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Soil-targeted interventions could alleviate locust and grasshopper pest pressure in West Africa

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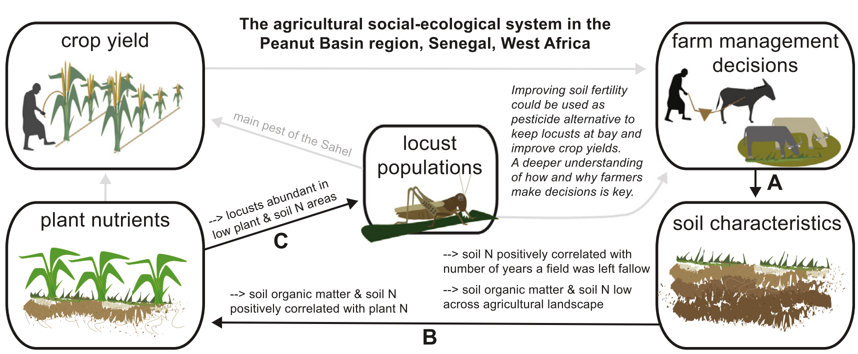
HIGHLIGHTS

- Locusts and grasshoppers cause devastating impacts on food security globally.
- Understanding human-environment feedbacks opens novel management opportunities.
- We explored connections among land use, soil, plant nutrients, and locusts.
- Counterintuitively, locusts were most abundant in areas with low-nitrogen plants.
- Land use that promotes soil organic matter and nitrogen may suppress outbreaks.

GRAPHICAL ABSTRACT



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ABSTRACT

Agricultural land use has intended and unintended consequences for human livelihoods through feedbacks within coupled human and natural systems. In Senegal, West Africa, soils are a vital resource for livelihoods and food security in smallholder farming communities. In this study, we explored the connections among land use, soil conditions, plant nutrient content, and the abundance of several locust and grasshopper species. We worked in two rural farming villages in the Kaffrine region of Senegal. *Oedaleus senegalensis* was least abundant in groundnut areas where plant N was highest and abundance was negatively correlated with plant N across land use types. Overall, grasshoppers were most numerous in grazing and fallow areas. There was little variation in soil properties across land use types and soil organic matter (SOM) and inorganic soil N content were low throughout. SOM was positively correlated with soil inorganic N concentration, which in turn was positively correlated with plant N content. Of the management practices we surveyed, fallowing fields was important for soil N and SOM replenishment. These results corroborate other research indicating that land use, management practices, soil and plant nutrients, and insect herbivore abundance are mechanistically coupled. Although further research is needed, improving soil fertility could be used as an alternative to pesticides to keep locusts at bay and improve crop yields.

1. Introduction

Social and ecological systems have been intimately coupled through agriculture for thousands of years. In particular, land use has both

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intended and unintended impacts on human livelihoods through feedbacks within the social-ecological system (SES) (Ostrom, 2007); also referred to as coupled human and natural system (CHANS) (Liu et al., 2007, 2013). Understanding these complexities, particularly through dialogue with farmers, can open opportunities for novel pest management approaches (Altieri, 2004). Agricultural practices alter the physical and chemical composition of soil which affects plant characteristics, including their nutrient contents (Wani et al., 1995; Welbaum et al., 2004; McLauchlan, 2006; Liu et al., 2016). In turn, vegetation productivity, nutrient contents, and diversity influence the growth, reproduction, and behavior of insect herbivores, leading to changes in population size and migratory capacity (White, 1993; Mattson Jr., 1980; Ode, 2006; Van Der Heijden et al., 2008; Behmer, 2009; Cease et al., 2017).

Pest management using a whole systems approach recognizes that insect population dynamics are a function of linked ecological processes in the natural plant-soil system, and thus should be managed using ecosystem-based strategies rather than relying exclusively on external "therapeutic" tactics (e.g. pesticides) (Lewis et al., 1997). Numerous studies have shown that land use practices (e.g. improvements in soil fertility through organic matter management and increasing the length of fallow) can reduce crop pest infestations and outbreaks (Litsinger, 1989; Altieri and Nicholls, 2003; Saito et al., 2006; Wyckhuys and O'Neil, 2007; Wyckhuys et al., 2017). Additionally, research on insect herbivores suggests a strong link between soil fertility and the success of biocontrol efforts (Hovick and Carson, 2015). Such habitat management can create favorable ecosystem-level conditions that control insect herbivores, in part, through trophic cascades that enhance natural enemy abundance or activity (Power, 1992; Liman et al., 2017). However, while many studies have explored the links between land use, soil conditions, plant nutrients, and pest population dynamics, few have considered these approaches for transboundary migratory pests. Due to the complexity of managing transboundary migratory pests, such as locusts and migratory grasshoppers, that can cover vast areas and remain a challenge to predict, most strategies are implemented at national and international scales. These approaches can preclude involvement of the stakeholder most affected, farmers (Lockwood et al., 2001). Here, we explore these links (Fig. 1) within subsistence farming communities in Senegal, West Africa where there are severe outbreaks of the Senegalese grasshopper (*Oedaleus senegalensis* Krauss 1877; Acrididae), a non-model locust (Song, 2011).

Cheke (1990) described *Oedaleus senegalensis* as the main pest of the Sahel. In a span of seven years (1986 to 1992) grasshopper control costs in the Sahel, predominantly for *O. senegalensis*, totaled US$177 million (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. In addition to their unique phenotypic plasticity, there is growing evidence that *Oedaleus* grasshoppers prefer and have the fastest growth rates when consuming plants with low N content (*O. asiaticus*: Cease et al., 2012, 2015, 2017; *O. senegalensis*: 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 N is often depleted by continuous crop cultivation through the removal of soil organic matter (SOM), compaction, and erosion (Agbenin and Goladi, 1997; Doran and Zeiss, 2000; Hall, 2014). In Senegal, soils are especially vulnerable to N loss due to their low SOM and clay content, and 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 et al., 1998; Christophersen et al., 1998; Tschakert and Khouma, 2004; Goudou et al., 2012; Touré et al., 2013b). 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. In these ways, agricultural practices can impact soil nutrients that are available to plants and potentially their nutrient content and susceptibility to herbivory (Ode, 2006; Liu et al., 2016).

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 et al., 2013). The two most common crops are grown in a yearly 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 N fixing legumes 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 (Boys, 1978; Coop et al., 1991; Maiga et al., 2008; Touré et al., 2013a; Bal et al., 2015), potentially due to their preference for lower N leaf tissue (e.g., Cease et al., 2012).

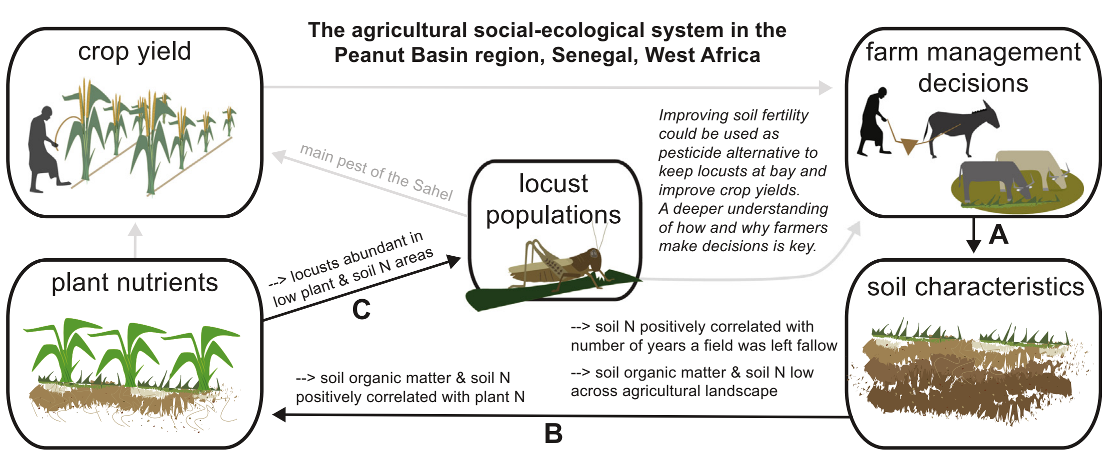

Fig. 1. This figure presents our conceptual framework for the agricultural social-ecological system. Starting on the upper right, farmers make decisions about land management over time which includes past crops types, livestock stocking rates, timing of planting and nutrient applications, etc. These impact soil characteristics (A). Soil characteristics, including nutrient content and organic matter, impact the nutrients available in crops (B). The current crop cover provides a food source for locusts, which have specific dietary preferences (C), and thus can ultimately impact crop yields. These impacts can then feed back into and update farm management decisions into the future. Black arrows (A, B, and C) are connections we tested in this study; grey arrows are connections we did not explicitly test. Black text along arrows indicates significant findings; italicized text indicates our overall conclusion.

