Adding a soil fertility dimension to locust and grasshopper management, a case study in West Africa

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Abstract

In Senegal, West Africa, soils are a vital resource for livelihoods and food security in smallholder farming communities. Low nitrogen (N) soils pose obvious challenges for crop production but may also, counterintuitively, promote the abundance of agricultural pests like the Senegalese locust, *Oedaleus senegalensis*. In this study I investigated how the abundance of locusts and grasshoppers are impacted by soil fertility through plant nutrients and how these variables change across land use types. We worked in two rural farming villages in the Kaffrine region of Senegal. Overall, there was little variation in soil properties and an agricultural landscape low in soil organic matter (SOM) and inorganic soil nitrogen. I corroborated that SOM is a significant driver of soil inorganic N, which had a positive relationship to plant N content. Of the management practices we surveyed, fallowing fields was important for soil nutrient restoration and years spent fallow was significantly correlated to inorganic soil N and SOM. *O. senegalensis* was least abundant in groundnut areas where plant N was highest. Additionally, I found a significant negative correlation between *O. senegalensis* abundance and plant N, suggesting that plant nutrients are an important driver of their populations. Grasshoppers, excluding *O. senegalensis*, were more numerous in grazing areas and fallow areas, perhaps due to a higher diversity of ecological niches and host plants. These results connect land use, soil, and vegetation to herbivores and suggest that improving soil fertility could be used as an alternative to pesticides to keep locusts at bay and improve crop yields.

Key words

Social ecological systems, soil fertility, locust, grasshopper, nitrogen, plant nutrients, land-use, Senegal, West Africa

1. Introduction

Social and ecological systems have been intimately coupled through agriculture for thousands of years. In particular, land use has both intended and unintended impacts on human livelihoods through feedbacks within the coupled human and natural system (CHANS) (Liu et al. 2007; 2013). Understanding these complexities can open opportunities for novel management approaches. Agricultural practices alter the physical and chemical composition of soil which affects plant characteristics, including their nutrient contents (Mclauchlan, 2006; Wani et al. 1995; Welbaum et al. 2004). In turn, crop nutrient contents and ratios, particularly the carbon to nitrogen (N) ratio, influence the growth, reproduction, and behavior of insect herbivores, leading to changes in population size and migratory capacity (Cease et al., 2017; Mattson, 1980; Ode, 2006; White, 1993). However, as yet, few studies have explored these connections among land use, soil conditions, plant nutrient contents, and population dynamics of migratory pests. Here, we quantify these links within subsistence farming communities in Senegal, West Africa where Senegalese locust outbreaks are severe (*Oedaleus senegalensis* Krauss 1877; Acrididae).

O. senegalensis is considered to be the main pest of the Sahel (Cheke, 1990), capable of causing crop losses totaling hundreds of millions of dollars (Maiga et al., 2008). Locusts are grasshoppers that, when exposed to specific environmental cues, will develop into gregarious and migratory phenotypes that can spread across continents and cause significant economic losses (Uvarov, 1957; Pener, 1983; Cullen et al., 2017). This type of shock impacts social and ecological resilience (Chuku and Okoye, 2009) and is especially damaging for farmers in smallholder systems, as in Senegal. In addition to their unique phenotypic plasticity, there is growing evidence that *Oedaleus* locusts prefer and have fastest growth rates when consuming plants with low N content (Cease et al., 2017, 2015, 2012; Le Gall et al., unpublished data), in contrast to the dominant paradigm of N limitation of terrestrial herbivores (White, 1993). Therefore, practices that decrease plant N content locally have the potential to increase locust populations that are capable of spreading to neighboring and distant areas.

Soil properties and nutrient availability impact vegetation productivity and diversity which produces shifts in the abundance of herbivores (Van Der Heijden et al., 2008; Ode, 2006). Soil N is particularly important because it is limiting to primary producers in many terrestrial ecosystems and plays a large role in determining plant chemistry. For example, N additions have been shown to increase the protein concentration in plant tissue (reviewed in Liu et al., 2016). Total soil N is often depleted by continuous crop cultivation through the removal of soil organic matter (SOM), compaction, and erosion (Agbenin & Goladi, 1997; Hall, 2014; Doran & Zeiss, 2000). In Senegal, soils are especially vulnerable to N loss due to their low SOM and clay content, and both low cation exchange and water holding capacities (FAO, 2001). Other factors like drought, lack of resources for land restoration or fertilizer inputs, exacerbate poor agricultural soil (Bationo at al., 1998; Goudou et al., 2012; Christophersen et al., 1998; Tschakert and Khouma, 2004; Touré et al., 2013). In response to these challenges, common soil management practices include manure application, fallowing, and crop rotations. Chemical fertilizer is used in small doses depending on the financial capital of the farmer. Resource limitations impact the soil nutrients available to plants and potentially their nutrient expression and susceptibility to herbivory (Liu et al., 2016; Ode, 2006).

In the West Central Agricultural Region of Senegal, staple crops are grown each year during one summer rainy season from May through September. The Sahelo-Sudanian climate of this region averages 250–750 mm of annual rainfall (Sijmons K et al., 2013). The two most common crops are grown in a rotation of pearl millet (*Pennisetum glaucum*) and groundnuts (*Arachis hypogaea*). Both crops are successful in this region due to their tolerance of drought, sandy soil, low nutrient availability, and high temperatures (Andrews and Kumar, 1992; Singh, 1999; Vadez et al., 2012). Groundnuts are not as reliant on soil N due to their symbiotic relationship with N-fixing bacteria and typically have a higher leaf N content than millet. Millet is most vulnerable to herbivory by *O. senegalensis*, which targets grasses including cereal crops, likely due to their preference for lower N leaf tissue (Cease et al., 2012).

The plant diversity available to *O. senegalensis* and other grasshoppers is arranged as a heterogeneous landscape of discrete land use types: agricultural cropland, fallow fields, and grazing areas dominated by grasses and woody-shrubs. *O. senegalensis* can be found across different land use types, but is most abundant in fallow and millet fields, and has been previously documented to preferentially move as nymphs from other field types into fallow areas (Toure et al., 2013). Anecdotally from farmer accounts, *O. senegalensis* may persist in high numbers in common-pool livestock grazing areas and move into crop fields after crops have sprouted (interviews 2016). How *O. senegalensis* and other grasshoppers are distributed throughout these land use types has not been tested, nor do we understand the potential mechanisms regulating these patterns.

In this research, we took a mixed methods approach combining biophysical data with quantitative surveys and qualitative interviews, to address the CHANS from a holistic perspective. We set out to test the hypothesis that management practices resulting in lower soil fertility will promote *O. senegalensis* outbreaks by lowering plant N (and correspondingly, protein) content (Cease et al., 2012, 2015). Specifically, we asked, what is the relationship between agricultural land use and management, soil properties, plant N content, and grasshopper abundance? We explored this question in a mixed smallholder agricultural landscape in Senegal, west Africa because locusts in the genus *Oedaleus,* have a much lower protein preference relative to other acridids tested to date (Behmer, 2009; Cease et al., 2012; Le Gall et al. unpublished data). We predicted they will be most sensitive to plant N, compared to other grasshopper species which would be unaffected or positively associated with plant N. Additionally, we predicted that land management practices would influence soil inorganic N and areas with higher soil N would produce plants with higher N content, ultimately driving the abundance of locust.

