UCLA
UCLA Previously Published Works

Title
Reduce pests, enhance production: benefits of intercropping at high densities for okra farmers in Cameroon

Permalink
https://escholarship.org/uc/item/8rq6914p

Journal
Pest Management Science, 73(10)

ISSN
0031-613X

Authors
Singh, Akanksha
Weisser, Wolfgang W
Hanna, Rachid
et al.

Publication Date
2017-10-01

DOI
10.1002/ps.4636

Copyright Information
This work is made available under the terms of a Creative Commons Attribution-NoDerivatives License, available at https://creativecommons.org/licenses/by-nd/4.0/

Peer reviewed

eScholarship.org Powered by the California Digital Library
University of California

Research Article

Received: 23 August 2016 Revised: 25 May 2017 Accepted article published: 5 June 2017 Published online in Wiley Online Library:

(wileyonlinelibrary.com) DOI 10.1002/ps.4636

Reduce pests, enhance production: benefits of intercropping at high densities for okra farmers in Cameroon

Akanksha Singh,[a,b*] Wolfgang W Weisser,[a] Rachid Hanna,[b] Raissa Houmgny[b] and Sharon E Zytynska[a]

Abstract

BACKGROUND: Intercropping can help reduce insect pest populations. However, the results of intercropping can be pest- and crop-species specific, with varying effects on crop yield, and pest suppression success. In Cameroon, okra vegetable is often grown in intercropped fields and sown with large distances between planting rows (∼ 2 m). Dominant okra pests include cotton aphids, leaf beetles and whiteflies. In a field experiment, we intercropped okra with maize and bean in different combinations (okra monoculture, okra–bean, okra–maize and okra–bean–maize) and altered plant densities (high and low) to test for the effects of diversity, crop identity and planting distances on okra pests, their predators and yield.

RESULTS: We found crop identity and plant density, but not crop diversity to influence okra pests, their predators and okra yield. Only leaf beetles decreased okra yield and their abundance reduced at high plant density. Overall, okra grown with bean at high density was the most economically profitable combination.

CONCLUSIONS: We suggest that when okra is grown at higher densities, legumes (e.g. beans) should be included as an additional crop. Intercropping with a leguminous crop can enhance nitrogen in the soil, benefiting other crops, while also being harvested and sold at market for additional profit. Manipulating planting distances and selecting plants based on their beneficial traits may thus help to eliminate yield gaps in sustainable agriculture.
© 2017 Society of Chemical Industry

Supporting information may be found in the online version of this article.

Keywords: intercropping; crop identity; high plant density; pests; predators; yield

1 INTRODUCTION

Agriculture is the primary driver of current deforestation, responsible for ∼80% of deforestation worldwide.[1] With the world human population estimated to increase by 2.3 billion by 2050, there is a growing demand for food, putting high pressure on remaining forest resources.[2] It is well known that current intensive agricultural practices are not sustainable in the long term as they contribute to depleting ecosystem services and increased greenhouse emissions.[3] Hence, efforts are needed to link traditional non-intensive practices with modern ecological knowledge, to understand the ecology of these systems and develop effective agricultural designs. Intercropping is a practice that has been carried out traditionally in many parts of the world, especially in the tropics and subtropics.[4] In Africa, the majority of farmers are small-land holders with farm sizes of <2 ha, producing the majority of the continent's food via traditional practices such as intercropping.[5] Intercropping has recently received a theoretical boost from functional biodiversity research that has shown that plant communities with more species show higher ecosystem functioning than plant communities with little species diversity.[6] A number of these functions are relevant for agriculture, including higher abundances of naturally occurring predators[7] and plant productivity.[8] Hence, intercropping systems provide vast possibilities to experiment with, and produce, effective farming designs that are sustainable and profitable.