The plant diversity available to *O. senegalensis* and other grasshoppers in this region is arranged as a heterogeneous landscape of discrete land use types: agricultural cropland, fallow fields, and grazing areas dominated by grasses and woody-shrubs. *Oedaleus senegalensis* can be found across different land use types, but is most abundant in fallow and millet fields (Touré et al., 2013a). Anecdotally from Senegalese farmer accounts, *O. senegalensis* may persist in high numbers in common-pool livestock grazing areas and move into crop fields after crops have sprouted (Survey 2016), a pattern found in northern Nigeria (Amatobi et al., 1988). However, how *O. senegalensis* and other grasshoppers are distributed throughout various land use types in relation to plant nutrients has not been tested.

We used a mixed methods approach, combining biophysical data, farmer surveys, and farmer interviews, to explore the relationship among management practices, soil and plant properties, and grasshopper abundance across this agricultural landscape. This integrated, participatory approach aimed to identify the common agricultural practices in the region as well as the effects of those practices on grasshopper abundance and the fertility of the mixed crop-livestock agroecosystem. We tested the hypothesis that management practices that decrease soil fertility will promote *O. senegalensis* outbreaks by reducing 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.

2. Materials and methods

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 mm in the dry season (November–April) to an average of 737 mm during the rainy season (May–October). Dry season temperatures average ~ 27 °C compared to rainy season average of ~29 °C (D'Alessandro et al., 2015). The woody shrubland savanna landscape is topographically flat and marked by agriculture expansion that has replaced native dry 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 (FAO, 2001; Goudou et al., 2012).

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 grazing areas are part of centuries-old livestock transhumance corridors that play a vital role in mixed land use for sustaining livestock (Kitchell et al., 2014; Turner et al., 2016).

2.2. Field survey approach: soil, plants, grasshoppers, people

To participate in the study, farmers needed to farm a combination of millet, groundnut, fallow fields, and graze livestock (the dominant land use types across the landscape). Collectively, we also aimed for participants' fields to be spatially well-distributed throughout village farm areas. Given these criteria, randomly sampling participants was not practical. Therefore, with the help of village leaders and local contacts from the national plant protection agency, La Direction de la Protection des Végétaux (DPV), we selected 5–6 farmers from each village that best met these inclusion criteria in June of 2015.

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 because their plans had changed from 2015 when they were selected for the study. For example, some farmers had planned to leave fields fallow but later lent the land to relatives who needed fields to grow their crops. Crop and fallow fields ranged from 1.5 to 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. In each field or grazing area, we sampled soils and plants in three 5 m × 5 m plots randomly distributed across the field. We sweep netted for grasshoppers within 20 m of the 5 × 5 m plots. Precipitation data (in mm) were gathered from rain gauge logs kept by the chief offices in each village.

We selected this time period because it was within about two weeks of the first rains in the region—the time when crop sprouting coincides with hatching of the first generation of *O. senegalensis*. This species has three generations per year during the rainy season. The first-generation hatches from diapause eggs after the first rains; the first and second generations migrate north as adults following the Inter-Tropical Convergence Zone; the third generation migrates back south at the end of the rainy season (Launois, 1978 and Launois and Rainey, 1979; Lecoq, 1978; Popov, 1980; Launois and Launois-Luong, 1989; Maiga et al., 2008). The abundance and survival of first-generation nymphs, and their crop defoliation rates, are key factors affecting the level of crop loss locally in their southern range (e.g. Gossas and Gnibi, Senegal), as well as their northern range where they migrate (e.g. Richard Toll, Senegal) (Popov, 1988; Coop and Croft, 1993; Fisker et al., 2007; Bal et al., 2015).

2.3. Soil sampling and analysis.

All soils were collected between July 27 and August 5, 2016 (Fig. 2). In each 5 m × 5 m plot, we collected two separate soil cores (4 cm diameter) at depths 0–7 cm and 8–15 cm and homogenized cores by depth into two soil samples (one soil sample per depth per plot). We carefully collected a separate 0–5 cm depth sample to estimate bulk density of the surface soil, making sure to not lose any soil from the core. Soils were immediately placed in cooler with ice for 2–10 h prior to being

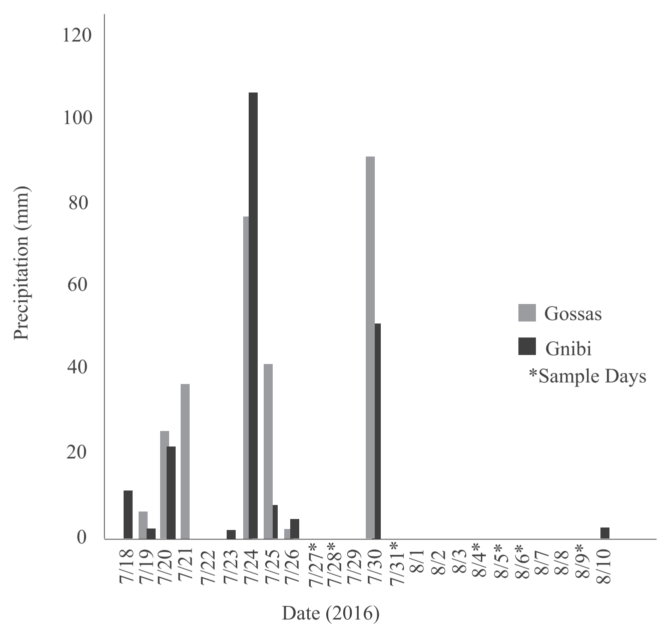

Fig. 2. July and August 2016 precipitation data (mm) for our study sites. Asterisk (*) indicates sample collection dates.

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–4 mm sized gravel. We then subdivided the samples into two plastic bags for later measurement of initial 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. These air-dried soil samples were used to estimate soil inorganic N pools and other soil properties. The other half of the samples were incubated in the dark at 29 ± 2 °C for 26 days at moisture levels between 10 and 20% weight addition of sample mass. These incubated soils were used to estimate rates of net potential N mineralization and nitrification.

All soil samples were brought to Arizona State University (ASU) laboratory facilities on 7 Aug and were stored at 24 °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), air-dried soil moisture (SM), soil organic matter (SOM), pH, and electrical conductivity (EC) using standard soil methods (SSSA, 2017).

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. Then we placed the solution 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 for sand (%) and 7 h for clay (%). We accounted for accuracy in sand readings by sieving the soil after 7 h with a 53-micron mesh sieve and determined sand weight by removing sand remaining in the sieve and drying it overnight at 105 °C. Organic matter content was low enough in these soils (0.71–1.30%) that we did not remove organic matter before textural analysis. We measured pH on a 10 g soil subsample diluted 1:2 with 20 mL DI using a pH meter (Mettler-Toledo). We measured EC on the same sample in a 1:3 water solution (Hatch Conductivity Probe model 17,250) to a precision of 1400–1600 μS/cm.

For N extractions, one 10 g subsample from the air-dried soil (initial inorganic N concentration) and the incubating soil from each plot (to calculate net N transformations) were shaken for 1 h in 50 mL 2 N KCl, set aside for 18–24 h, filtered through pre-leached Whatman #1 filters, and then frozen immediately for later analysis. Net potential N mineralization was calculated as the difference between the sum of NH_4^+ and NO_3^- concentrations on air-dried and incubated soil. Net potential nitrification was calculated as the difference of only NO_3^- between air-dried and incubated soil. Extractable NO_{3-}, and ammonium NH_4^+ concentrations 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 air-dried soil before and after baking samples for 5 h at 550 °C in a Thermolyne 6000 muffle furnace.

2.4. Plant sampling and analysis

In each 5 m × 5 m plot, we used the relevé method (MNDNR, 2013) to visually assess total cover of vegetation and the three most abundant plant species, categorized into ordinal cover classes (by %: 0 = 0 (none), 0.1–2 (rare), 2 = 3–10 (very sparse), 3 = 11–40 (sparse), 4 = 41–70 (moderate), 5 = 71–100 (dense)). We calibrated percent cover estimates between observers to reduce observer bias (Morrison, 2016). Additionally, we collected 3 to 5 g (wet mass) of leaves from several individuals of each of the dominant three species scattered throughout the plot for nutrient analysis. These species included the crop in production (millet or groundnut) in the actively farmed fields, as well as the grasses, sedges, forbs, or shrubs present as weeds and groundcover. We removed leaves from stems on site, kept them separate by species, and placed them in a cooler with ice after collection for <10 h before placing them in a drying oven at 60° ± 5 °C for 36–48 h. 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 s 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 were analyzed separately for each individual plant collected. We later averaged the nutrients (unweighted) of the leaves of the top three plants at the site level for some of the statistical analyses to estimate the average nutrients available to grasshoppers within a given 5 × 5 m plot. Grasshopper populations large enough to be economically important would, out of necessity, have to feed on the top three most abundant plants.