2. Methodology

2.1 Field sites

Our research was conducted in the Kaffrine region of Senegal (14°06'18.7"N 15°32'29.8"W). The area is known as the 'West Central Agricultural Region', or Peanut Basin (Tappan et al. 2004). Precipitation in this region ranges from an average of 2.14 mm in the dry season (November-April) to an average of 736.05 mm during the rainy season (May-October). Dry season temperatures average ~27°C compared to rainy season average of ~29°C (World Bank, 2015). The woody shrubland savanna landscape is topographically flat and marked by agriculture expansion that has replaced native forests (Mbow et al., 2008). Soils are classified as Arenosols, characterized by high sand content, high permeability, low water and nutrient storage capacity and prone to wind and water erosion (Goudou et al., 2012; FAO, 2011). We worked with two villages, Gossas (14°29'44.5"N 16°04'01.2"W) and Gnibi (14°26'11.5"N 15°39'13.6"W). These villages were chosen because of the prevalence and persistence of *O. senegalensis* in these areas and their similar population size (10,000-13,000 people according to Senegal Census Data, 2013). In both villages, households individually manage farming areas while grazing areas surrounding the villages are open access, and can be used by anyone in the village or migrating pastoralists. These areas are part of centuries-old livestock transhumance corridors which play a vital role in mixed land use for sustaining livestock (Kitchell et al., 2014).

Fig. 1

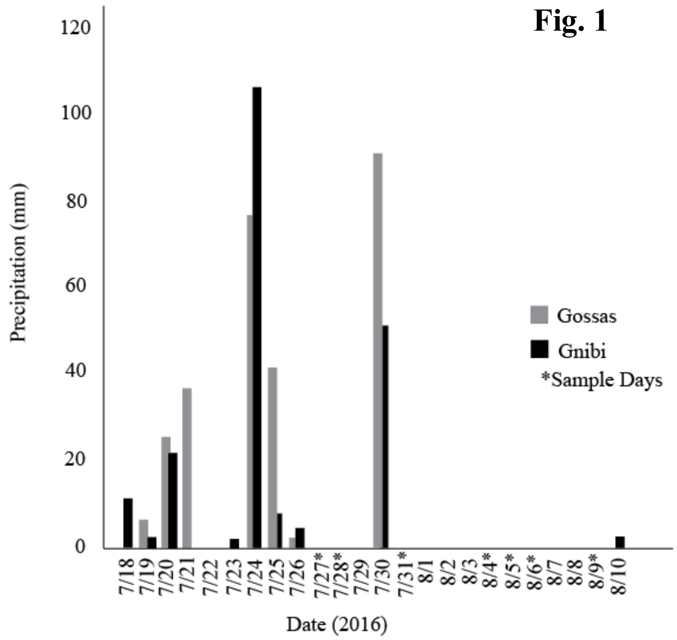

Fig. 1 July and August 2016 precipitation data (mm) for our study sites. Asterisk (*) indicates sample collection dates.

To select participants for this study, in June of 2015 we collaborated with village leaders and local contacts from the national plant protection agency, La Direction de la Protection des Végétaux (DPV). We identified participants whose fields were distributed spatially throughout the village's farming areas, and who farmed a combination of millet, groundnut, fallow fields, and grazed livestock, which were the dominant land use types across the landscape. The village leaders selected 5-6 farmers for each village that best met these criteria for inclusion in the study.

2.2 Field Survey Experimental Design

In July-August 2016, we worked with 4 farmers from Gossas and 5 farmers from Gnibi. We aimed to sample from a millet, groundnut, and fallow field all under each participants' management. Out of the 9 participants, 2 Gnibi and 2 Gosass farmers did not have a fallow field in 2016. Crop and fallow fields ranged from 1.5 – 10 ha in area. Because grazing areas are not managed at the level of the household, we selected and sampled two grazing areas for each village. Fallow fields are areas taken out of crop production and set aside to restore soil fertility. In each field or grazing area, we sampled soils, plants, and grasshoppers from or around three 5 m x 5 m plots randomly distributed across the field. Precipitation data was gathered from rain gauge (mm) logs kept by the village chief offices in each village.

2.3 Soil Sampling and Analysis

All soils were collected between July 27 and August 5, 2016 (Fig. 1). In each 5 m x 5 m plot, we collected two separate soil cores (4 cm diameter, 16 cm length) at depths 0-7 cm and 8-15 cm and homogenized cores by depth into two soil samples. We collected a separate 0-5 cm core to estimate bulk density of the surface soil. Soils were immediately placed in cooler with ice for 2-10 hours prior to being transported back to the DPV Nganda phytosanitary station. At the station, we stored soil samples in a refrigerator at 8°C ± 2°C for <8 h prior to sieving. Samples were hand sieved to remove organic matter and rocks to 4 mm. No samples contained substantial amounts of 2 mm-4mm sized gravel. We then subdivided the samples into two plastic bags to measure plant-available inorganic N, and net potential N transformations (net potential N mineralization and net potential nitrification). Half of the samples were air dried in containers with desiccant and stored at 29 ± 2° C while in Senegal. The other half of the samples were incubated in the dark at 29 ± 2° C for 26 days at moisture levels between 10 – 20 % weight addition of sample mass.

All soil samples were hand carried back to Arizona State University (ASU) laboratory facilities on 7 Aug and were stored at 22° ± -16° C until processing, which occurred within 17- 26 days of sample collection. We measured inorganic N (NO_3- + NH_4+ = total inorganic N), texture, bulk density (BD), soil moisture (SM), soil organic matter (SOM), pH, and electrical conductivity (EC) using standard soil methods (Chemical and Physical volumes of Methods SSSA Book Series:5).

We measured soil texture, pH, and EC on air-dried soil subsamples. To determine particle size, we used the hydrometer method. We shook 40 g of soil with 100 ml of 50 g l^{-1} (5%) sodium hexametaphosphate for 24 h and placed in sedimentation cylinders and carefully added 900 ml of deionized water. Using a suspension plunger we manually mixed the solution and took hydrometer readings at 40 s and 7 h. We calculated sand (%) using the known percentage of silt (%) and clay (%) subtracted from 100%. We accounted for accuracy in sand readings by sieving the soil after 7h with a 53-micron mesh sieve and determined sand weight by removing remaining sediment and drying it overnight at 105°C. We did not destroy organic matter before analysis; however, organic matter was low enough (0.71-1.30%) that the error would not have significantly affected the results. We measured pH on a 10 g soil subsample diluted 1:2 with 20 ml DI using a pH meter (Miller-Toledo). We measured EC on the same sample in a 1:3 water solution (Hatch Conductivity Probe model 17250) to a precision of 1400-1600 µS/cm.

