to growth rate and N acquisition strongly affect rhizobiome composition and function while traits such as litter composition correspond with net decomposition or accrual of SOM (Tamura and Tharayil, 2014; Emmett et al., 2020).

Furthermore, to fully realize the benefits of plant species diversity requires a comprehensive understanding of smallholder management decision-making and the effects of varying practices on the belowground processes we are attempting to manage. We found that the magnitude and consistency of soil OM accrual under PP intercropping was more variable on smallholder farms than in the research station experiments. This can be attributed to the greater variation in management practices across working farms compared to the research station (Tittonell and Giller, 2013). Indeed, management by PP and NPP farmers was highly variable, likely reflecting differences in livestock ownership, manure access, fodder requirements and ability to purchase fertility inputs. Application rates for N fertilizer varied by 3-fold in PP fields and it is possible that the higher N rates undermined desmodium N fixation rates. Use of N fertilizer in conjunction with legumes needs to be carefully calibrated since most legumes down-regulate N fixation in the presence of greater soil N availability (Ardley and Sprent, 2021). Furthermore, given that extractable P was < 20 ppm in many PP fields, investments in P fertilizer rather than high rates of N could be warranted. Lastly, added to these variations in soil amendment rates, aggressive harvesting of desmodium could undermine the capacity of this system to rebuild soil fertility. This large variation in farmer practices points to the need for research aimed at developing management recommendations that optimize the capacity of companion plants to provide the targeted ecosystem services. In the case of PP intercropping, guidelines on how to avoid overharvesting desmodium while optimizing fertilizer additions are needed.

5. Conclusions

We found that the perennial legumes included in PP intercropping promoted the formation of protected OM and increased accrual of N-rich OM reserves as well as plant available P. Our findings suggest that strategies to incorporate perennial legumes into intercropping systems could play a significant role in restoring soil function and fertility in smallholder farming systems. Affordable farming technologies such as PP intercropping, which provides a wide range of ecosystem services beyond immediate yield improvements are essential for addressing the recalcitrant problems of soil degradation, poverty, and malnutrition in smallholder farming communities worldwide. A large body of research demonstrates that intercropping boosts grain yields, provides protein-rich food/fodder, and increases income. The PP intercropping system provides these benefits for smallholder farmers in SSA while also effectively reversing the trajectory of soil degradation. Reforming government policies to support the refinement and adoption of PP intercropping could greatly expand the pool of smallholders in SSA who can implement this management system. To expedite the availability of new intercropping systems that can reverse soil degradation while meeting the needs of smallholder farmers worldwide, research characterizing the belowground functions of candidate species needs to be conducted in collaboration with agronomists who are familiar with regional farming systems and expert farmers who can play a crucial role in the development of locally relevant innovations.

Declaration of Competing Interest

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

Acknowledgements

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107566.

References

Ahn, P.M., Gieger, L.C., 1987. Kenya Soil Survey- Soils of Laikipia District. Ministry of Agriculture, National Agricultural Laboratories, Kabete, Kenya.

Alami, Y., Achouak, W., Marol, C., Heulin, T., 2000. Rhizosphere soil aggregation and plant growth promotion of sunflowers by an exopolysaccharide-producing Rhizobium sp strain isolated from sunflower roots. Appl. Environ. Microbiol. 66, 3393–3398.

Ardley, J., Sprent, J., 2021. Evolution and biogeography of actinorhizal plants and legumes: a comparison. J. Ecol. 109, 1098–1121.

Barbier, E.B., Hochard, J.P., 2018. Land degradation and poverty. Nat. Sustain. 1, 623–631.

Bedoussac, L., Journet, E.P., Hauggaard-Nielsen, H., Naudin, C., Corre-Hellou, G., Jensen, E., Prieur, L., Justes, E., 2015. Ecological principles underlying the increase of productivity achieved by cereal-grain legume intercrops in organic farming. A review. Agron. Sustain. Dev. 35, 911–935.