2.5. Locust sampling

We collected grasshoppers from 7/28/16 to 8/9/16, between 10 am–6 pm (when grasshoppers were active), with temperature averaging 34 °C ± 2 °C, relative humidity of 54% ± 7%, and wind speed of 2 ± 1 (m/s) (when sweep netting would not be impeded by wind). These dates were 1.5–2.5 weeks after the first rains when *O. senegalensis* were predominantly nymphs. While the nymphs in our study were not forming marching bands, nymphs can migrate locally among fields (Touré et al., 2013a). Therefore, this survey likely captured locusts in their preferred habitat type and not necessarily where they hatched (similar to Touré et al., 2013a). We estimated grasshopper abundance and diversity with sweep net surveys within 20 m of each plot where vegetation and soil samples were taken. We surveyed grasshoppers next to, as opposed to inside of, our plots in areas where team members had not recently walked to ensure grasshoppers were undisturbed. The same researcher conducted all surveys by evenly sweeping 20 times, each sweep a 180° arc approximately 1 m apart along a straight transect. These methods are similar to Cease et al. (2012).

2.6. Farmer surveys

To explore the potential relationship between farmer management practices, soil properties, and plant N content, we conducted verbal surveys with farmers and village leaders. In 2016, we first spoke with village leaders to learn general property rights regimes for the villages and history of the grazing areas. We then verbally surveyed 9 farmers, in total, at the time we collected biophysical data from their fields. We asked 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 is fluent in Wolof, the most common language spoken in Senegal.

From the 2016 survey results, we calculated 'years fallow' as the number of years a particular field has spent out of crop production during the farmers' memory. Thus, years that a field was fallow were not necessarily continuous. Fertilizer use was defined as whether the farmer uses synthetic or organic manure in his management practice in general, not on the day of our survey. If farmers cleared crop residue from their field we characterized as 'residue removal' and 'burning' was indicated by residue burned in place on the field of origin. 'Land use history' captured the length of crop rotations, e.g. what was grown on that particular piece of land, and for how many years. 'Alternative crops' included any other crops besides millet and groundnut grown in that field outside of the rainy season. Results from these 2016 surveys are cited as (Survey 2016).

We conducted an additional 12 interviews in 2017 to gain further insight into the social system that could influence agricultural

Table 1
Soil characteristics across land use types. Values indicate mean (SD) of 9 farmer fields. Letters show post hoc significant differences between land use types from Tukey HSD comparisons following ANOVAs. Farmer was used as random variable. Bolded values indicate P < 0.05 here and throughout all tables.

Variable	Fallow	Grazing	Groundnut	Millet	DF	F value	P value
Sand (%)	83.1 (2.8) (a)	80.2 (5.1) (a)	(86.9) (1.8) (b)	87.8 (23.0) (b)	3	8.3	<**0.001**
Silt (%)	12.9 (1.2) (a,c)	13.1 (2.6) (b,c)	10.3 (1.8) (b)	9.6 (2.8) (b)	3	5.7	**0.005**
Clay (%)	4.0 (2.1) (a,c)	6.7 (3.6) (c)	2.9 (1.2) (a,b)	2.6 (0.6) (b)	3	4.4	**0.01**
BD (g/cm^3)	1.7 (0.1)	1.7 (0.1)	1.6 (0.1)	1.7 (0.1)	3	1.4	0.3
SOM (%)	0.9 (0.3) (a,b)	1.3 (0.5) (a)	0.8 (0.1) (b)	0.7 (0.1) (b)	3	5.8	**0.004**
pH	5.6 (0.5)	5.9 (0.41)	5.6 (0.4)	5.6 (0.2)	3	1.1	0.4
EC (mS/cm)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)	0.02 (0.02)	3	2.1	0.9
Total N (mg/kg)	8.0 (2.7)	12.4 (4.6)	9.9 (5.1)	10.3 (4.3)	3	0.6	0.6
NO_3^- (mg/kg)	4.5 2.0)	6.5 (2.7)	5.7 (3.9)	6.0 (3.3)	3	0.2	0.8
NH_4^+ (mg/kg)	2.4 (0.5)	3.8 (1.7)	3.2 (2.0)	2.8 (1.4)	3	0.7	0.6
Net mineralization (mg/kg)	5.2 (5.0)	1.1 (3.1)	6.1 (4.4)	8.0 (4.2)	3	2.9	0.06
Net nitrification (mg/kg)	6.4 (4.6)	3.0 (3.7)	7.8 (5.5)	8.0 (3.7)	3	2.0	0.1

management practices. These interviews differed from the quantitative 2016 surveys in that they were semi-structured with open-ended questions about soil and land management, use of fallow, locust control strategies as well as concepts of sustainability. 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. Insights from these 2017 open-ended interviews are cited as (Interviews 2017).

2.7. 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 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 plant samples and ground cover (3 plots per field) were averaged across each field before statistical analyses.

To test the importance of land use type on field-level soil, plant, and grasshopper parameters, we used multiple one-way 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. Grasshopper abundance data was transformed using $z = \log(y + 1)$ because there were some zeros in the datasets (Warton, 2005). Kruskal-Wallis was used to test the relationship between the abundance of the all grasshopper species besides *O. senegalensis*, and land use type, as well as for grasshopper species diversity and land use type. To test the correlation between locust and grasshopper abundance and plant nutrients, we used Pearson's correlation tests.

To evaluate the relationships among soil physical properties, plant cover, soil inorganic N, and plant N content, we used multiple linear mixed-effect models (LMEs). In different models we tested the relationship between the non-correlated independent variables (see Appendix A) and the dependent variables, either total soil inorganic N (initial $NO_3^- + NH_4^+$) or plant N content. In all cases we used 'village' as a random factor. We used another LME to explore the relationship between binary (residue removal, burning, fertilizer use, alternative crops) and ordinal (land use history) farmer management practices and 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 $\Delta AICc \leq 2$ of the best one (e.g. the model with the lowest AICc value (Burnham and Anderson, 2002)). We determined a priori that certain variables were of interest and important for testing our original hypotheses; these were left in all models (Appendix A).

3. Results

3.1. Land use differences in soil, plants, and grasshoppers (Fig. 1, arrow A)

Across this mixed agricultural landscape, soils were sandy, nitrogen poor, moderately acidic, moderately dense, and had low EC and SOM (Table 1). Most soil characteristics varied minimally across land use types, except texture and SOM (Table 1). Actively cultivated fields were sandier than either grazed or fallow fields, and were generally lower in organic matter.

At the time of sampling, the dominant plants in the cropped fields were either millet or groundnut, followed by weeds. These non-

Table 2
Vegetation cover across land use type. Values are the mean (SD) cover of the top three dominant plants, regardless of plant family from ANOVAs. Rank score scale (%): 0 = 0, 1 = 1–2, 2 = 3–10, 3 = 11–40, 4 = 41–70, 5 = 71–100.

Ground cover	Fallow	Grazing	Groundnut	Millet	DF	F value	P value
Vegetation cover	2.8 (1.0) (a,c)	3.3 (1.2) (a)	2.1 (0.8) (b,c)	1.7 (0.8) (b)	3	8.9	<**0.001**
% Cover	11–40%	40–70%	11–40%	3–10%			
Coverage class	(Sparse)	(Moderate)	(Sparse)	(Very sparse)			
Manure	1.5 (0.8) (a,c)	1.2 (0.6) (a)	0.5 (0.7) (b)	0.9 (0.5) (b,c)	3	7.4	**0.001**
% Cover	3–10%	3–10%	0–1%	0–1%			
Coverage class	(Very sparse)	(Very sparse)	(Rare)	(Rare)			
Litter	1.1 (0.5)	1.1 (0.7)	1.2 (0.4)	1.0 (0.3)	3	0.5	0.7
% Cover	3–10%	3–10%	3–10%	3–10%			
Coverage class	(Very sparse)	(Very sparse)	(Very sparse)	(Very sparse)			
Rock	0.0 (0.3)	0.6 (1.3)	0.3 (0.9)	0.5 (1.0)	3	0.8	0.5
% Cover	0%	0–1%	0–1%	0–1%			
Coverage class	(None)	(Rare)	(Rare)	(Rare)			

cropped plants dominated fallow and grazing areas along with woody shrubs in the *Acacia* genus. The average field vegetation cover was sparse between 11 and 40% and highest coverage was in grazing areas (Table 2). We identified six different plant families and four functional groups: grasses, forbs, legumes, sedges, and shrubs (Table 3). Total plant N content was highest in fields cropped with groundnut, an N-fixing legume (Fig. 3B; Table 3).

Eleven species of grasshoppers were found across all land use types (Table 4). *Oedaleus senegalensis* was the most abundant and only species to vary significantly with land use type, being highest in fallow and lowest in groundnut fields (Table 4).