For N extractions, one 10 g subsample from each plot was shaken for 1 hr in 50 mL 2N KCl, set aside for 18-24 hours, filtered through pre-leached Whatman #1 filters, and then frozen immediately for later analysis. Air-dried initial samples were extracted first followed by the incubating samples, which were also extracted as described above. Net potential N mineralization was calculated as the difference between the sum of NH_4^+ and NO_3^- concentrations before and after each incubation period. Net potential nitrification was calculated as the difference between NO_3^- concentrations before and after each incubation period. Extractable NO_3-, and ammonium NH4+ were analyzed using a microplate reader based on the Weatherburn (1967) protocol, as adapted by (Doane and Horwáth, 2003).

We measured bulk density (soil dry weight [g] / 65.35 cm^3 core volume) and gravimetric soil moisture from an intact soil core (0-5 cm depth) that was carefully collected from each plot to ensure no loss of soil particles in the field. Soil organic matter was calculated by weighing dried soil before and after baking samples for 5 hours at 550°C in a Thermolyne 6000 muffle furnace.

2.4 Plant Sampling and Analysis

In each 5 m x 5 m plot, we visually assessed total cover of vegetation and the three most abundant plant species (Figure 1; *Relevé* method Minnesota Department of Natural Resources, 2013). We calibrated percent cover estimates between observers to reduce observer bias (Morrison 2016). Additionally, we collected three to five g (wet mass) of leaves from several individuals of each of the dominant three species scattered throughout the plot for nutrient analysis. This includes the crop in production (millet or groundnut) and the native grasses, sedges, forbs, or shrubs present as weeds and groundcover in fallow areas. The field team removed leaves from stems on site, kept them separate by species, and placed them in a cooler with ice after collection for <10 hours before placing them in a drying oven at 60°± 5°C for 36-48 hours. Dried samples were hand carried back to ASU laboratory facilities and stored in paper bags until being ground using a Retsch MM 400 ball mill for 30 seconds at 200 rpm. We then analyzed ground plant samples for carbon (C) and N content using a Perkin-Elmer model 2400 CHN analyzer at the Goldwater Environmental Lab at ASU. Plant CHN data was analyzed separately for each individual plant collected and later averaged at the site level for some of the statistical analysis.

2.5 Locust Sampling

We estimated grasshopper abundance and diversity with sweep net surveys within 20 m of each plot where vegetation and soil samples were taken. The same researcher conducted all surveys by evenly sweeping 20 times, each a 180° arc approximately 1 m apart along a straight line.

2.6 Farmer Surveys

To explore the potential relationship between farmer management practices, soil properties, and plant N content, we administered interviews with farmers and village leaders. In 2016, we spoke with leaders to learn general property rights regimes for the villages and history of the grazing areas. Additionally, we interviewed 9 farmers on site at the time of soil sampling to ask questions about questions about yearly and seasonal farming practices like crop rotation, residue removal, fertilizer use, and other factors. Each farmer was asked about the history and management of the land, using an interpreter (B. Manneh), who was fluent in Wolof, the most common language spoken in Senegal. Every interview started with a set of general questions about yearly farming practices to get more detailed information about how the land is managed over seasons. These were followed by questions about soil and pest management, use of fallow, and concepts of sustainability. We conducted an additional 12 interviews in 2017 to gain further insight into the social system that strongly influences the ecological one we sampled from in 2016. Participants included 7 out of the original 9 farmers, 2 other farmers representing the original participants who couldn't be present at the time, and 3 DPV staff members. These interviews included more detailed questions about soil and land management as well as locust control strategies. For reference, years fallow takes into consideration the years a particular field has spent out of crop production (not necessarily continuous). Fertilizer use was defined by if the farmer uses synthetic or organic manure in his management practice in general, not on the day of our survey.

2.8 Statistical methods

All statistical analyses were carried out in RStudio version 1.0.143. Data quality assurance was a multi-step effort to check for missing values, inconsistencies, and outliers. Soil texture did not differ between depths (0-7 and 8-15 cm), so separate soil depth samples were combined before in statistical analyses and the 0-5 cm depth bulk density estimate was applied to all 15 cm. In the plant dataset, two outliers (out of 225 samples) were removed from analysis due to suspected instrumental error. Soil samples (2 cores per plot, 3 plots per field), grasshoppers (sweep nets around the 3 plots per field) and both plant samples and cover (3 plots per field) were averaged across each field before statistical analyses.

To test the importance of land use type on site-level soil, plant, and grasshopper parameters, we used multiple linear models (ANOVAs) to assess the relationship between the independent variable (land use type) and dependent variables (soil inorganic N, SOM, SM, BD, pH, EC, soil texture, plant nutrients, and grasshopper abundance and diversity). We plotted all residuals to assess assumptions of normality and homogeneity of variance; data were log transformed as needed to meet these assumptions or a non-parametric alternative was used (Kruskal-Wallis). Kruskal-Wallis was used on testing the differences of GH species by land use type. Specifically, used for Acropha sp., Acrotylus sp., and Chrotogonus senegalensis, as well as for species diversity where abundance data did not meet assumptions of normality.

To evaluate how soil and groundcover properties influenced soil inorganic N and plant N, we used multiple linear mixed-effect models (LMEs) to test the relationship between the non-correlated independent variables (see appendix A) on the dependent variables, total inorganic N (initial NO_3^- + NH_4^+) and plant N content, with 'village' as a random factor. We used another LME to explore the relationship between binary and ordinal farmer management practices (residue removal, burning, fertilizer use, land use history, alternative crops) on soil total inorganic N. Grazing areas were removed from analysis for questions about farmer management because these sites were not directly managed or under cultivation. A final LME was used to predict locust abundance from the plant, soil, and land use variables surveyed. We selected models using the information criterion approach and accepted all models within ΔAICc ≤ 2 of the best one (e.g. the model with the lowest AICc value (Burnham and Anderson 2002)). Alternative models can be found in the appendix section.

To test the correlation between locust and grasshopper abundance and plant nutrients, we did a separate analysis from the LME's above, using linear regressions and Pearson's Correlation Tests. Spearman's rank correlation were used when data did not meet normality assumptions (Acrotylus sp.~ Plant N, C:N).

3. Results

3.1 Land use differences in soil, plants, and grasshoppers

Across this mixed agricultural landscape, soils were sandy, low in SOM with pH less than 6, as expected for Arenosols (FAO, 2011). The soil type characteristics were consistent with other studies (Tschakert et al., 2000; Goudou et al., 2012) and overall, nitrogen poor, moderately acidic, high in BD, with low EC as expected. Most soil characteristics varied minimally across land use types, except texture and SOM (Table 1). Actively cultivated crops were sandier than either grazed or fallow fields, and were generally lower in organic matter.

Table 1. Soil characteristics across land use types. Values indicate mean (SE) of 9 farmer fields. Letters show post hoc significant differences between land use types from Tukey HSD comparisons following ANOVAs.