Intercropped fields have higher vegetation diversity than monocultures and this has been shown to reduce insect pests, by increasing the diversity and abundance of predators and parasitoids,[7,9,10] through the use of barrier crops that obstruct pest movement,[11] or by growing crops that repel[12,13] or trap pests.[14,15] Furthermore, as stated by the 'resource concentration' hypothesis[9] pest numbers can simply be reduced due to their reduced colonization of diverse fields. Root[9] suggested that herbivores with a narrow host ranges are more likely to find, remain and increase in density in pure crop fields. Although most studies

* *Correspondence to: A Singh, Technische Universität München, Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, School of Life Sciences Weihenstephan, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany. E-mail: akankshaa.singh9@gmail.com*

a *Terrestrial Ecology Research Group, Department for Ecology and Ecosystem Management, Technische Universität München, Freising, Germany*

b *International Institute for Tropical Agriculture (IITA), Yaoundé, Cameroon*

 © 2017 Society of Chemical Industry

have recorded pest densities to be higher in monocultures, such hypotheses cannot be generalized and do not consistently predict the influence of crop diversity on arthropods.[10,16–18]

Increasing vegetation diversity can, however, also reduce pest suppression by hindering predator host-searching due to increasing vegetation complexity or, due to alternative herbivore prey species that distract predators (e.g. parasitoid wasps) away from target pests.[19–22] Pest numbers can also increase in intercropped fields with the presence of additional crops or undesirable weeds that act as refuges for the pests.[10,23] Additionally, the response of pests to intercropping can be species-specific and vary with their host-finding mechanisms, such as differences in their olfactory or visual cues.[24] Most pest-colonization hypotheses apply to specialist pests; yet, crops are attacked by several polyphagous pests, e.g. certain polyphagous whitefly or aphid species. Throughout, we use the description by Cates[25] to define herbivores with different host plant feeding ranges. Polyphagous herbivores are defined as those that feed on multiple plant families, oligophagous herbivores are those that feed on multiple genera within the same plant family and monophagous herbivores are those that feed on one or more plant species within the same genus. Polyphagous aphids and whiteflies often respond to the spectra of greenish-yellow light reflected by vegetation, or to the contrast in the plant–soil landscape,[26–29] as they have not developed host-specific olfactory cues. The relevance of visual cues in host-searching abilities has also been shown for oligophagous leaf beetles.[30,31] Therefore, it is evident that in intercropping systems the identity of the additional crop species, and of the pest, can be crucial in determining the pest suppression success of the intercropped field design.

Higher plant densities in a crop field could reduce pest abundances, if the lack of plant–soil contrast and homogenous visual cues hinder pest host-searching. Monoculture studies on plant density have shown that pests locate their host plants more effectively in high plant density plots.[32–34] As pest abundances can influence natural predators,[35,36] higher plant density may cascade up to influence predator abundances. In intercropped fields, although the effect of plant density has been studied on crop yield,[37,38] its effect on pests or predators is often overlooked. Some studies have used additive designs to test for the effect of diversity on pests, where primary crop density does not change but secondary species are added to the plot, increasing total plant density in an intercropped plot.[4,39–41] The interpretation of any density effect from such a design is unclear as total plant density is not constant between treatments and the results observed may only be driven by diversity. To our knowledge, only one study to date has tested for the effect of diversity and density on pest assemblages (but not on plant yield or predators), where abundance of the cucumber beetle was found to be higher in monocultures irrespective of plant density.[42] Hence, as pest/predator responses to diversity are species-specific and affected by density, understanding the impact of diversity and density together can be important for pest suppression in an intercropping system.

Aside from the regulation of pest and predator numbers, intercropping can also increase crop yield by facilitative plant–plant interactions, which are positive interactions between physiologically independent plants mediated through the abiotic environment or other organisms.[43,44] Such interactions occur in most legume–cereal intercropping systems and are prevalent worldwide, because nitrogen-fixing legumes improve soil fertility and transfer nitrogen to co-occurring plants, e.g. 98% of cowpea in Africa and 90% of soybean in Colombia are intercropped, often with staple cereal crops.[4] Although there is ample literature on how intercropping can improve yield and reduce pest damage, most intercropping studies have measured biocontrol or crop yield parameters separately, and to date, only 26 studies have measured these two together.[45] Hence, there is little data to measure the effect of biocontrol services on yield and specifically how these are altered by plant density.