3.2. Relationship between soil properties, inorganic soil N, and plant N (Fig. 1, arrow B)

SOM and EC were the only significant predictors of total inorganic soil N content (Table 5). Out of the farmer management practices we surveyed, only years fallow was significantly related to soil inorganic

Table 3
Plant nutrient variation by plant family across land use type; values indicate mean (SD). Letters show post hoc significant differences from Tukey HSD comparisons following ANOVAs. Not present in field (NP).

Plant family	Functional type	Fallow	Grazing	Groundnut	Millet	N	DF	F value	P value
		Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)				
All plants									
%N		3.3 (0.8) (a)	3.5 (0.9) (a)	4.2 (1.2) (b)	3.5 (0.7) (a)	222	3	6.8	<**0.002**
%C		40.2 (4.2)	40.8 (3.9)	40.1 (4.1)	40.3 (3.4)		3	0.1	1
C:N Ratio		12.9 (3.2) (a)	12.5 (3.3) (a)	10.0 (2.2) (b)	12.0 (2.8) (a)		3	8.9	<**0.001**
Poaceae (millet only)									
%N	Grass	4.5 (NA)	NP	NP	3.4 (0.7)	27	1	2.5	0.1
%C		34.7 (NA)			42.3 (2.1)		1	13	**0.001**
C:N Ratio		7.7 (NA)			13.2 (3.1)		1	2.8	0.1
Poaceae (excluding millet)									
%N	Grass	3.4 (0.7)	3.5 (0.7)	3.4 (0.8)	3.3 (0.4)	43	3	0.4	0.7
%C		42.0 (2.0)	41.2 (3.6)	39.8 (0.8)	42.2 (2.7)		3	0.6	0.6
C:N Ratio		13.0 (2.7)	12.1 (2.6)	12.4 (4.4)	13.1 (2.0)		3	0.4	0.7
Fabaceae (groundnut only)									
%N	Legume	NP	NP	4.9 (1.4)	4.1 (0.5)	29	1	3.2	0.1
%C				42.5 (2.6)	42.3 (0.2)		1	0	0.9
C:N ratio				9.2 (2.4)	10.3 (1.1)		1	1.9	0.2
Fabaceae (excluding groundnut)									
%N	Legume	3.4 (0.6)	3.4 (1.1)	4.3 (0.7)	2.7	22	3	2.1	0.1
%C		42.3 (1.1)	42.1 (0.9)	40.7 (0.7)	41.8		3	0.8	0.5
C:N ratio		12.6 (2.1)	13.6 (4.0)	9.8 (2.2)	15.3		3	2.3	0.1
Combretaceae									
%N	Shrub	3.3 (0.0)	4.5 (1.8)	3.6 (0.4)	NP	7	2	3.8	0.1
%C		47.0 (0.4)	43.2 (6.9)	46.1 (0.5)	NP		2	0.4	0.7
C:N Ratio		14.1 (0.3)	11.2 (6.6)	12.8 (1.7)	NP		2	0.4	0.7
Commelinaceae									
%N	Forb	3.2 (0.2)	3.7 (0.6)	3.7 (0.7)	NP	37	2	1.3	0.3
%C		39.4 (2.3)	37.1 (3.1)	37.4 (2.2)	NP		2	1.5	0.2
C:N Ratio		12.2 (0.5)	10.2 (1.7)	10.4 (2.4)	NP		2	1.7	0.2
Convolvulaceae									
%N	Forb	3.2 (0.7)	3.1 (1.0)	3.6 (0.2)	3.7 (0.7)	30	3	1.7	0.2
%C		35.9 (3.8)	35.5 (3.8)	36.7 (2.8)	37.1 (3.2)		3	0.3	0.8
C:N Ratio		11.7 (3.0)	12.6 (4.4)	10.3 (0.8)	10.3 (2.1)		3	1.3	0.3
Cyperaceae									
%N	Sedge	2.4 (0.3)	NP	3.2 (0.1)	2.9 (0.3)	8	2	11.4	**0.02**
%C		43.6 (2.0)		43.1 (0.8)	43.4 (2.0)		2	0.1	0.9
C:N Ratio		18.6 (2.0)		13.7 (0.8)	14.9 (2.0)		2	7.7	**0.04**
Malvaceae									
%N	Forb	6.1	NP	NP	NP	1			
%C		42.4							
C:N Ratio		6.9							
Rubiaceae									
%N	Forb	2.6 (1.1) (a)	3.5 (0.2) (b)	3.4 (0.1) (b)	3.1 (0.4) (b)	10	3	24.3	<**0.01**
%C		35.1 (5.2)	37.2 (4.0)	32.2 (2.8)	35.4 (4.3)		3	1.5	0.3
C:N Ratio		14.7 (5.2) (a)	10.8 (0.7) (b,c)	9.5 (1.2) (b)	11.4 (0.1) (c)		3	58.7	<**0.001**
Unknown forb sprout									
%N	Forb	NP	NP	3.8 (0.1)	3.4	3			
%C				40.4 (0.0)	41.9				
C:N Ratio				10.8 (0.4)	12.2				

N content (Table 5). Total inorganic soil N was positively correlated with N content of non-nitrogen fixing plants (Table 5).

3.3. Plant nutrients and grasshopper abundance (Fig. 1, arrow C)

Plant N and live vegetation cover were negatively and positively correlated, respectively, with *O. senegalensis* abundance (statistics shown in Table 5; Fig. 4 illustrates the relationship between grasshoppers and plant N). Two models were considered to explain *O. senegalensis* abundance (Appendix A; Table 5) and plant N and live vegetation cover were significant in both, with model 2 showing a marginally-significant impact of soil inorganic N ($p = 0.05$).

Oedaleus senegalensis abundance was negatively correlated with plant N content (Pearson's correlation test: $t = -2.73$, df $= 25$, $p = 0.01$, $r = -0.48$; Fig. 4A; Table 6) and positively correlated with plant C:N ratio (Pearson's correlation test: $t = 3.72$, df $= 25$, $p = 0.001$, $r = 0.60$; Fig. 4B). Abundance of the top three other grasshopper species, *Acrotylus* sp., *Acorypha sp.*, and *Acrida bicolor*, were not significantly correlated with plant N or C:N when compared individually (Table 6), but when grouped, they were positively correlated with plant C:N ratio (Pearson's correlation test: $t = 2.45$, df $= 25$, $p = 0.02$, $r = 0.44$; Fig. 4D).

4. Discussion

Our results indicate that, in the West Central Agricultural Region of Senegal, land use influenced grasshopper abundance and distribution, especially *O. senegalensis*, likely through soil-plant interactions. *Oedaleus senegalensis* abundance was negatively correlated with plant N (Fig. 4A; Table 5), supporting the finding that *Oedaleus* species prefer low N environments (Cease et al., 2012). Our soil and plant data corroborated the pattern well-described in terrestrial ecosystems: positive correlations between SOM, soil N, and plant N. Therefore, while more studies are needed to better understand this agroecosystem, our study suggests managing soils to increase SOM and N could be a potential tool for locust management that would simultaneously increase crop yield.

We found that soil characteristics were relatively homogenous across the agroecosystem and consistent with other studies in this region (Tschakert and Khouma, 2004; Goudou et al., 2012). Low soil N was ubiquitous. Cropped fields contained on average 8.0–12.4 kg N/ha, which is well below the recommended N application for pearl millet of 60 kg/ha (Singh and Thakare, 1986; Bagayoko et al., 2011). The common annual crop rotation between groundnut and millet likely is responsible for the continuity of soil inorganic N content across fields. 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/ha (Bationo et al., 1998). The expense of fertilizer, lack of quality seeds, labor constraints, and alternative uses for crop residue (e.g. building fences, livestock fodder) makes restorative practices like mulching, cover cropping, or intercropping rarely feasible (Survey 2016). Even if the crop residue is not being used for alternative purposes such as building fences and livestock fodder, it is oftentimes still removed from the fields. 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. As such, the land is typically left bare November–May with little organic matter build up over time, making it vulnerable to nutrient loss via biomass removal, wind erosion, and non-stable aggregates due to continuous plowing.

Despite these constraints, we found that soil texture and organic matter (SOM) did differ across the agroecosystem based on management practices. Farmers mainly use manure to fertilize their crops and, when budgets allow, will apply synthetic fertilizer in micro-doses, by hand next to sprouts (Hayashi et al., 2008; Interviews 2017). 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 longer the land is fallow, the higher the levels of SOM and total inorganic N (Table 5). SOM plays a vital role in soil functioning and therefore is considered a key indicator of soil health (Reeves, 1997). However, due to limited land for growing crops, fallowing fields is usually done only after soil health has greatly declined. 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]".