Variable	Fallow	Grazing	Groundnut	Millet	P Value
Sand (%)	83.1 (2.8) (a)	80.2 (5.1) (a)	(86.9) (1.8) (b)	87.8 (23.0) (b)	**0.003
Silt (%)	12.9 (1.2) (a,c)	13.1 (2.6) (b,c)	10.3 (1.8) (b)	9.6 (2.8) (b)	*0.01
Clay (%)	4.0 (2.1) (a,c)	6.7 (3.6) (c)	2.9 (1.2) (a,b)	2.6 (0.6) (b)	*0.02
BD (g/cm³)	1.7 (0.1)	1.7 (0.1)	1.6 (0.1)	1.7 (0.1)	0.3
SOM (%)	0.9 (0.3) (a,b)	1.3 (0.5) (a)	0.8 (0.1) (b)	0.7 (0.1) (b)	*0.01
pH	5.6 (0.5)	5.9 (0.41)	5.6 (0.4)	5.6 (0.2)	0.4
EC (mS/cm)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)	0.02 (0.02)	0.9
SM (%)	4.8 (1.3)	3.6 (1.9)	4.5 (1.3)	5.1 (2.6)	0.5
Total N (mg/kg)	8.0 (2.7)	12.4 (4.6)	9.9 (5.1)	10.3 (4.3)	0.8
NO3 (mg/kg)	4.5 2.0)	6.5 (2.7)	5.7 (3.9)	6.0 (3.3)	0.9
NH4 (mg/kg)	2.4 (0.5)	3.8 (1.7)	3.2 (2.0)	2.8 (1.4)	0.6
Net Min (mg/kg)	5.2 (5.0)	1.1 (3.1)	6.1(4.4)	8.0 (4.2)	0.1
Net Nit (mg/kg)	6.4 (4.6)	3.0 (3.7)	7.8 (5.5)	8.0 (3.7)	0.3

At the time of sampling, the dominant plants in the cropped fields were either millet or groundnut, followed by native plants (as weeds). These native plants dominated fallow and grazing areas along with woody shrubs in the acacia genus. The average field vegetation cover was between 11-40 % and highest coverage was in grazing areas (Table 2). We surveyed from about six different plant families and four functional groups, grasses, forbs, legumes, sedges, and shrubs (Supplemental Table 1). As expected, total plant N content was highest in fields cropped with groundnut, a N-fixing legume (Table 7; Fig 2B).

Fig. 2

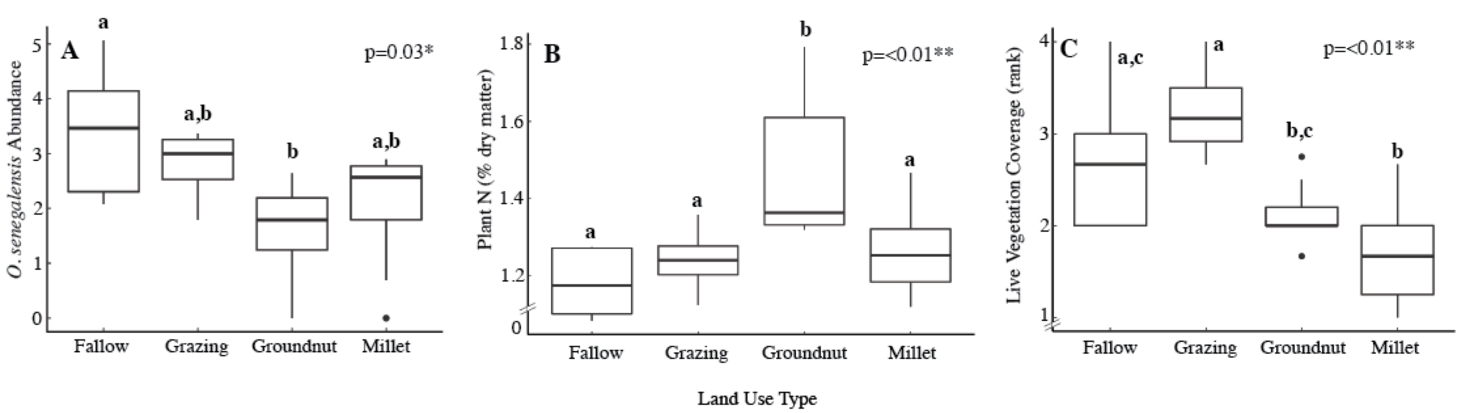

Fig. 2 Plant, vegetation cover, and grasshopper differences across land use types. *O. senegalensis* abundance across land use types (A). Plant N content is an average N (%) of all plants regardless of functional type (B). Vegetation cover by rank score across land use types (C). Letters represent Tukey HSD significant differences. All figures are box plots showing mean and quartile ranges corresponding to the first (bottom whisker) and third quartiles (top) (the 25th and 75th percentiles).

Table 2: Vegetation coverage data across land use type; values indicate mean of the top three dominant plants regardless of plant family (SE).

Ground Cover	Fallow	Grazing	Groundnut	Millet	F Value	P Value
Veg Cover (rank score)	2.8 (1.0) (a,c)	3.3 (1.2) (a)	2.1 (0.8) (b,c)	1.7 (0.8) (b)	7.9	***<0.001
% Cover (density class)	11- 40% (Sparse)	40- 70% (Moderate)	11- 40% (Sparse)	3-10 % (Very Sparse)		
Manure (rank score)	1.5 (0.8) (a,c)	1.2 (0.6) (a)	0.5 (0.7) (b)	0.9 (0.5) (b,c)	7.4	*0.01
% Cover (density class)	3-10 % (Very Sparse)	3-10 % (Very Sparse)	0-1 % (Rare)	0-1 % (Rare)		
Litter (rank score)	1.1 (0.5)	1.1 (0.7)	1.2 (0.4)	1.0 (0.3)	0.5	0.7
% Cover (density class)	3-10 % (Very Sparse)	3-10 % (Very Sparse)	3-10 % (Very Sparse)	3-10 % (Very Sparse)		
Rock (rank score)	0.0 (0.3)	0.6 (1.3)	0.3 (0.9)	0.5 (1.0)	0.8	0.5
% Cover (density class)	0% (None)	0-1 % (Rare)	0-1 % (Rare)	0-1 % (Rare)		

Eleven species of grasshoppers were found across all land use types (Table 7). As expected, *O. senegalensis* was the most abundant species, ranging from 8 - 158 in fallow fields fields, 6 - 29 in grazing areas, 1- 14 in groundnut fields, and 1 - 18 in millet. The diversity in the grasshopper community was similar to expected for this region (Gupta, 1983). *O. senegalensis* was the only locust species present. The other grasshopper species are not known to migrate or cause economic damage to crops. Across the grasshopper community, only the abundance of two species varied significantly with land use type (Table 7). *O. senegalensis* was significantly less abundant in groundnut fields compared to fallow and millet fields, and grazed areas (Fig. 2A). Interestingly, there was no difference in live vegetation cover (%) between fallow and groundnut areas (Fig. 2C) suggesting *O. senegalensis* is not avoiding groundnut fields because of lower levels of vegetation.

Table 3. Results of mixed model regression between total inorganic N and soil variables.