Beedy, T.L., Snapp, S.S., Akinnifesi, F.K., Sileshi, G.W., 2010. Impact of Gliricidia sepium intercropping on soil organic matter fractions in a maize-based cropping system. Agric. Ecosyst. Environ. 138, 139–146.

Berthrong, S.T., Buckley, D.H., Drinkwater, L.E., 2013. Agricultural management and labile carbon additions affect soil microbial community structure and interact with carbon and nitrogen cycling. Microb. Ecol. 66, 158–170.

Blake, G.R., Hartge, K.H., 1986. Bulk Density1. In: Klute, A. (Ed.), Methods of Soil Analysis: Part 1—Physical and Mineralogical Methods. Soil Science Society of America, American Society of Agronomy. Madison, WI, pp. 363–375.

Blesh, J., Ying, T.Y., 2020. Soil fertility status controls the decomposition of litter mixture residues. Ecosphere 11, 11.

Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. Trends Ecol. Evol. 28, 230–238.

Boudreau, M.A., 2013. Diseases in intercropping systems. Annu. Rev. Phytopathol. 51 (51), 499–519.

Briones, A.M., Okabe, S., Umemiya, Y., Ramsing, N.B., Reichardt, W., Okuyama, H., 2003. Ammonia-oxidizing bacteria on root biofilms and their possible contribution to N use efficiency of different rice cultivars. Plant Soil 250, 335–348.

Brooker, R.W., Bennett, A.E., Cong, W.F., Daniell, T.J., George, T.S., Hallett, P.D., Hawes, C., Iannetta, P.P.M., Jones, H.G., Karley, A.J., Li, L., McKenzie, B.M., Pakeman, R.J., Paterson, E., Schob, C., Shen, J.B., Squire, G., Watson, C.A., Zhang, C. C., Zhang, F.S., Zhang, J.L., White, P.J., 2015a. Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology. New Phytol. 206, 107–117.

Brooker, R.W., Bennett, A.E., Cong, W.-F., Daniell, T.J., George, T.S., Hallett, P.D., Hawes, C., Iannetta, P.P.M., Jones, H.G., Karley, A.J., Li, L., McKenzie, B.M., Pakeman, R.J., Paterson, E., Schoeb, C., Shen, J., Squire, G., Watson, C.A., Zhang, C.,

Zhang, F., Zhang, J., White, P.J., 2015b. Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology. New Phytol. 206, 107–117.

Bu, R.Y., Lu, J.W., Ren, T., Liu, B., Li, X.K., Cong, R.H., 2015. Particulate organic matter affects soil nitrogen mineralization under two crop rotation systems. 10.

Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48, 1079–1087.

Cadotte, M.W., Dinnage, R., Tilman, D., 2012. Phylogenetic diversity promotes ecosystem stability. Ecology 93, S223–S233.

Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P., O'Connor, M.I., Gonzalez, A., 2011. The functional role of producer diversity in ecosystems. Am. J. Bot. 98, 572–592.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67.

Castro-Diez, P., Godoy, O., Alonso, A., Gallardo, A., Saldana, A., 2014. What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. Ecol. Lett. 17, 1–12.

Christensen, B.T., 2001. Physical fractionation of soil and structural and functional complexity in organic matter turnover. Eur. J. Soil Sci. 52, 345–353.

Conceicao, P.C., Dieckow, J., Bayer, C., 2013. Combined role of no-tillage and cropping systems in soil carbon stocks and stabilization. Soil Tillage Res. 129, 40–47.

Crews, T.E., Rumsey, B.E., 2017. What agriculture can learn from native ecosystems in building soil organic matter: a review. Sustainability 9, 578.

Crews, T.E., Blesh, J., Culman, S.W., Hayes, R.C., Jensen, E.S., Mack, M.C., Peoples, M.B., Schipanski, M.E., 2016. Going where no grains have gone before: from early to mid-succession. Agric. Ecosyst. Environ. 223, 223–238.