Fallowing is known to be a sustainable agroecological strategy for maintaining soil fertility and macroinvertebrate diversity, reducing soil erosion and temperature, and controlling weeds (Kleinman et al., 1995; Rossi et al., 2010; Lal and Stewart, 2013). Additionally, increasing the length of fallow has been shown to reduce infestation and outbreaks of pests affecting a range of crops (e.g. banana [banana weevils], rice [root aphids and nematodes], and maize [fall armyworm], among others) (Litsinger, 1989; Saito et al., 2006; Wyckhuys and O'Neil, 2007). However, while fallowing may significantly increase soil N over time, the time scale necessary to sufficiently improve soils for maximum crop production (Mertz, 2002) and the interactions among soil nitrogen, crop yield, and pest management in Sub-Saharan Africa are not well understood (Snapp et al., 2014; Burke et al., 2017). Importantly, surplus land available for feasibly growing crops is limited in Africa (Chamberlin et al., 2014), which restricts the capacity for leaving fields fallow. For the agroecosystem studied in Senegal, the fallowing time scale may be too long to sustainably replenish nutrient reserves for plants or increase their tissue N before farmers need to cultivate the field due to land constraints (Interviews 2017). In addition, fallow fields may provide refuges for grasshoppers to lay eggs without them being disturbed by weeding or plowing (Amatobi et al., 1988).

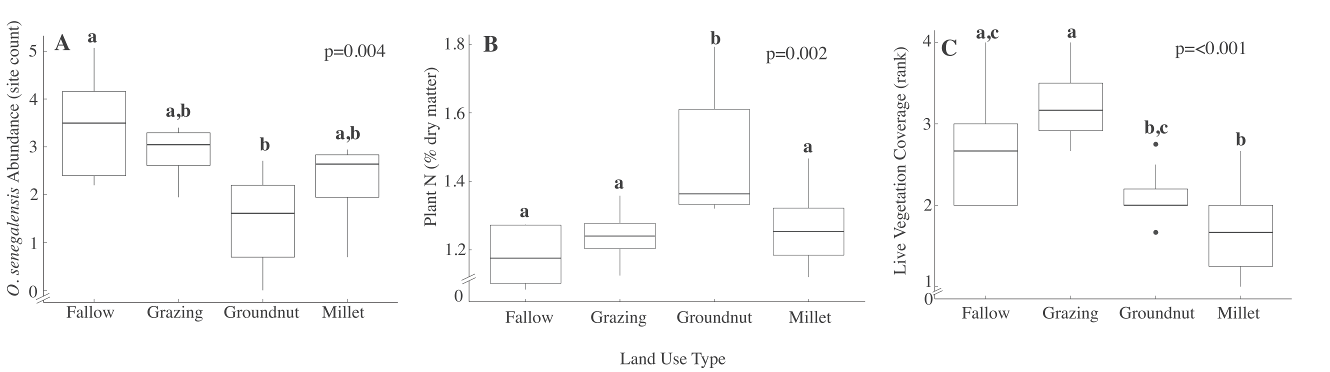

Fig. 3. *O. senegalensis* abundance (A), plant N (B) and vegetation cover by rank score across land use types (C) across land use types. Plant N content is the mean N content (%) of all plants regardless of functional type. Letters represent Tukey HSD significant differences. All figures are box plots showing mean and quartile ranges corresponding to the first (bottom whisker) and third quartiles (top) (the 25th and 75th percentiles).

Table 4
Grasshopper abundance, diversity and plant nutrients across land use type. Data are mean (SD). 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. All statistics were run with log(n + 1) transformation to account for zeros.

Grasshopper Spp.	Fallow	Grazing	Groundnut	Millet	DF	F (♦) or Chi-squared value	p value
Acorypha spp	2.6 (3.2)	1.8 (2.4)	0.1 (0.3)	1.6 (2.9)	3	4.4	0.2
Acrida bicolor	17.6 (36.0)	25.8 (30.6)	0.3 (0.5)	0.9 (1.3)	3	6.2	0.1
Acrotylus spp	0.8 (1.8)	8.3 (16.5)	0.1 (0.3)	1.2 (1.6)	3	4.1	0.3
Catantops stramineus	0.0 (0.0)	1.0 (0.0)	0.0 (0.0)	0.0 (0.0)	–	–	–
Chrotogonus senegalensis	1.4 (2.1)	0.3 (0.5)	1.2 (1.0)	0.6 (0.7)	3	4.3	0.2
Cryptocatantops haemorrhoidalis	0.0 (0.0)	0.0 (0.0)	1.0 (0.0)	0.0 (0.0)	–	–	–
Diabolocatantops axillaris	0.0 (0.0)	0.0 (0.0)	1.0 (0.0)	0.0 (0.0)	–	–	–
Oedaleus senegalensis	54.2 (62.1) (a)	19.0 (10.2) (a,b)	5.1 (4.8) (b)	10.8 (6.4) (a,b)	3	5.9♦	**<0.01**
Ornithacris cavroisi	0.0 (0.0)	1.0 (0.0)	0.0 (0.0)	1.0 (0.0)	–	–	–
Pyrgomorpha cognata	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.0 (0.0)	–	–	–
Unknown nymph	4.5 (3.5)	2 (0.0)	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)	3	2.7	0.4
Mean abundance	78.4 (96.6)	56.3 (34.6)	8.1 (4.5)	16.1 (7.3)	3	4.6	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)	3	6.8	**0.002**
%C	40.2 (4.2)	40.8 (3.9)	40.1 (4.1)	40.3 (3.4)	3	0.1	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)	3	8.9	**<0.001**

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. 3B). The N contents of non-nitrogen fixing plants was positively correlated with total soil inorganic N (Table 5). Plant nutrient content was, in turn, correlated with grasshopper distributions. *Oedaleus senegalensis* were most abundant in land use types where plant N was the lowest (Fig. 3A), including non-groundnut cultivated areas, suggesting that these areas provide a

Table 5
Results of regression analyses between site-averaged soil, farmer, plant, and locust data. Shown are all acceptable models based on an information criterion approach using Akaike weights and the significant variables. See appendix for a full list of models.

Model	Dependent variable	Model number	AIC	AICc	ΔAICc	AkaikeWt.	Predictor variables	DF	F value	P value
Soil variable models	Total inorganic N	4	114.84	122.84	0	0.74	**Soil organic matter**	**20**	**8.1**	**0.01**
							BD	20	1.2	0.29
							Electrical conductivity	**20**	**11.6**	**<0.01**
							pH	20	0.4	0.52
							Rock cover	20	3.3	0.09
Farmer management variable models	Total inorganic N	3	78.58	104.29	0	0.48	Residue removed	9	0.5	0.51
							Fertilizer use	9	0.6	0.45
							Years groundnut	9	0.2	0.64
							Years spent fallow	**9**	**6.8**	**0.03**
							Years millet	9	1.7	0.23
							Years beans	9	1.2	0.30
		4	87.56	105.56	1.28	0.26	Residue removed	10	0.6	0.45
							Fertilizer use	10	0.4	0.53
							Years spent fallow	**10**	**5.5**	**0.04**
							Years millet	10	1.0	0.34
							Alternative crop	10	0.6	0.45
		5	80.41	106.12	1.83	0.19	Residue removed	9	1.3	0.28
							fertilizer use	9	0.2	0.66
							Years groundnut	9	0.7	0.42
							Years spent fallow	**9**	**5.6**	**0.04**
							Years beans	9	1.4	0.27
							Alternative crop	9	1.3	0.28
Plant soil variable models	Plant N content	2	−24.9	−24.41	0	0.53	**Total inorganic soil N**	**171**	**3.8**	**0.05**
							Manure cover	171	0.1	0.71
							Litter cover	171	0.3	0.58
		5	−24.72	−24.06	0.35	0.44	**Total inorganic soil N**	**170**	**3.8**	**0.05**
							Crop type	170	1.8	0.15
Locust plant soil variable models	*O. senegalensis*	2	85.01	107.29	2.06	0.24	**Plant N content**	**16**	**12.0**	**<0.01**
							Total inorganic soil N	**16**	**4.3**	**0.05**
							Live vegetation cover	**16**	**11.0**	**<0.01**
							Rock cover	16	3.1	0.10
							Manure cover	16	0.1	0.76
							Litter cover	16	0.1	0.78
							Crop type	16	2.8	0.07
		3	91.49	105.24	0	0.66	**Plant N content**	**18**	**9.8**	**0.01**
							Total inorganic soil N	18	3.5	0.08
							Live vegetation cover	**18**	**9.0**	**0.01**
							Rock cover	18	2.5	0.13
							Manure cover	18	0.1	0.78
							Litter cover	18	0.1	0.80
							Years spent fallow	18	1.8	0.20