Factors	DF	F value	P value
(Intercept)	19	26.0	<0.001
SOM (%)	**19**	**8.1**	***0.01**
BD (g/cm^3)	19	1.1	0.3
EC (mS/cm)	**19**	**11.6**	**<0.01**
pH	19	2.1	0.2
Dung Cover (%)	19	0.2	0.7
Rock Cover (%)	19	3.2	0.1

3.2 Drivers of inorganic soil N and plant N content

SOM and EC were the only significant main effects on total inorganic soil N pools (Table 3). Out of the farmer management practices we surveyed (residue removal,

Table 4. Results of mixed model regression between total inorganic N and farmer management factors.

Factors	DF	F value	P value
(Intercept)	9	20.9	0.0
Residue Removed	9	0.5	0.5
Fertilizer Use	9	0.6	0.5
Years Spent Groundnut	9	0.2	0.6
Years Spent Fallow	**9**	**6.8**	***0.03**
Years Spent Millet	9	1.7	0.2
Years Spent Beans	9	1.2	0.3

fertilizer use, land use history, alternative crops), only years fallow was significantly related to soil inorganic N content (Table 4). Total inorganic soil N had a significant effect on plant N content (non-nitrogen fixing plants) (Table 5).

3.4 Plant nutrients and grasshopper abundance

Plant N and live vegetation cover had significant effects on *O. senegalensis* abundance (Table 6). *O. senegalensis* abundance was negatively correlated with plant N content (Pearson's correlation test: t=-2.1, df=23, p=0.045, r=-0.4; Fig 3A) and positively correlated with plant C:N ratio (Pearson's correlation test: t=3.3, df =23, p=0.003, r=0.6; Fig 3B). Out of the ten other grasshopper species we surveyed, *Acrotylus* spp, was the only other one negatively correlated with plant N (Spearman's rank correlation: S= 157.2, p= 0.005, r=-0.9; Fig 3D) and positively with CN ratio (Spearman's rank correlation: S=12.9, p=<0.01, r=0.8; Fig 3E). The top two other species, *Acorypha spp* and *Acrida bicolor,* were not significantly correlated with plant N or C:N ratio when tested alone (Fig 3E&F).

Table 5. Results of mixed model regression between plant N content (non-N fixing species) soil N and ground cover factors.

Factors	DF	F-value	p-value
(Intercept)	171	6219.9	<.0001
Total Inorganic Soil N	**171**	**3.8**	***0.05**
Dung Cover	171	0.1	0.7
Litter Cover	171	0.3	0.5763

Table 6. Results of mixed model regression between O. senegalensis abundance and environmental factors.

Factors	DF	F value	P value
(Intercept)	16	193.1	<.0001
Plant N Content	**16**	**6.9**	***0.02**
Total Inorganic Soil N	16	0.9	0.4
Live Vegetation Cover	**16**	**17.6**	**<0.001**
Rock Cover	16	1.6	0.226
Dung Cover	16	0.2	0.6322
Litter Cover	16	0.2	0.6323
Years Spent Fallow	16	1.5	0.233

Fig. 3

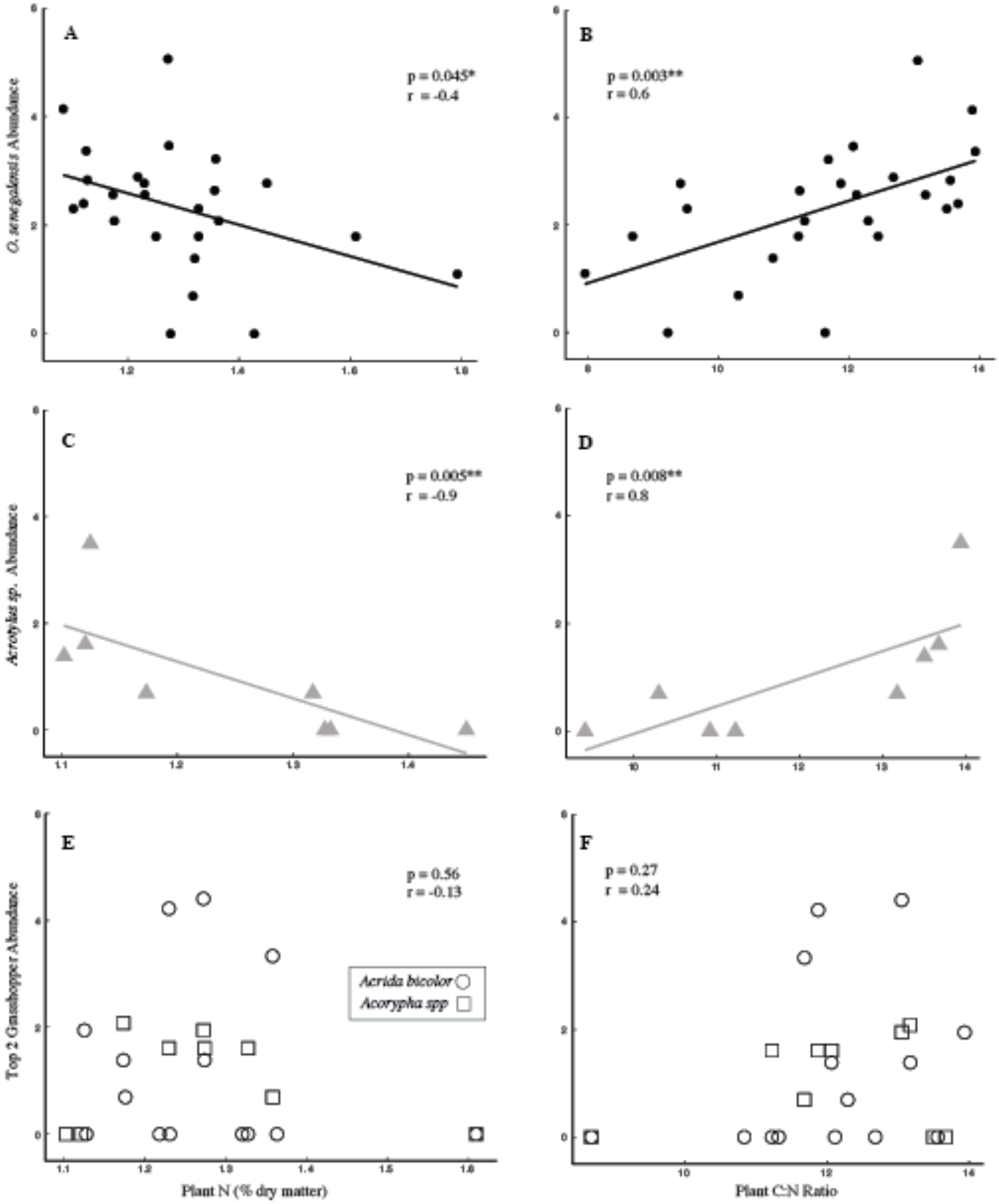

Fig. 3 Relationships between grasshopper abundance and plant nutrient content. *O. senegalensis* abundance and plant N and C:N (panels A and B) and the top three most abundant grasshopper species (excluding *O. senegalensis*) and plant N and C:N (panels C and D). In panel C and D, the significant line is for *Acrotylus spp,* the only other grasshopper with a significant correlation with plant nutrients.