Cu, S.T.T., Hutson, J., Schuller, K.A., 2005. Mixed culture of wheat (Triticum aestivum L.) with white lupiu (Lupinus albus L.) improves the growth and phosphorus nutrition of the wheat. Plant Soil 272, 143–151.

DeLuca, T.H., Zabinski, C.A., 2011. Prairie ecosystems and the carbon problem. Front. Ecol. Environ. 9, 407–413.

Diaz, S., Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655.

Drinkwater, L.E., Letourneau, D.K., Workneh, F., Vanbruggen, A.H.C., Shennan, C., 1995. Fundamental differences between conventional and organic tomato agroecosystems in California. Ecol. Appl. 5, 1098–1112.

Drinkwater, L.E., Snapp, S.S., 2007. Nutrients in agroecosystems: rethinking the management paradigm. In: Sparks, D.L. (Ed.), Advances in Agronomy, Vol. 92. Elsevier Academic Press Inc, San Diego, 163-+.

Droppelmann, K.J., Snapp, S.S., Waddington, S.R., 2017. Sustainable intensification options for smallholder maize-based farming systems in sub-Saharan Africa. Food Secur. 9, 133–150.

Duchene, O., Vian, J.-F., Celette, F., 2017. Intercropping with legume for agroecological cropping systems: Complementarity and facilitation processes and the importance of soil microorganisms. A review. Agric. Ecosyst. Environ. 240, 148–161.

Emmett, B.D., Youngblut, N.D., Buckley, D.H., Drinkwater, L.E., 2017. Plant phylogeny and life history shape rhizosphere bacterial microbiome of summer annuals in an agricultural field. Front. Microbiol. 8, 8.

Emmett, B.D., Buckely, D.H., Drinkwater, L.E., 2020. Plant growth rate and nitrogen uptake shape rhizosphere bacterial community composition and activity in an agricultural field. New Phytol. 225, 960–973.

Finney, D.M., Kaye, J.P., 2017. Functional diversity in cover crop polycultures increases multifunctionality of an agricultural system. J. Appl. Ecol. 54, 509–517.

Funk, J.L., Larson, J.E., Ames, G.M., Butterfield, B.J., Cavender-Bares, J., Firn, J., Laughlin, D.C., Sutton-Grier, A.E., Williams, L., Wright, J., 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biol. Rev. 92, 1156–1173.

Gan, H., Drinkwater, L.E. *In preparation.* Perennial grass-legume mixtures significantly increase SOM reserves after only two growing seasons. To be submitted to Agrictulure, Ecosystems and Environment.

Garland, G., Bunemann, E.K., Oberson, A., Frossard, E., Snapp, S., Chikowo, R., Six, J., 2018. Phosphorus cycling within soil aggregate fractions of a highly weathered tropical soil: a conceptual model. Soil Biol. Biochem. 116, 91–98.

Gee, G.W., Bauder, J.W., 1979. Particle-size analysis by hydrometer - simplified method for routine textural analysis and a sensitivity test of measurement parameters. Soil Sci. Soc. Am. J. 43, 1004–1007.

Hamilton, M.L., Kuate, S.P., Brazier-Hicks, M., Caulfield, J.C., Rose, R., Edwards, R., Torto, B., Pickett, J.A., Hooper, A.M., 2012. Elucidation of the biosynthesis of the di-C-glycosylflavone isoschaftoside, an allelopathic component from Desmodium spp. that inhibits Striga spp. development. Phytochemistry 84, 169–176.

Hawkes, C.V., Wren, I.F., Herman, D.J., Firestone, M.K., 2005. Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. Ecol. Lett. 8, 976–985.

Haynes, R., Beare, M., 1997. Influence of six crop species on aggregate stability and some labile organic matter fractions. Soil Biol. Biochem. 29, 1647–1653.