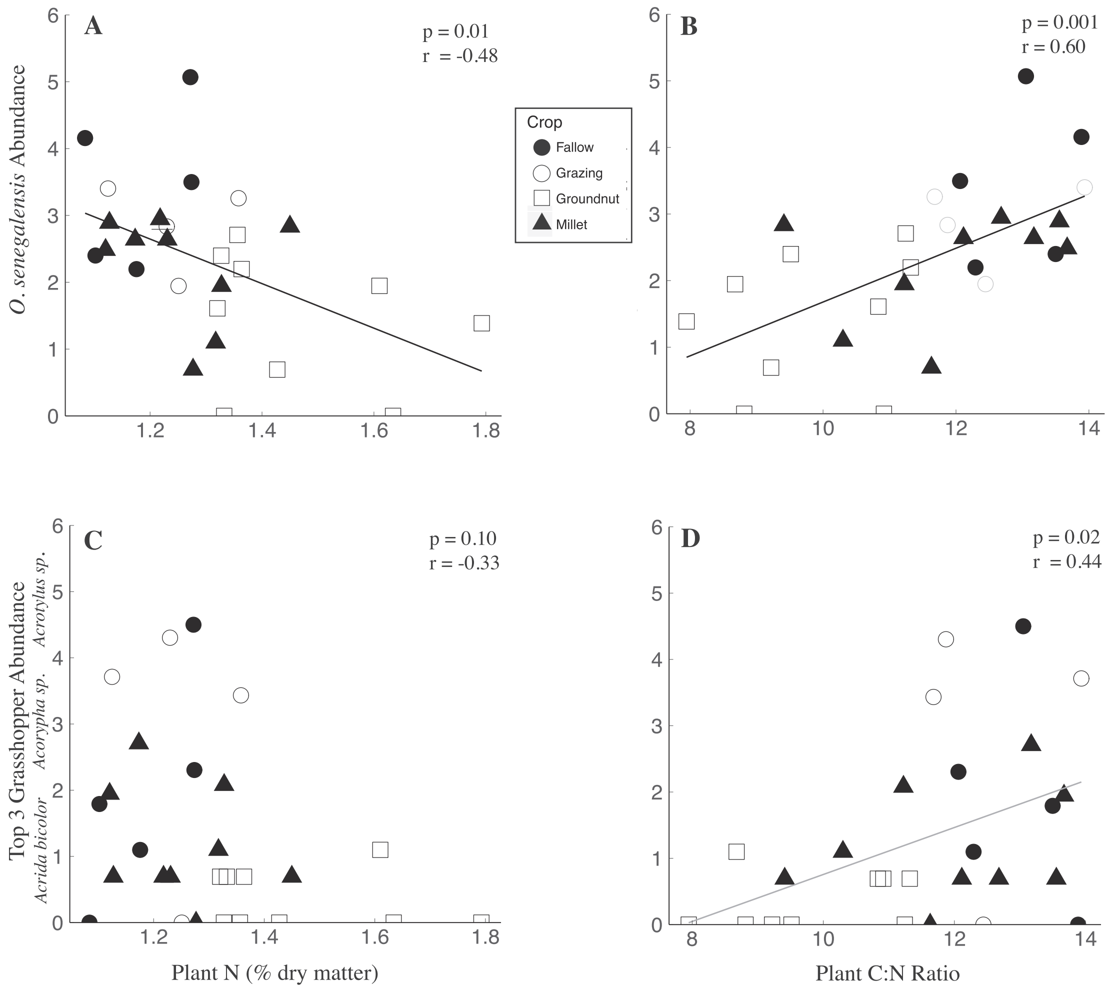

Fig. 4. Relationships between grasshopper abundance and plant nutrient content. Shown are *O. senegalensis* (panels A and B) and the top three most abundant grasshopper taxa (excluding *O. senegalensis*), including *Acrotylus sp*, *Acorypha sp.*, and *Acrida bicolor*. (panels C and D). Trend lines are shown where the relationship is significant. Symbols illustrate different land use types. All statistics were run with log(n + 1) transformation to account for zeros.

more optimal nutritional landscape. The density of the top three most abundant other grasshopper species, *Acrotylus sp.*, *Acorypha sp.*, and *Acrida bicolor* was positively correlated with plant C:N (Fig. 4D), though not with plant N (Fig. 4C). These three species are of less economic importance compared to *O. senegalensis* but have been noted to cause minor crop damage in conjunction with a complex of other species (COPRA 1982). While the pattern was not as strong as for *O. senegalensis*, this result suggests an overall tendency for grasshoppers to prefer low-N plants or environments. In addition to being a more optimal nutritional landscape, these low-N environments could be favorable by creating a trophic cascade that suppresses natural enemies (e.g., Liman et al., 2017) and/or altering plant defenses (Müller and Krauss, 2005). Plant N was not correlated with live vegetation cover, but live vegetation cover was a significant positive predictor of *O. senegalensis* abundance (Table 5). However, it is important to note that the vegetation cover was relatively low across all survey areas (Table 2). Because *O. senegalensis* is a semiarid grasshopper with a tendency to bask and lay eggs in patches of bare sand (Cheke et al., 1980;

Table 6

Correlation between grasshopper species, plant N content and plant C:N ratio. Spearman's rank correlation tests were used for all species besides *O. senegalensis* where we used a Pearson's correlation test.

Species	Plant preference	Plant N (P value)	Plant N (rho)	Plant C:N (P value)	Plant C:N (rho)
Acorypha sp.	Mixed	0.4	−0.2	0.2	0.2
Acrida bicolor	Mixed/Graminivorous	0.2	−0.2	0.1	0.4
Acrotylus spp	Mixed	0.1	−0.9	0.2	0.3
Catantops stramineus	Mixed	Insufficient n	–	–	–
Chrotogonus senegalensis	Mixed	0.2	0.3	0.2	−0.3
Cryptocatantops haemorrhoidalis	Mixed/Non-Graminivorous	Insufficient n	–	–	–
Diabolocatantops axillaris	Mixed	Insufficient n	–	–	–
Ornithacris cavroisi	Mixed	Insufficient n	–	–	–
Pyrgomorpha cognata	Mixed	Insufficient n	–	–	–
Unknown nymph	NA	Insufficient n	–	–	–
		Plant N (P value)	Plant N (r)	Plant C:N (P value)	Plant C:N (r)
Oedaleus senegalensis	Graminivorous	**0.01**	−0.5	**0.001**	0.6

Duranton and Lecoq, 1980; Lecoq, 1984), there is likely an optimal patchiness of ground cover and bare soil with too much vegetation cover negatively impacting *O. senegalensis*. There was no difference in grasshopper species diversity across the different land use types (Table 4) and the grasshopper community diversity was similar to expected for this region (COPR, 1982).

Our surveys represent a snapshot in time, about two weeks after the first rains. We picked this time point because it is when most grasshoppers are nymphs and when the crops are vulnerable to leaf damage by *O. senegalensis* (Popov, 1988; Coop and Croft, 1993; Fisker et al., 2007; Maiga et al., 2008). Previous research suggests that *O. senegalensis* density and defoliation level prior to the millet maturing is a significant predictor of grain weight and resultant yield loss at harvest, likely mediated by diminished photosynthetic-active leaf area (Coop and Croft, 1993; Bal et al., 2015). Because nymphs can migrate locally among fields to select their preferred habitat (Touré et al., 2013a), the distribution of grasshoppers in our study likely reflects their preferred landscape at the time of sampling. While grasshoppers are notoriously mobile and we cannot extrapolate the results of our surveys across the entire rainy season, our data corroborate previous surveys (Amatobi et al., 1988; Touré et al., 2013a). A three-year study conducted in Senegal from July to November found that *O. senegalensis* density was highest in fallow fields, followed by millet, and lowest in beans and groundnut (Touré et al., 2013a). Another study in Nigeria included weekly surveys during the 1977 and 1978 rainy seasons and found that *O. senegalensis* density was highest in grazing and fallow fields relative to millet and sorghum fields (Amatobi et al., 1988). These studies indicate a consistent correlation between land use and *O. senegalensis* populations; however, more studies are needed to understand the mechanisms regulating these patterns. Future research should include grasshopper nutrient and host plant choice tests, as well as studies testing additional potential factors that may cause locusts to select these fields, like egg laying sites and egg survival, alkaloids, or predators.

Organic matter inputs help build up soil nutrient pools (Puttaso et al., 2011) and our results suggest this may suppress locust populations. However, the natural accumulation of manure from livestock and native plant biomass may not be enough to regenerate soil nutrients. Therefore, more active conservation along with synthetic and organic fertilizers may be of greater benefit than passive fallow rotations, especially if fallow areas are harboring locusts. Potential ways to improve soil quality include Zai pits (Slingerland and Stork, 2000), composting (McClintock and Diop, 2005), Quesungual slash and mulch systems (Castro et al., 2009), and diversification of agroecosystems (Altieri et al., 2015). While there are criticisms of conservation agriculture approaches in Africa (Giller et al., 2009) especially where adoption has been low (Twomlow et al., 2008), this research may encourage new perspectives because of the connection between soil fertility and the prevalence of agricultural pests.