Table 7. Grasshopper abundance, diversity and plant nutrients across land use type. Letters indicate post hoc significant differences from Nemenyi's test following Kruskal-Wallis rank sum test for all species besides *O. senegalensis* where we used an ANOVA followed by Tukey HSD.

Grasshopper Spp. Abundance	Fallow	Grazing	Groundnut	Millet	P Value
Acorypha spp	4.3 (3.1)	3.5 (2.1)	1	4.7 (3.5)	0.7
Acrida bicolor	29.3 (45.6) (a,b)	34.3 (31.0) (a)	1 (b)	1.6 (1.3) (a,b)	*0.02
Acrotylus spp	4	33	1	2.2 (1.6)	0.3
Catantops stramineus	0	1	0	0	
Chrotogonus senegalensis	2.3 (2.3)	1	1.7 (.8)	1.25 (0.5)	0.7
Cryptocatantops haemorrhoidalis	0	0	1	0	-
Diabolocatantops axillaris	0	0	1	0	-
Oedaleus senegalensis	54.2 (62.1) (a)	19.0 (10.2) (a,b)	6.6 (4.5) (b)	10.7 (6.3) (a,b)	*0.03
Ornithacris cavroisi	0	1	0	1	-
Pyrgomorpha cognata	0	0	0	1	-
Unknown nymph	4.5 (3.5)	2	1.5 (0.7)	1.0 (0.0)	-
Grasshopper Diversity					
Shannon's Diversity H	0.8 (0.3)	0.9 (0.1)	0.6 (0.3)	0.8 (0.5)	0.4
Mean Abundance	78.4 (96.6)	56.3 (34.6)	8.1 (4.5)	16.1 (7.3)	0.2
Plant Nutrients					
%N	3.3 (0.8) (a)	3.5 (0.9) (a)	4.2 (1.2) (b)	3.5 (0.7) (a)	**0.004
%C	40.2 (4.2)	40.8 (3.9)	40.1 (4.1)	40.3 (3.4)	1.0
C:N Ratio	12.9 (3.2) (a)	12.5 (3.3) (a)	10.0 (2.2) (b)	12.0 (2.8) (a)	**0.002

4. Discussion

An optimal nutrient landscape for locusts is determined by aboveground-belowground feedbacks. Grasshoppers, especially *O. senegalensis*, were influenced by soil-plant interactions and therefore indirectly by land use. Their avoidance of groundnut areas where plant N was highest, and their negative correlation with plant N, supports the unusual finding that *Oedaleus* species prefer low N diets (Cease et al. 2012). While their abundance was significantly impacted by the amount of live vegetation cover, the areas with variation in plant N content did not differ in their vegetation coverage (Fig. 2). Suggesting plant nutrient content is more important than density of plants. Farmers directly influence groundcover and plant N by deciding how land is used. Their management practices indirectly impact soil N through SOM, thus offering a new tool for locust management from the bottom up.

On a landscape level, soil characteristics are relatively homogenous with the exception of texture and SOM. The common crop rotation between groundnut and millet is potentially keeping consistent, albeit low, levels of soil inorganic N from year to year. Our results show fields with averages between 8.0- 12.4 kg/ha of total N. This is well below the recommended nitrogen application for Pearl Millet of 60 kg per hectare (Bagayoko et al., 2011; Singh and Thakare, 1986). There are serious constraints that restrict nutrient additions and soil conservation practices in this subsistence farming system. Sub-Saharan Africa uses the lowest rate of fertilizer in the world at about 8 kg nutrients per hectare (Bationo et al. 1998). The expense of fertilizer, lack of quality seeds, labor constraints, and alternative uses for crop residue, makes restorative practices like mulching, cover cropping, or intercropping rarely feasible (interviews, 2016). For example, there are many alternative uses for crop residue that take priority over soil fertility management. Our interviews found a strong management paradigm that the land should be "clean" (cleared or burned) before the next planting season. Farmers noted that clearing millet stalks and shrubs makes it easier for plowing the following season and some residue may harbor other pests or snakes (interviews, 2017). As such, the land is typically left bare November-May with leftover residue used for animal feed, building material, or fuel, which leads to little organic matter build up over time (interviews, 2017). In rare cases, residue is left on the field until the next rainy season. Soil amendments from mulches, compost, and crop residue, cover and polycropping, and no-till, are all common soil regenerative practices in conservation agriculture (CA). The constraints on CA and low synthetic fertilizer input, make the soil vulnerable to nutrient loss via biomass removal, wind erosion, and non-stable aggregates due to continuous plowing.

Farmers mainly use manure to fertilize their crops and, when budgets allow, will apply synthetic fertilizer via micro-doses (interviews, 2017; Hayashi et al. 2008). In addition to manure application, many farmers fallow land "when the soil gets tired" and to "let the soil rest" when yields decline (interviews, 2017). The cycle of continuous cultivation that lowers soil N can drive farmers to rotate fields out of cultivation, leaving native plants to colonize in place of higher N crops like groundnut. This cycle was affirmed in our interviews with farmers. For example, one farmer told us, "bad soil means plants will be weak" and "if you don't get what you want from the harvest, the power has decreased on the land, and I leave it [fallow]".

The strategy of fallowing thus produces a tradeoff. Our study showed that the longer the land is fallow, the higher the levels of SOM and total inorganic N (Table 4). SOM plays a vital role in soil functioning and therefore is considered a key indicator of soil health (Reeves 1997) and our results corroborate the well-established link between SOM and soil N (Table 3). Fallowing may significantly increase soil N over time but the time scale necessary to improve soils through this method may be too long to sustainably replenish nutrients reserves for plants or increase their tissue N before farmers need to cultivate the field due to land constraints. Another limitation on regeneration through fallow is insecure land tenure and village specific rules that dictate cultivation requirements. In some cases land can be turned over to a new owner after three years continuous cultivation, or if land isn't cultivated for several years (1-5, depending on location and village chief), farmers can lose rights to the land (interviews, 2016).

Plant nitrogen content and C:N ratios varied significantly across the land use types. The plants in groundnut fields had higher leaf N content (and lower C:N ratio) than plants in other areas (Fig. 2B). We predicted that soils with higher levels of inorganic N would support plants with higher N content. Indeed, non-nitrogen fixing plant N content was significantly influenced by total soil inorganic N (Table 5).

O. senegalensis were most abundant in land use types where plant N was the lowest (Fig. 2A). They were more abundant in non-groundnut cultivated areas, potentially indicating that these other areas provide a more optimal nutritional landscape. Our data suggest that *O. senegalensis* is more impacted by plant N than the other grasshopper species (Fig. 3). Future studies may more deeply address the other factors that are potentially causing locust to avoid groundnut fields, like secondary alkaloids or predators. With the exception of *Acrotylus sp.*, the abundances of other grasshopper species were not correlated with plant N, though a larger sample sizes is needed to strengthen this conclusion. *Acrotylus sp.* was the only other species that may also show a nutritional preference for plants with high carbon ratios. This genus contains about 20 species present throughout Africa, S. Europe, and S.W. Asia. They are of less economic importance compared to *O. senegalensis* and have been noted to cause crop damage in minor significance in conjunction with a complex of other species (Gupta, 1983). There was no difference in species diversity across the different land use types, with *O. senegalensis* being the most abundant species overall (Table 7).