Holden, S.T., Fisher, M., 2015. Subsidies promote use of drought tolerant maize varieties despite variable yield performance under smallholder environments in Malawi. Food Secur. 7, 1225–1238.

Iverson, A.L., Marin, L.E., Ennis, K.K., Gonthier, D.J., Connor-Barrie, B.T., Remfert, J.L., Cardinale, B.J., Perfecto, I., 2014. Do polycultures promote win-wins or trade-offs in agricultural ecosystem services? A meta-analysis. J. Appl. Ecol. 51, 1593–1602.

Jilling, A., Kane, D., Williams, A., Yannarell, A.C., Davis, A., Jordan, N.R., Koide, R.T., Mortensen, D.A., Smith, R.G., Snapp, S.S., Spokas, K.A., Grandy, A.S., 2020. Rapid and distinct responses of particulate and mineral-associated organic nitrogen to conservation tillage and cover crops. Geoderma 359, 114001.

John, B., Yamashita, T., Ludwig, B., Flessa, H., 2005. Storage of organic carbon in aggregate and density fractions of silty soils under different types of land use. Geoderma 128, 63–79.

Kates, R.W., Dasgupta, P., 2007. African poverty: a grand challenge for sustainability science. Proc. Natl. Acad. Sci. USA 104, 16747–16750.

Kebede, Y., Baudron, F., Bianchi, F., Tittonell, P., 2018. Unpacking the push-pull system: assessing the contribution of companion crops along a gradient of landscape complexity. Agric. Ecosyst. Environ. 268, 115–123.

Khan, Z., Midega, C., Pittchar, J., Pickett, J., Bruce, T., 2011. Push-pull technology: a conservation agriculture approach for integrated management of insect pests, weeds and soil health in Africa UK government's foresight food and farming futures project. Int. J. Agric. Sustain. 9, 162–170.

Khan, Z.R., AmpongNyarko, K., Chiliswa, P., Hassanali, A., Kimani, S., Lwande, W., Overholt, W.A., Pickett, J.A., Smart, L.E., Wadhams, L.J., Woodcock, C.M., 1997. Intercropping increases parasitism of pests. Nature 388, 631–632.

Khan, Z.R., Pickett, J.A., van den Berg, J., Wadhams, L.J., Woodcock, C.M., 2000. Exploiting chemical ecology and species diversity: stem borer and striga control for maize and sorghum in Africa. Pest Manag. Sci. 56, 957–962.

Khan, Z.R., Pickett, J.A., Wadhams, L., Muyekho, F., 2001. Habitat management for the control of cereal stem borers in maize in Kenya.

Khan, Z.R., Hassanali, A., Overholt, W., Khamis, T.M., Hooper, A.M., Pickett, J.A., Wadhams, L.J., Woodcock, C.M., 2002. Control of witchweed Striga hermonthica by intercropping with Desmodium spp., and the mechanism defined as allelopathic. J. Chem. Ecol. 28, 1871–1885.

Khan, Z.R., Amudavi, D.M., Midega, C.A.O., Wanyarna, J.M., Pickett, J.A., 2008a. Farmers' perceptions of a 'push-pull' technology for control of cereal stemborers and Striga weed in western Kenya. Crop Prot. 27, 976–987.

Khan, Z.R., Midega, C.A.O., Amudavi, D.M., Hassanali, A., Pickett, J.A., 2008b. On-farm evaluation of the 'push-pull' technology for the control of stemborers and striga weed on maize in western Kenya. Field Crops Res. 106, 224–233.

Khan, Z.R., Midega, C.A.O., Bruce, T.J.A., Hooper, A.M., Pickett, J.A., 2010. Exploiting phytochemicals for developing a 'push-pull' crop protection strategy for cereal farmers in Africa. J. Exp. Bot. 61, 4185–4196.