We call for more work to understand the additional benefits of soil-targeted interventions for migratory pest management. There are opportunities to alter management techniques like passive fallowing or clearing and burning residue during land preparation, which could lead to higher retention of nutrients in the system (and decrease grasshopper oviposition sites). Yet we do not downplay the constraints smallholders face in their adoption of otherwise seemingly beneficial techniques and practices. Especially when adoption is risky or requires upfront investment or when land tenure is insecure (Robinson et al., 2018), adoption may be prohibitive for many farmers in developing regions. Interventions are often suggested due to their perceived social benefit, but it is also difficult to understand all the private costs and benefits of uptake, or their inherent uncertainties, from the smallholders' perspective. Thus, a deeper understanding of how and why farmers make decisions and integrate new practices in smallholder systems is key. The complexities of coupled human-natural systems like this one illustrate the interconnectivity of not just ecological processes but the important social dimension that must be incorporated to achieve sustainability goals (Lockwood et al., 2001; Toleubayev et al., 2007) (Fig. 1).

5. Conclusions

The sustainability challenge for West African farmers is to secure dietary needs with limited options for increasing soil fertility and controlling pests (Abate et al., 2000; Giller et al., 2009). Our main findings indicate fields and grazing areas with low-N plants supported higher locust population densities and thus, increased capacity for crop damage. Plant N content, especially non-N fixing species, is significantly related to soil inorganic N, which can be tied back to farm management decisions. However, our respondents note that recent decades have brought new challenges: climate change, land degradation, and, notably, Senegalese locusts. In Senegal, locusts are second only to drought in their impacts on agricultural productivity (D'Alessandro et al., 2015). Maintaining the status quo will likely leave many vulnerable.

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Data accessibility

Data will be available from the Dryad Digital Repository upon publication.

References

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., 2004. Linking ecologists and traditional farmers in the search for sustainable agriculture. Front. Ecol. Environ. 2 (1), 35–42. https://www.jstor.org/stable/3868293.

Altieri, M.A., Nicholls, C.I., 2003. Soil fertility management and insect pests: harmonizing soil and plant health in agroecosystems. Soil Tillage Res. 72 (2), 203–211. https://doi.org/10.1016/S0167-1987(03)00089-8.

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.

Amatobi, C.I., Apeji, S.A., Oyidi, O., 1988. Effects of farming practices on populations of two grasshopper pests *Kraussaria angulifra* Krauss and *Oedaleus senegalensis* Krauss (Orthoptera: Acrididae) in Northern Nigeria. Int. J. Pest. Manage. 34 (2), 173–179. https://doi.org/10.1080/09670878809371237 (*formerly*: Tropical Pest Management).

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. Afr. J. Agric. Res. 6, 1141–1150. https://doi.org/10.5897/AJAR10.711.

Bal, A.B., Ouambama, Z., Moumouni, A., Dieng, I., Maiga, I.H., Gagare, S., Axelsen, J.A., 2015. A simple tentative model of the losses caused by the Senegalese grasshopper, *Oedaleus senegalensis* (Krauss 1877) to millet in the Sahel. Int. J. Pest. Manag. 61 (3), 198–203. https://doi.org/10.1080/09670874.2015.1031201.

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. https://doi.org/10.1016/S0167-8809(98)00129-7.

Behmer, S.T., 2009. Insect herbivore nutrient regulation. Annu. Rev. Entomol. 54, 165–187. https://doi.org/10.1146/annurev.ento.54.110807.090537.

Boys, H.A., 1978. Food selection by Oedaleus senegalensis (Acrididae: Orthoptera) in grassland and millet fields. Entomol. Exp. Appl. 24 (3), 278–286. https://doi.org/10.1111/j.1570-7458.1978.tb02783.x.

Burke, W.J., Jayne, T.S., Black, J.R., 2017. Factors explaining the low and variable profitability of fertilizer application to maize in Zambia. Agric. Econ. 48 (1), 115–126. https://doi.org/10.1111/agec.12299.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd edition. Springer-Verlag, New York.

Castro, A., Rivera, M., Ferreira, O., Pavon, J., García, E., Amézquita Collazos, E., Ayarza, M.A., Barrios, E., Rondón, M.A., Pauli, N., Baltodano, M.E., 2009. Quesungual slash and mulch agroforestry system (QSMAS): improving crop water productivity, food security and resource quality in the sub-humid tropics. Project completion report (PN15). Challenge Program on Water and Food. 2009 . https://hdl.handle.net/10568/3906.

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 335, 467–469. https://doi.org/10.1126/science.1214433.

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. Bioscience 65, 551–558. https://doi.org/10.1093/biosci/biv048.

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.

Chamberlin, J., Jayne, T.S., Headey, D., 2014. Scarcity amidst abundance? Reassessing the potential for cropland expansion in Africa. Food Policy 48, 51–65. https://doi.org/10.1016/j.foodpol.2014.05.002.

Cheke, R.A., 1990. A migrant pest in the Sahel: the Senegalese grasshopper *Oedaleus senegalensis*. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 328, 539–553. https://doi.org/10.1098/rstb.1990.0126.

Cheke, R.A., Fishpool, L.D.C., Ritchie, J.M., 1980. An ecological study of the egg-pods of *Oedaleus senegalensis* (Krauss) (Orthoptera: Acrididae). J. Nat. Hist. 14 (3), 363–371. https://doi.org/10.1080/00222938000770311.

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. Afr. J. Agric. Res. Spec. Rev. 4, 1524–1535.

Coop, L.B., Croft, B.A., 1993. Pearl millet injury by five grasshopper species (Orthoptera: Acrididae) in Mali. J. Econ. Entomol. 86 (3), 891–898. https://doi.org/10.1093/jee/86.3.891.

Coop, L.B., Croft, B.A., Murphy, C.F., Miller, S.F., 1991. Decision support system for economic analysis of grasshopper treatment operations in the African Sahel. Crop Prot. 10 (6), 485–495. https://doi.org/10.1016/S0261-2194(91)80138-6.

COPR, 1982. The Locust and Grasshopper Agricultural Manual. Centre for Overseas Pest Research, London.

Cullen, D.A., Cease, A.J., Latchininsky, A.V., Ayali, A., Berry, K., Buhl, J., De Keyser, R., Foquet, B., Hadrich, J.C., Matheson, T., Ott, S.R., 2017. From molecules to management: mechanisms and consequences of locust phase polyphenism. Advances in Insect Physiology. 53, pp. 167–285. https://doi.org/10.1016/bs.aiip.2017.06.002.

D'Alessandro, S., Fall, A.A., Grey, G., Simpkin, S., Wane, A., 2015. Senegal Agricultural Risk Assessment. World Bank Group Report Number 96296-SN.

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., Zeiss, M.R., 2000. Soil health and sustainability: managing the biotic component of soil quality. Appl. Soil Ecol. 15, 3–11. https://doi.org/10.1016/S0929-1393(00)00067-6.

Duranton, J.F., Lecoq, M., 1980. Ecology of locusts and grasshoppers (Orthoptera, Acrididae) in Sudanese West Africa. 1. Discriminant factors and ecological requirements of acridian species. Acta Oecol. 1, 151–164.

Fisker, E.N., Bak, J., Niassy, A., 2007. A simulation model to evaluate control strategies for the grasshopper *Oedaleus senegalensis* in West Africa. Crop Prot. 26 (4), 592–601. https://doi.org/10.1016/j.cropro.2006.04.026.

Food and Agriculture Organization of the United Nations (FAO), 2001. Soil Carbon Sequestration for Improved Land Management. World Soil Resources Report. FAO, Rome, p. 96.

Giller, K.E., Witter, E., Corbeels, M., Tittonell, P., 2009. Conservation agriculture and smallholder farming in Africa: the heretics' view. Field 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.

Hall, S.J., 2014. Soils and the future of food: challenges and opportunities for feeding nine billion people. The Soil Underfoot. 50–69. CRC Press.

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. Agroecosyst. 80, 257–265. https://doi.org/10.1007/s10705-007-9141-3.

Hovick, S.M., Carson, W.P., 2015. Tailoring biocontrol to maximize top-down effects: on the importance of underlying site fertility. Ecol. Appl. 25 (1), 125–139. https://doi.org/10.1890/13-2050.1.

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.

Kleinman, P.J.A., Pimentel, D., Bryant, R.B., 1995. The ecological sustainability of slash-and-burn agriculture. Agric. Ecosyst. Environ. 52 (2–3), 235–249. https://doi.org/10.1016/0167-8809(94)00531-I.

Lal, R., Stewart, B.A., 2013. Principles of Sustainable Soil Management in Agroecosystems. CRC Press.

Launois, M., 1978. Modelisation ecologique et simulation operationnelle en acridologie. Application a *Oedaleus senegalensis* (Krauss, 1877). Ministere de la Cooperation et GERDAT, France.