Conclusion

Areas containing low-N plants supported higher locust population densities and thus, capacity for crop damage. The plants, especially non-N fixing species, are impacted by low soil N, which can be tied back to farmer management decisions. For farmers in West Africa, the sustainability challenge is to meet food security needs with limited options for increasing soil fertility and controlling pests (Abate et al., 2000; Giller et al., 2009). As demonstrated in our interviews, farmers have extensive knowledge of how to produce food under the pressures of low input and rain-fed conditions. However, with a changing climate and locust second only to drought, as the most common and expensive agricultural risk, sustaining the status quo leaves many vulnerable (D'alessandro et al., 2015).

Organic matter inputs are one of the most promising amendments to build up soil nutrient pools (Puttaso et al., 2011). However, the slow accumulation of manure from grazing livestock and integration of native plant biomass in fallow areas may not be enough to regenerate soil nutrients in the short time frame they are left fallow. More active conservation practices mixed with synthetic and organic fertilizers may be of greater benefit than passive fallow rotations, especially if fallow areas are harboring locusts. Other studies have suggested adaptations to traditional and conservation agriculture techniques as ways to improve soil quality without increasing synthetic fertilizer use. For example integrating Zai pits (Slingerland and Stork, 2000), composting (Mcclintock and Diop, 2005) and diversified crop rotations as viable options for replenishing soil nutrients (Altieri et al., 2015; Twomlow et al., 2008). While there are criticisms of conservation agriculture approaches in Africa (Giller et al., 2009) where adoption has been low (Twomlow et al., 2008), this research may encourage new perspectives because of the connection to the prevalence of agricultural pests.

We call for more work to understand the additional positive benefits of pest management by way of the soil. There are opportunities to alter management techniques like passive fallowing, clearing and burning residue during land preparation, which could lead to higher retention of nutrients in the system. However, a deeper understanding of how and why farmers make decisions and integrate new practices in smaller holder systems is key. The complexities of CHANS like this one, illustrate the interconnectivity of not just ecological processes but the important social human dimension in facing sustainability challenges.

References cited

Abate, T., van Huis, A., Ampofo, J.K.O., 2000. Pest Management Strategies in Traditional Agriculture: An African Perspective. Annu. Rev. Entomol. 45, 631–659. https://doi.org/10.1146/annurev.ento.45.1.631

Agbenin, J.O., Goladi, J.T., 1997. Carbon, nitrogen and phosphorus dynamics under continuous cultivation as influenced by farmyard manure and inorganic fertilizers in the savanna of northern Nigeria. Agric. Ecosyst. Environ. 63, 17–24. https://doi.org/10.1016/S0167-8809(96)01123-1

Altieri, M.A., Nicholls, C.I., Henao, A., Lana, M.A., Altieri, M.A., Nicholls, C.I., Henao, A., Lana, M.A., 2015. Agroecology and the design of climate change-resilient farming systems. Agron. Sustain. Dev 35, 869–890. https://doi.org/10.1007/s13593-015-0285-2

Andrews, D.J., Kumar, K.A., 1992. Pearl Millet for Food, Feed, and Forage. Adv. Agron. 48, 89–139. https://doi.org/10.1016/S0065-2113(08)60936-0

Bagayoko, M., Maman, N., Palé, S., Sirifi, S., Taonda, S.J.B., Traore, S., Mason, S.C., 2011. Microdose and N and P fertilizer application rates for pearl millet in West Africa. African J. Agric. Res. 6, 1141–1150. https://doi.org/10.5897/AJAR10.711

Bationo, A., Lompo, F., Koala, S., 1998. Research on nutrient flows and balances in west Africa: state-of-the-art. Agric. Ecosyst. Environ. 71, 19–35.

Behmer, S.T., 2009. Insect Herbivore Nutrient Regulation. Annu. Rev. Entomol. 54, 165–187. https://doi.org/10.1146/annurev.ento.54.110807.090537

Cease, A.J., Elser, J.J., Fenichel, E.P., Hadrich, J.C., Harrison, J.F., Robinson, B.E., 2015. Living With Locusts: Connecting Soil Nitrogen, Locust Outbreaks, Livelihoods, and Livestock Markets. @BULLET Biosci. 65. https://doi.org/10.1093/biosci/biv048

Cease, A.J., Elser, J.J., Ford, C.F., Hao, S., Kang, L., Harrison, J.F., 2012. Heavy Livestock Grazing Promotes Locust Outbreaks by Lowering Plant Nitrogen Content. Science (80-.). 335, 467–469.

Cease, A.J., Harrison, J.F., Hao, S., Niren, D.C., Zhang, G., Kang, L., Elser, J.J., 2017. Nutritional imbalance suppresses migratory phenotypes of the Mongolian locust (Oedaleus asiaticus). R. Soc. Open Sci. 4. https://doi.org/10.1098/rsos.161039

Cheke, R.A., 1990. A Migrant Pest in the Sahel: The Senegalese Grasshopper Oedaleus senegalensis. R. Soc. 328, 539–553.

Christophersen, K.A., Rands, B., Hadj, A., Winterbottom, B., 1998. USAID/Senegal natural resources management “limited scope” impact assessment report. USAID/Senegal.

Chuku, C.A., Okoye, C., 2009. Increasing resilience and reducing vulnerability in sub-Saharan African agriculture: Strategies for risk coping and management. African J. Agric. Res. Spec. Rev. 4, 1524–1535.

D ’alessandro, S., Fall, A.A., Grey, G., Simpkin, S., Wane, A., n.d. SENEGAL AGRICULTURAL SECTOR RISK ASSESSMENT.

Doane, T.A., Horwáth, W.R., 2003. Spectrophotometric Determination of Nitrate with a Single Reagent. Anal. Lett. 36, 2713–2722. https://doi.org/10.1081/AL-120024647

Doran, J.W., Elliott, E.T., Paustian, K., n.d. Soil microbial activity, nitrogen cycling, and long-term changes in organic carbon pools as related to fallow tillage management.

Doran, J.W., Zeiss, M.R., 2000. Soil health and sustainibility: managing the biotic component of soil quality. Appl. Soil Ecol. 15, 3–11. https://doi.org/10.1016/S0929-Get

Giller, K.E., Witter, E., Corbeels, M., Tittonell, P., 2009. Conservation agriculture and smallholder farming in Africa: The heretics’ view. F. Crop. Res. 114, 23–34. https://doi.org/10.1016/j.fcr.2009.06.017

Goudou, D., Gué/Traoré, J., Ouédraogo, M., Segda, Z., Badiane Ndour, N.Y., Sall, M., Gueye, F., Sissoko, K., Zougmoré, R., Moussa, A.S., 2012. Village Baseline Study: Site Analysis Report for Kaffrine – Kaffrine, Senegal (SE0112). CGIAR Res. Progr. Clim. Chang. Agric. Food Secur.

Gupta, V.K., 1983. The Locust and Grasshopper Agricultural Manual 1982. Orient. Insects 17, 78–126. https://doi.org/10.1080/00305316.1983.10433700

Hall, S.J., 2014. The Soil Underfoot: Soils and the Future of Food Challenges and Opportunities for Feeding Nine Billion People. Taylor & Francis Group.