Khan, Z.R., Midega, C.A.O., Hassanali, A., Pickett, J.A., Wadhams, L.J., 2007. Assessment of different legumes for the control of Striga hermonthica in maize and sorghum. Crop Sci. 47, 730–736.

Khan, Z.R., Midega, C.A.O., Njuguna, E.M., Arnudavi, D.M, Wanyama, J.M., Pickett, J.A., 2008c. Economic performance of the `push-pull' technology for stemborer and Striga control in smallholder farming systems in western Kenya. Crop Prot. 27, 1084–1097.

Khan, Z.R., Midega, C.A.O., Pittchar, J.O., Murage, A.W., Birkett, M.A., Bruce, T.J.A., Pickett, J.A., 2014. Comparison of two doses of ropivacaine hydrochloride for lumbosacral epidural anaesthesia in goats undergoing laparoscopy assisted embryo transfer. Int. Sch. Res. Not. 2014, 937018.

Kifuko-Koech, M., Pypers, P., Okalebo, J.R., Othieno, C.O., Khan, Z.R., Pickett, J.A., Kipkoech, A.K., Vanlauwe, B., 2012. The impact of Desmodium spp. and cutting regimes on the agronomic and economic performance of Desmodium-maize intercropping system in western Kenya. Field Crops Res. 137, 97–107.

King, A.E., Blesh, J., 2018. Crop rotations for increased soil carbon: perenniality as a guiding principle. Ecol. Appl. 28, 249–261.

Laforest-Lapointe, I., Paquette, A., Messier, C., Kembel, S.W., 2017. Leaf bacterial diversity mediates plant diversity and ecosystem function relationships. Nature 546, 145–147, 145-+.

Lal, R., 2009. Soil degradation as a reason for inadequate human nutrition. Food Secur. 1, 45–57.

Lavallee, J.M., Soong, J.L., Cotrufo, M.F., 2020. Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. Glob. Change Biol. 26, 261–273.

Le Bagousse-Pinguet, Y., Soliveres, S., Gross, N., Torices, R., Berdugo, M., Maestre, F.T., 2019. Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. Proc. Natl. Acad. Sci. USA 116, 8419–8424.

Li, L., Li, S., Sun, J., Zhou, L., Bao, X., Zhang, H., Zhang, F., 2007. Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. Proc. Natl. Acad. Sci. USA 104, 11192–11196.

Li, L., Tilman, D., Lambers, H., Zhang, F.-S., 2014. Plant diversity and overyielding: insights from belowground facilitation of intercropping in agriculture. New Phytol. 203, 63–69.

Li, Y.P., Ye, W., Wang, M., Yan, X.D., 2009. Climate change and drought: a risk assessment of crop-yield impacts. Clim. Res. 39, 31–46.

von Lutzow, M., Kogel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B., Flessa, H., 2006. Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions - a review. Eur. J. Soil Sci. 57, 426–445.

Maillard, E., Angers, D.A., Chantigny, M., Lafond, J., Pageau, D., Rochette, P., Levesque, G., Leclerc, M.L., Parent, L.E., 2016. Greater accumulation of soil organic carbon after liquid dairy manure application under cereal-forage rotation than cereal monoculture. Agric. Ecosyst. Environ. 233, 171–178.

Malezieux, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., Ozier-Lafontaine, H., Rapidel, B., de Tourdonnet, S., Valantin-Morison, M., 2009. Mixing plant species in cropping systems: concepts, tools and models. A review. Agron. Sustain. Dev. 29, 43–62.

Marriott, E.E., Wander, M., 2006a. Qualitative and quantitative differences in particulate organic matter fractions in organic and conventional farming systems. Soil Biol. Biochem. 38, 1527–1536.

Marriott, E.E., Wander, M.M., 2006b. Total and labile soil organic matter in organic and conventional farming systems. Soil Sci. Soc. Am. J. 70, 950–959.