Launois, M., Launois-Luong, M.H., 1989. *Oedaleus senegalensis* (Krauss 1877) sauteriau ravageur du Sahel. Collection Acridologie Operationnelle no 4. Ministere des Affaires Etrangeres des Pays-Bas et CIRAD/PRIFAS, France.

Launois, M., Rainey, R.C., 1979. An ecological model for the study of the grasshopper *Oedaleus senegalensis* in West Africa. Philos. Trans. R. Soc. Lond. B 287 (1022), 345–355. https://doi.org/10.1098/rstb.1979.0066.

Lecoq, M., 1978. Biologie et dynamique d'un peuplement acridien de zone soudanienne en Afrique de l'Ouest (Orthopt., Acrididae). Ann. Soc. Entomol. Fr. 14 (4), 603–681.

Lecoq, M., 1984. Ecology of locusts and grasshoppers (Orthoptera, Acrididae) in Sudanese West Africa. 2. Ecological niches. Acta Oecol. 5, 229–242.

Lewis, W.J., van Lenteren, J.C., Phatak, S.C., Tumlinson, J.H., 1997. A total system approach to sustainable pest management. Proc. Natl. Acad. Sci. U. S. A. 94, 12,243–12,248. https://doi.org/10.1073/pnas.94.23.12243.

Liman, A.S., Dalin, P., Björkman, C., 2017. Enhanced leaf nitrogen status stabilizes omnivore population density. Oecologia 183 (1), 57–65. https://doi.org/10.1007/s00442-016-3742-y.

Litsinger, J.A., 1989. Second generation insect pest problems on high yielding rices. Int. J. Pest. Manag. 35 (3), 235–242. https://doi.org/10.1080/09670878909371372 (*formerly*: Tropical Pest Management).

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 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-05873-180,226.

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.

Lockwood, J.A., Showler, A.T., Latchininsky, A.V., 2001. Can we make locust and grasshopper management sustainable? J. Orthopt. Res. 10 (2), 315–329. https://www.jstor.org/stable/3503748.

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. Soc. Entomol. Fr. 44, 271–288. https://doi.org/10.1080/00379271.2008.10697563.

Mattson Jr., W.J., 1980. Herbivory in relation to plant nitrogen content. 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. Chang. 64, 210–221. https://doi.org/10.1016/j.gloplacha.2008.09.008.

McClintock, N.C., Diop, A.M., 2005. Soil fertility management and compost use in Senegal's peanut basin. Int. J. Agric. Sustain. 3, 79–91. https://doi.org/10.1080/14735903.2005.9684746.

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.

Mertz, O., 2002. The relationship between length of fallow and crop yields in shifting cultivation: a rethinking. Agrofor. Syst. 55 (2), 149–159. https://doi.org/10.1023/A:1020507631848.

MNDNR (Minnesota Department of Natural Resources), 2013. A Handbook for Collecting Vegetation Plot Data in Minnesota: The Relevé Method. 2nd ed. Minnesota Biological Survey, Minnesota Natural Heritage and Nongame Research Program, and Ecological Land Classification Program. Biological Report 92. Minnesota Department of Natural Resources, St. Paul.

Morrison, L.W., 2016. Observer error in vegetation surveys: a review. J. Plant Ecol. 9 (4), 367–379. https://doi.org/10.1093/jpe/rtv077.

Müller, C.B., Krauss, J., 2005. Symbiosis between grasses and asexual fungal endophytes. Curr. Opin. Plant Biol. 8 (4), 450–456. https://doi.org/10.1016/j.pbi.2005.05.007.

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.

Ostrom, E., 2007. A diagnostic approach for going beyond panaceas. Proc. Natl. Acad. Sci. U. S. A. 104 (15), 181–187. https://doi.org/10.1073/pnas.0702288104.

Pener, M.P., 1983. Endocrine aspects of phase polymorphism in locusts. Endocrinology of Insects. 1. Alan R. Liss, New York, pp. 379–394.

Popov, G.B., 1980. Studies on Oviposition, Egg Development and Mortality in *Oedaleus senegalensis* (Krauss), (Orthoptera, Acridoidea) in the Sahel. Miscellaneous Report No. 53. Centre for Overseas Pest Research College House, London, UK.

Popov, G.B., 1988. Sahelian Grasshoppers (No. 5). Overseas Development Natural Resources Institute.

Power, M.E., 1992. Top-down and bottom-up forces in food webs: do plants have primacy. Ecology 73 (3), 733–746. https://doi.org/10.2307/1940153.

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. Agroecosyst. 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. 43, 131–167. https://doi.org/10.1016/S0167-1987(97)00038-X.

Robinson, B.E., Masuda, Y.J., Kelly, A., Holland, M.B., Bedford, C., Childress, M., Fletschner, D., Game, E.T., Ginsburg, C., Hilhorst, T., Lawry, S., 2018. Incorporating land tenure security into conservation. Conserv. Lett. 11 (2), e12383. https://doi.org/10.1111/conl.12383.

Rossi, J.P., Celini, L., Mora, P., Mathieu, J., Lapied, E., Nahmani, J., Ponge, J.F., Lavelle, P., 2010. Decreasing fallow duration in tropical slash-and-burn agriculture alters soil macroinvertebrate diversity: a case study in southern French Guiana. Agric. Ecosyst. Environ. 135 (1–2), 148–154. https://doi.org/10.1016/j.agee.2009.08.012.

Saito, K., Linquist, B., Keobualapha, B., Phanthaboon, K., Shiraiwa, T., Horie, T., 2006. Cropping intensity and rainfall effects on upland rice yields in northern Laos. Plant Soil 284 (1–2), 175–185. https://doi.org/10.1007/s11104-006-0049-5.

Sijmons, K., Kiplimo, J., Förch, W., Thornton, P.K., Zougmoré, A.S., 2013. CCAFS Site Atlas – Kaffrine. CCAFS site atlas series pp. 1–23.

Singh, A.L., 1999. Mineral nutrition of groundnut. Adv. Plant Physiol. 2, 161–200.

Singh, L., Thakare, R.B., 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. https://doi.org/10.1007/BF01074366.

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. https://doi.org/10.1300/J064v16n02_06.

Snapp, S., Jayne, T.S., Mhango, W., Benson, T., Ricker-Gilbert, J., 2014. Maize-nitrogen Response in Malawi's Smallholder Production Systems. Malawi Strategy Support Program Working Paper.

Song, H., 2011. Density-dependent phase polyphenism in nonmodel locusts: a minireview. Psyche 2011. https://doi.org/10.1155/2011/741769 (16 pages).

SSSA, 2017. Methods of Soil Analysis, Book Series 5. Soil Science Society of America.

Tappan, G.G., Sall, M., Wood, E.C., Cushing, M., 2004. Ecoregions and land cover trends in Senegal. J. Arid Environ. 59 (3), 427–462. https://doi.org/10.1016/j.jaridenv.2004.03.018.

Toleubayev, K., Jansen, K., van Huis, A., 2007. Locust control in transition: the loss and reinvention of collective action in post-Soviet Kazakhstan. Ecol. Soc. 12 (2), 38. https://www.jstor.org/stable/26267902.

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

Touré, A., Temgoua, E., Guenat, C., Elberling, B., 2013b. 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.

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.

Turner, M.D., McPeak, J.G., Gillin, K., Kitchell, E., Kimambo, N., 2016. Reconciling flexibility and tenure security for pastoral resources: the geography of transhumance networks in eastern Senegal. Hum. Ecol. 44 (2), 199–215. https://doi.org/10.1007/s10745-016-9812-2.

Twomlow, S., Hove, L., Mupangwa, W., Masikati, P., Mashingaidze, N., 2008. Precision Conservation Agriculture for Vulnerable Farmers in Low-potential Zones. International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Bulawayo. Zimbabwe.

Uvarov, B., 1957. The aridity factor in the ecology of locusts and grasshoppers of the old world. Arid Zone Research: Human and Animal Ecology, pp. 164–198.

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.

Warton, D.I., 2005. Many zeros does not mean zero inflation: comparing the goodness-of-fit of parametric models to multivariate abundance data. Environmetrics 16 (3), 275–289. https://doi-org.ezproxy1.lib.asu.edu/10.1002/env.702.

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. https://doi.org/10.1080/07352680490433295.

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

Wyckhuys, K.A., O'Neil, R.J., 2007. Local agro-ecological knowledge and its relationship to farmers' pest management decision making in rural Honduras. Agric. Hum. Values 24 (3), 307–321. https://doi.org/10.1007/s10460-007-9068-y.

Wyckhuys, K.A.G., Burra, D.D., Tran, D.H., Graziosi, I., Walter, A.J., Nguyen, T.G., Trong, H.N., Le, B.V., Le, T.T.N., Fonte, S.J., 2017. Soil fertility regulates invasive herbivore performance and top-down control in tropical agroecosystems of Southeast Asia. Agric. Ecosyst. Environ. 249, 38–49. https://doi.org/10.1016/j.agee.2017.08.006.