Hayashi, K., Abdoulaye, T., Gerard, B., Bationo, A., 2008. Evaluation of application timing in fertilizer micro-dosing technology on millet production in Niger, West Africa. Nutr. Cycl. Agroecosystems 80, 257–265. https://doi.org/10.1007/s10705-007-9141-3

Kitchell, E., Turner, M.D., McPeak, J.G., 2014. Mapping of pastoral corridors: practices and politics in eastern Senegal. Pastoralism 4, 1–14. https://doi.org/10.1186/s13570-014-0017-2

Liu, J., Dietz, T., Carpenter, S.R., Alberti, M., Folke, C., Moran, E., Pell, A.N., Deadman, P., Kratz, T., Lubchenco, J., Ostrom, E., Ouyang, Z., Provencher, W., Redman, C.L., Schneider, S.H., Taylor, W.W., 2007. Complexity of Coupled Human and Natural Systems. Science (80-.). 317, 1513–1516. https://doi.org/10.1126/science.1144004

Liu, J., Hull, V., Batistella, M., DeFries, R., Dietz, T., Fu, F., Hertel, T.W., Izaurralde, R.C., Lambin, E.F., Li, S., Martinelli, L.A., McConnell, W.J., Moran, E.F., Naylor, R., Ouyang, Z., Polenske, K.R., Reenberg, A., de Miranda Rocha, G., Simmons, C.S., Verburg, P.H., Vitousek, P.M., Zhang, F., Zhu, C., 2013. Framing Sustainability in a Telecoupled World. Ecol. Soc. 18, 26. https://doi.org/10.5751/ES-05873-180226

Liu, J., Wu, N., Wang, H., Sun, J., Peng, B., Jiang, P., Bai, E., 2016. Nitrogen addition affects chemical compositions of plant tissues, litter and soil organic matter. Ecology 97, 1796–1806. https://doi.org/10.14315/evth-2014-0505

Maiga, I.H., Lecoq, M., Kooyman, C., 2008. Ecology and management of the Senegalese grasshopper Oedaleus senegalensis (Krauss 1877) (Orthoptera: Acrididae) in West Africa: review and prospects. Ann. la Société Entomol. Fr. 44, 271–288. https://doi.org/10.1080/00379271.2008.10697563

Mattson, W.J., 1980. Herbivory in Relation to Plant Nitrogen Content HERBIVORY IN RELATION +41 74 TO PLANT NITROGEN CONTENT'. Source Annu. Rev. Ecol. Syst. 11, 119–161.

Mbow, C., Mertz, O., Diouf, A., Rasmussen, K., Reenberg, A., 2008. The history of environmental change and adaptation in eastern Saloum–Senegal—Driving forces and perceptions. Glob. Planet. Change 64, 210–221. https://doi.org/10.1016/j.gloplacha.2008.09.008

Mcclintock, N.C., Diop, A.M., n.d. Soil Fertility Management and Compost Use in Senegal's Peanut Basin.

Mclauchlan, K., 2006. The Nature and Longevity of Agricultural Impacts on Soil Carbon and Nutrients: A Review. Ecosystems 9, 1364–1382. https://doi.org/10.1007/s10021-005-0135-1

Ode, P.J., 2006. PLANT CHEMISTRY AND NATURAL ENEMY FITNESS: Effects on Herbivore and Natural Enemy Interactions. Annu. Rev. Entomol. 51, 163–185.

https://doi.org/10.1146/annurev.ento.51.110104.151110

Puttaso, A., Vityakon, P., Saenjan, P., Trelo-ges, V., Cadisch, G., 2011. Relationship between residue quality, decomposition patterns, and soil organic matter accumulation in a tropical sandy soil after 13 years. Nutr. Cycl. Agroecosystems 89, 159–174. https://doi.org/10.1007/s10705-010-9385-1

Reeves, D.W., 1997. The role of soil organic matter in maintaining soil quality in continuous cropping systems. soil& Tillage Res. Soil Tillage Res. Reeues/Soil Tillage Res. 43, 131–167.

Sijmons K, Kiplimo J, Förch W, Thornton P K, Zougmoré, A.S., 2013. CCAFS Site Atlas – Kaffrine. CCAFS site atlas series. The.

Singh, A.L., 1999. Mineral Nutrition of Groundnut. Adv. Plant Physiol. 2, 161–200.

Singh and Thakare, 1986. Yield response and nitrogen uptake of pearl millet (Pennisetum americanum (L.) Leeke) cultivars to nitrogen application in the savanna region of Nigeria. Fertil. Res. 10, 113–118.

Slingerland, M.A., Stork, V.E., 2000. Determinants of the Practice of Zaï and Mulching in North Burkina Faso. J. Sustain. Agric. 16, 53–77.

Touré, A., Temgoua, E., Guenat, C., Elberling, B., 2013. Land Use and Soil Texture Effects on Organic Carbon Change in Dryland Soils, Senegal. Open J. Soil Sci. 3, 253–262. https://doi.org/10.4236/ojss.2013.36030

Toure, M., Ndiaye, M., Dongue, A., 2013. Effect of cultural techniques: Rotation and fallow on the distribution of Oedaleus senegalensis (Krauss, 1877)(Orthoptera: Acrididae) in Senegal. African J. Agric. Res. 8, 5634–5638. https://doi.org/10.5897/AJAR11.2353

Tschakert, P., Khouma, M., 2004. Biophysical potential for soil carbon sequestration in agricultural systems of the Old Peanut Basin of Senegal. J. Arid Environ. 59, 511–533. https://doi.org/10.1016/j.jaridenv.2004.03.026

Twomlow, S., Hove, L., Mupangwa, W., Masikati, P., Mashingaidze, N., 2008. Precision conservation agriculture for vulnerable farmers in low-potential zones.

Vadez, V., Hash, T., Bidinger, F.R., Kholova, J., 2012. Phenotyping pearl millet for adaptation to drought. Front. Physiol. 3, 1–12. https://doi.org/10.3389/fphys.2012.00386

Van Der Heijden, M.G.A., Bardgett, R.D., Van Straalen, N.M., 2008. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol. Lett. 11, 296–310. https://doi.org/10.1111/j.1461-0248.2007.01139.x

Wani, S.P., Rupela, D.P., Lee, K.K., 1995. Sustainable agriculture in the semi-arid tropics through biological nitrogen fixation in grain legumes. Plant Soil 174, 29–49.

Weatherburn, M.W., 1967. Phenol-hypochlorite reaction for determination of ammonia. Anal. Chem. 39, 971–974. https://doi.org/10.1021/ac60252a045

Welbaum, G.E., Sturz, A. V., Zhongmin, D., Nowak, J., 2004. Managing Soil Microorganisms to Improve Productivity of Agro-Ecosystems. CRC. Crit. Rev. Plant Sci. 23, 175–193.

White, T.C.R., 1993. The Inadequate Environment : Nitrogen and the Abundance of Animals. Springer-Verlag Berlin.