Marschner, B., Brodowski, S., Dreves, A., Gleixner, G., Gude, A., Grootes, P.M., Hamer, U., Heim, A., Jandl, G., Ji, R., Kaiser, K., Kalbitz, K., Kramer, C., Leinweber, P., Rethemeyer, J., Schaeffer, A., Schmidt, M.W.I., Schwark, L., Wiesenberg, G.L.B., 2008. How relevant is recalcitrance for the stabilization of organic matter in soils? J. Plant Nutr. Soil Sci. -Z. Fur Pflanzenernaehr. Und Bodenkd. 171, 91–110.

Martin-Guay, M.O., Paquette, A., Dupras, J., Rivest, D., 2018. The new green revolution: sustainable intensification of agriculture by intercropping. Sci. Total Environ. 615, 767–772.

Midega, C.A.O., Khan, Z.R., Van den Berg, J., Ogol, C., Bruce, T.J., Pickett, J.A., 2009. Non-target effects of the 'push-pull' habitat management strategy: parasitoid activity and soil fauna abundance. Crop Prot. 28, 1045–1051.

Midega, C.A.O., Khan, Z.R., Amudavi, D.M., Pittchar, J., Pickett, J.A., 2010. Integrated management of Striga hermonthica and cereal stemborers in finger millet (Eleusine coracana (L.) Gaertn.) through intercropping with Desmodium intortum. Int. J. Pest Manag. 56, 145–151.

Midega, C.A.O., Pittchar, J., Salifu, D., Pickett, J.A., Khan, Z.R., 2013. Effects of mulching, N-fertilization and intercropping with Desmodium uncinatum on Striga hermonthica infestation in maize. Crop Prot. 44, 44–49.

Midega, C.A.O., Salifu, D., Bruce, T.J., Pittchar, J., Pickett, J.A., Khan, Z.R., 2014. Cumulative effects and economic benefits of intercropping maize with food legumes on Striga hermonthica infestation. Field Crops Res. 155, 144–152.

Midega, C.A.O., Bruce, T.J.A., Pickett, J.A., Pittchar, J.O., Murage, A., Khan, Z.R., 2015. Climate-adapted companion cropping increases agricultural productivity in East Africa. Field Crops Res. 180, 118–125.

Müller, C., Cramer, W., Hare, W.L., Lotze-Campen, H., 2011. Climate change risks for African agriculture. Proc. Natl. Acad. Sci. USA 108, 4313–4315.

Murage, A.W., Amudavi, D.M., Obare, G., Chianu, J., Midega, C.A.O., Pickett, J.A., Khan, Z.R., 2011. Determining smallholder farmers' preferences for technology dissemination pathways: the case of 'push-pull' technology in the control of stemborer and Striga weeds in Kenya. Int. J. Pest Manag. 57, 133–145.

Murage, A.W., Obare, G., Chianu, J., Amudavi, D.M., Midega, C.A.O., Pickett, J.A., Khan, Z.R., 2012. The effectiveness of dissemination pathways on adoption of "push-pull" technology in western Kenya. Q. J. Int. Agric. 51, 51–71.

Murage, A.W., Midega, C.A.O., Pittchar, J.O., Pickett, J.A., Khan, Z.R., 2015a. Determinants of adoption of climate-smart push-pull technology for enhanced food security through integrated pest management in eastern Africa. Food Secur. 7, 709–724.

Murage, A.W., Pittchar, J.O., Midega, C.A.O., Onyango, C.O., Khan, Z.R., 2015b. Gender specific perceptions and adoption of the climate-smart push-pull technology in eastern Africa. Crop Prot. 76, 83–91.

Nyawade, S.O., Gachene, C.K.K., Karanja, N.N., Gitari, H.I., Schulte-Geldermann, E., Parker, M.L., 2019a. Controlling soil erosion in smallholder potato farming systems using legume intercrops. Geoderma Reg. 17, e00225.