Okra (*Abelmoschus esculentus* Moench) is an economically important vegetable crop grown worldwide with a gross production value of over 5 million US dollars (USD),[46] and it is widely consumed in Cameroon. Okra is attacked by several pests, including the polyphagous cotton aphid (*Aphis gossypii* Glover (Hemiptera: Aphididae)) and an oligophagous leaf beetle (*Nisotra uniformis* Jacoby (Coleoptera: Chrysomelidae)).[47] A survey conducted by the International Institute of Tropical Agriculture (IITA) in Cameroon (2011) found that ∼62% of okra farmers practice intercropping and maize and bean were the most common crops grown along with okra. Common natural predators recorded on okra plants during the survey were spiders, syrphid larvae and lacewing larvae. Okra was always found to be planted in rows and often the fields were sparsely planted with a distance between two consecutive okra rows recorded to be as large as 2 m. However, the recommended row planting distance for okra ranges from 40 to 90 cm,[48,49] suggesting that planting at higher densities may not affect yield production. The effects of intercropping at different plant densities on okra pests and okra fruit yield are unknown. Thus, we conducted a field study in which we intercropped maize and bean with okra (two- and three-species combinations) at different plant densities (high and low). The aim of our study was to answer the following questions: (i) Does crop diversity, crop identity and plant density affect okra pests, their predators and the okra fruit yield? (ii) Does plant density mediate (alter) any effects of crop diversity and crop identity?

2 MATERIALS AND METHODS

2.1 Study site and study system

The field experiment was conducted at the IITA research station in Yaoundé, located in the central region of Cameroon (West Africa). The experiment was initiated on 15 April 2014 and terminated once all plants had yielded fruits and completed their life cycle. Conditions were as follows: average temperature 23.6 ± 0.07 °C (range 18.1–33.2 °C), average humidity $90.7 \pm 0.24\%$ (range 51.9–100%), average rainfall 7.6 ± 1.49 mm (range 0–90.7 mm) and natural light at ∼12: 12 h (light: dark).

We used three plant species, and the varieties used are popular commercially sold varieties in Cameroon. These were: okra (Clemson variety), maize (*Zea mays* L.; CMS8704 variety) and common beans (*Phaseolus vulgaris* L.; ECAPAN21 variety).

Okra is mostly grown in well-drained sandy and clay loam soils in a humid climate. The plants are annual erect herbs (2–4 m tall) with lobed and hairy leaves (up to 50 cm wide and 35 cm long). Okra plants are attacked by many pests at different growing stages such as the polyphagous cotton aphid, tobacco whitefly (*Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae)) and an oligophagous leaf beetle.[47]

Maize is an annual grass, usually with one stem (1–4 m tall).[50] It is a nutrient-demanding crop and requires large quantities of nitrogen during its growth.[51] In sub-Saharan Africa, dominant maize pests are stem and cob borer species belonging to the families Noctuidae, Pyralidae and Crambidae.[52] Maize plants are minor hosts of the cotton aphid, but are not attacked by the leaf beetle or the tobacco whitefly.[53]

 © 2017 Society of Chemical Industry

Common bean is a polymorphic, herbaceous annual plant.[54] We used the erect bush bean type for our experiment which grows up to 20–60 cm high and has a thin multi-branched stem.[55] Among the many bean pests in Africa, the bean stem maggot (*Ophiomyia* spp.) and bruchids (Family Chrysomelidae, sub-family Bruchinae) are considered dominant pests.[56] Bean plants are major hosts for the tobacco whitefly, minor hosts for the cotton aphid, but are not attacked by the leaf beetle.[57]

2.2 Experimental design

We used four crop species combinations: [1] okra monoculture, [2] okra–bean, [3] okra–maize and [4] okra–bean–maize. Hence, we had plots with three different diversities i.e. okra monoculture (1-sp), okra with one other crop species (2-sp) and okra with both crop species (3-sp). Each crop combination was grown at two different plant densities within a plot (high and low), resulting in eight treatment combinations, each with nine replicates, in total $4 \times 2 \times 9 = 72$ plots. A randomized-block design was used with nine spatial blocks each containing one replicate of each treatment; within a block different plot treatments were randomly distributed. Blocks 1–5 and 6–9 were set up on two consecutive days. Because of a lack of space, we could not include bean and maize monoculture plots in our study, and so we focus on the effect of intercropping on okra. The experimental field site (~ 1800 m^2) was situated on a hillside and was surrounded by cassava and plantain fields and set aside land.