Nyawade, S.O., Karanja, N.N., Gachene, C.K.K., Gitari, H.I., Schulte-Geldermann, E., Parker, M.L., 2019b. Short-term dynamics of soil organic matter fractions and microbial activity in smallholder potato-legume intercropping systems. Appl. Soil Ecol. 142, 123–135.

Oades, J.M., 1984. Soil organic-matter and structural stability - mechanisms and implications for management. Plant Soil 76, 319–337.

O'Brien, S.L., Jastrow, J.D., 2013. Physical and chemical protection in hierarchical soil aggregates regulates soil carbon and nitrogen recovery in restored perennial grasslands. Soil Biol. Biochem. 61, 1–13.

Oelmann, Y., Kreutziger, Y., Temperton, V.M., Buchmann, N., Roscher, C., Schumacher, J., Schulze, E.D., Weisser, W.W., Wilcke, W., 2007. Nitrogen and phosphorus budgets in experimental grasslands of variable diversity. J. Environ. Qual. 36, 396–407.

Ojiem, J.O., Vanlauwe, B., de Ridder, N., Giller, K.E., 2007. Niche-based assessment of contributions of legumes to the nitrogen economy of Western Kenya smallholder farms. Plant Soil 292, 119–135.

Philippot, L., Raaijmakers, J.M., Lemanceau, P., van der Putten, W.H., 2013. Going back to the roots: the microbial ecology of the rhizosphere. Nat. Rev. Microbiol. 11, 789–799.

Pituch, K.A., Stevens, J.P., 2016. Applied Multivariate Statistics for the Social Sciences. Routledge, New York, NY.

Poirier, V., Roumet, C., Munson, A.D., 2018. The root of the matter: linking root traits and soil organic matter stabilization processes. Soil Biol. Biochem. 120, 246–259.

Poole, N., 2017. Smallholder Agriculture and Market Participation. Practical Action, Rugby, UK.

Puget, P., Drinkwater, L.E., 2001. Short-term dynamics of root- and shoot-derived carbon from a leguminous green manure. Soil Sci. Soc. Am. J. 65, 771–779.

Reynolds, H.L., Packer, A., Bever, J.D., Clay, K., 2003. Grassroots Ecology: Plant-Microbe-Soil Interactions as Drivers of Plant Community Structure and Dynamics. Ecology 84, 2281–2291.

Romney, D.L., Thorne, P., Lukuyu, B., Thornton, P.K., 2003. Maize as food and feed in intensive smallholder systems: management options for improved integration in mixed farming systems of east and Southern Africa. Field Crops Res. 84, 159–168.

Sanchez, P.A., 2002. Ecology - soil fertility and hunger in Africa. Science 295, 2019–2020.

Schipanski, M.E., Drinkwater, L.E., 2011. Nitrogen fixation of red clover interseeded with winter cereals across a management-induced fertility gradient. Nutr. Cycl. Agroecosyst. 90, 105–119.

Schipanski, M.E., Drinkwater, L.E., 2012. Nitrogen fixation in annual and perennial legume-grass mixtures across a fertility gradient. Plant Soil 357, 147–159.

Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P.,

Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56.

Silberg, T.R., Chimonyo, V.G.P., Richardson, R.B., Snapp, S.S., Renner, K., 2019. Legume diversification and weed management in African cereal-based systems. Agric. Syst. 174, 83–94.

Snapp, S.S., Mafongoya, P.L., Waddington, S., 1998. Organic matter technologies for integrated nutrient management in smallholder cropping systems of Southern Africa. Agric. Ecosyst. Environ. 71, 185–200.

Snapp, S.S., Blackie, M.J., Gilbert, R.A., Bezner-Kerr, R., Kanyama-Phiri, G.Y., 2010. Biodiversity can support a greener revolution in Africa. Proc. Natl. Acad. Sci. USA 107, 20840–20845.

Soliveres, S., van der Plas, F., Manning, P., Prati, D., Gossner, M.M., Renner, S.C., Alt, F., Arndt, H., Baumgartner, V., Binkenstein, J., Birkhofer, K., Blaser, S., Bluthgen, N., Boch, S., Bohm, S., Borschig, C., Buscot, F., Diekotter, T., Heinze, J., Holzel, N., Jung, K., Klaus, V.H., Kleinebecker, T., Klemmer, S., Krauss, J., Lange, M., Morris, E. K., Muller, J., Oelmann, Y., Overmann, J., Pasalic, E., Rillig, M.C., Schaefer, H.M., Schloter, M., Schmitt, B., Schoning, I., Schrumpf, M., Sikorski, J., Socher, S.A., Solly, E.F., Sonnemann, I., Sorkau, E., Steckel, J., Steffan-Dewenter, I., Stempfhuber, B., Tschapka, M., Turke, M., Venter, P.C., Weiner, C.N., Weisser, W.W., Werner, M., Westphal, C., Wilcke, W., Wolters, V., Wubet, T., Wurst, S., Fischer, M., Allan, E., 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536, 456–459, 456-+.

Storkey, J., Doring, T., Baddeley, J., Collins, R., Roderick, S., Jones, H., Watson, C., 2015. Engineering a plant community to deliver multiple ecosystem services. Ecol. Appl. 25, 1034–1043.

Subbarao, G.V., Rondon, M., Ito, O., Ishikawa, T., Rao, I.M., Nakahara, K., Lascano, C., Berry, W.L., 2007. Biological nitrification inhibition (BNI) - is it a widespread phenomenon? Plant Soil 294, 5–18.

Tamura, M., Tharayil, N., 2014. Plant litter chemistry and microbial priming regulate the accrual, composition and stability of soil carbon in invaded ecosystems. New Phytol. 203, 110–124.

Tittonell, P., Giller, K.E., 2013. When yield gaps are poverty traps: the paradigm of ecological intensification in African smallholder agriculture. Field Crops Res. 143, 76–90.

Tully, K., Sullivan, C., Weil, R., Sanchez, P., 2015. The state of soil degradation in sub-Saharan Africa: baselines, trajectories, and solutions. Sustainability 7, 6523–6552.

van Ittersum, M.K., van Bussel, L.G.J., Wolf, J., Grassini, P., van Wart, J., Guilpart, N., Claessens, L., de Groot, H., Wiebe, K., Mason-D'Croz, D., Yang, H.S., Boogaard, H., van Oort, P.A.J., van Loon, M.P., Saito, K., Adimo, O., Adjei-Nsiah, S., Agali, A., Bala, A., Chikowo, R., Kaizzi, K., Kouressy, M., Makoi, J., Ouattara, K., Tesfaye, K., Cassman, K.G., 2016. Can sub-Saharan Africa feed itself? Proc. Natl. Acad. Sci. USA 113, 14964–14969.

Vanek, S.J., Drinkwater, L.E., 2013. Environmental, social, and management drivers of soil nutrient mass balances in an extensive andean cropping system. Ecosystems 16, 1517–1535.

Wander, M.M., Traina, S.J., Stinner, B.R., Peters, S.E., 1994. Organic and conventional management effects on biologically-active soil organic-matter pools. Soil Sci. Soc. Am. J. 58, 1130–1139.

Wang, Z.-g, Bao, X.-g, Li, X.-f, Jin, X., Zhao, J.-h, Sun, J.-h, Christie, P., Li, L., 2015. Intercropping maintains soil fertility in terms of chemical properties and enzyme activities on a timescale of one decade. Plant Soil 391, 265–282.

Yu, Y., Stomph, T.J., Makowski, D., Zhang, L.Z., van der Werf, W., 2016. A meta-analysis of relative crop yields in cereal/legume mixtures suggests options for management. Field Crops Res. 198, 269–279.