The plots measured 12.96 m^2 (3.6 × 3.6 m) and were 1.4 m from adjacent plots, on all sides. We manipulated plant density within a plot by varying the distances between planting rows. In low plant density (LD) plots the distance between planting rows was 0.9 m, i.e. five rows per plot. In high plant density (HD) plots the distance between planting rows was 0.4 m, i.e. 10 rows per plot. These distances were chosen because the recommended distance between rows for growing okra ranges from 0.4 to 1.0 m.[48,49] Within a row, the planting distance used was 40 cm for okra (10 plants/row), 20 cm for maize (19 plants/row) and 10 cm for bean plants (36 plants/row). Hence, for a crop combination, density was only changed due to the distance between rows, not within. Within an intercropped plot, we planted rows of okra alternating with rows of the other crops. Whenever the number of rows was unequal among species, okra was planted in the higher number rows, such that one of the outermost edges of plots always had a row of okra. For example, in LD plots (five rows total) for each two-species plot we had three rows of okra interspersed with two rows of maize (okra–maize combination) or two rows of bean (okra–bean combination). For the three-species plots, three rows of okra were interspersed with one row of bean and one of maize. For more information on the planting design see supplementary material (Table S1 and Fig. S1).

2.3 Experimental set-up

The field site was weeded and cleared, and then small gullies were dug around each plot to direct rain water away from the plot. The experiment was conducted during the wet season (optimal time for okra growth) and heavy rain water can cause soil erosion if allowed to run directly across the growing seedlings. Seeds were placed directly into the ground at a depth of 2.5 cm. We planted three seeds per hole, and removed any additional germinated seedling 2 weeks later to ensure we had one established plant per planting site. All invertebrates were allowed to colonize naturally.

2.4 Weeding and fertilizing

Weeding was done by hand, starting from day 18 and repeated every 3 weeks (four times in total during the experiment). Okra plants were fertilized twice, in weeks 4 and 6. Maize was fertilized once, in week 3. We used 9.5 g of 20: 10: 10 (N: P: K) solid fertilizer per plant (Yara company, Cameroon), for both maize and okra and this was placed into the soil next to each plant.

2.5 Data collection

Data was collected every 2 weeks, on weeks 3, 5, 7 and 9, each time over two consecutive days, i.e. in blocks 1–5 on one day and in blocks 6–10 the next day. At the plot level, we visually recorded weed cover (% weed ground cover) and crop cover (% of the plot surface covered by overhead canopy of the experimental plants).

We collected more specific data on the abundance of pest species and their natural enemies using a subset of plants in each plot. We selected three okra plants in LD and five okra plants in HD plots to account for differences in plant number. We used the same plants on each observation date. In total, data were collected from 288 okra plants. For these selected plants, on each observation date we counted the number of aphids (using a hand tally counter), leaf beetles, whiteflies, spiders and syrphid larvae. We also measured plant height and number of leaves. Carbon and nitrogen content of okra leaves was also measured from plants from which data had been collected during the experiment, see below.

Once okra fruits started to develop (week 8) we conducted observations of all plants every 2 days and harvested the fruits when they were at least 7 cm in length. A newly developed okra fruit pod can take 4–5 days to mature and one plant can produce multiple fruits (at different intervals) for up to 1 month, after its first fruit production. Thus, within a plot, not all fruits were harvested at the same time and fruits from a single plant were also harvested at multiple times. We aggregated the data to obtain total fruit number and total fruit fresh weight per plot for all plants within a plot. Further, fruits were separated into two categories per plot, marketable and unmarketable. We classified fruits as unmarketable when >50% of their surface was black (by bacterial, leaf beetle or cotton stainer bug (*Dysdercus* sp.) damage), when there was fruit borer damage and when the fruits were rotting. The remaining fruits were classified as marketable fruits. For maize, fruits were harvested once the ears (top part) were filled out and were round (weeks 12 and 13) (harvest method used by maize farmers in Cameroon; R. Houmgny, pers. comm.). We recorded the number and weight of maize fruits per plot. Bean fruits were harvested once the bean pods had turned fully yellow (week 11) and we recorded the total weight of bean pods per plot.

Further, we collected soil samples from the centre of each plot on week 8. The samples were air-dried for a week at room temperature and then analysed for carbon and nitrogen content in the soil analysis laboratory of IITA, Cameroon. Once all okra plants had stopped producing fruits (week 15), the experiment was terminated. The okra plants were harvested, dried in paper bags at 60 °C for 3 days and their biomass measured.

2.6 Yield calculations

Okra is sold by numbers and not by weight in Cameroon, hence the response variables were calculated using fruit number. HD plots had almost double the number of okra plants than LD plots and, okra monoculture plots had greater numbers of planted okra than intercropped plots. Hence, for unbiased investigation of the effect

 © 2017 Society of Chemical Industry

of our treatments on okra yield, we calculated the percentage marketable fruit (M_P) by dividing total number of marketable fruits per plot (M) with total number of fruits per plot (N_F), and multiplying the result with 100. We also calculated okra yield per plant per plot (Y) by dividing the total number of fruits per plot (N_F) with the total number of okra plants per plot (N).

Additionally, we calculated a modified version of the land equivalent ratio (LER). LER is used to judge the effectiveness of an intercrop and is defined as relative area required for sole crops to produce the same yield as intercropping.[58] A LER value >1 indicates that an intercrop gives better yield (over-yielding) than a monocrop. Calculating LER requires monocultures yield for all crop species. As we only had okra monoculture, here we calculated the 'relative land equivalent ratio' (RLER) per plot. This modified formula allowed for calculation focused on okra.

$$\mathrm{RLER} = \mathrm{Y}_{\mathrm{inter}}/\mathrm{Y}_{\mathrm{mono}}.$$

Here, Y_{inter} is the okra yield per m^2 in an intercropped plot and Y_{mono} is the okra yield per m^2 in a monoculture plot. Okra plants were grown in 50% of the area in HD and in 60% of the area in LD intercropped plots. Our total plot area was $3.6 \times 3.6 = 12.96\ m^2$. Hence, to derive Y_{inter} in a HD intercropped plot, okra yield per plot was divided by 50% of the plot area, i.e. $1.8 \times 3.6 = 6.48\ m^2$ and for a LD plot it was divided by 60% of the plot area, i.e. $2.16 \times 3.6 = 7.78\ m^2$. To derive Y_{mono} in a monoculture plot, okra yield per plot was divided by the total plot area ($12.96\ m^2$). RLER was calculated for each two- and three-species plot separately.

Further, we determined the market selling price of our crops. For this we first interviewed ten vegetable selling vendors and asked them the price at which they sell okra, maize and bean during the crops respective growing seasons (okra and maize are sold by numbers and bean is sold by weight in Cameroon). As the price is always as a range rather than a fixed number, we noted the highest price of the range. For example, when we were told that 10-15 okra fruits were sold for 100 Central African CFA francs (XAF) then we would note the price of 10 fruits to be 100 XAF. We averaged the selling price for each crop species across vendors, and used it to calculate the selling price of the produce from our plots (average selling price for each crop species was multiplied with total fruit number (okra and maize) or fruit weight (bean) per plot for the respective crop species). We also calculated the total inputs (seeds and fertilizer) cost per plot by adding price of total fertilizer and seed weight (for each crop species) used per plot (Table S2). Finally, we calculated the economic profit per plot by subtracting the total selling price by total input cost. The economic profit is presented in USD for ease of comparison, using the exchange rate of 1 USD to 584.58 XAF.

2.7 Data analysis

2.7.1 Response variables for which data were analysed

Invertebrate abundances (aphids, whiteflies, leaf beetles, spiders and syrphid larvae), plant height, plant biomass, soil CN ratio, okra yield (yield per plant and % marketable fruit per plot), RLER and economic profit were measured.

The values used for invertebrate abundances and plant height in our analyses are cumulative averages. We first calculated averages per plot from each reading (three plants for the LD or five for HD plots) for each of these variables. Then the average values of all readings were added, separately for each of these variables, to yield the cumulative average abundance per plant. Plant biomass values are also average values from each plot calculated from sample plants.

2.7.2 Selection of main explanatory variables to be used for data analysis

Diversity and crop combination are highly correlated variables, hence to avoid multicollinearity, we first analysed data to select one variable of these to be used for all our further analysis. Two separate models for each of the response variables were run to test for the effects of crop diversity (i.e. 1–3) and crop combination (okra, okra–bean, okra–maize, okra–bean–maize) separately. Diversity significantly affected only two response variables (Table S3) but crop combination affected seven response variables. Further, average adjusted R^2 values (range 0–1, with values closer to 1 providing a better fit of the model to the data) derived from different models of all response variables using crop diversity was 0.17 and from models using crop combination was 0.41. Thus, crop combination explained more variation than crop diversity for all response variables. Therefore, in all our analyses we used the main explanatory variable of crop combination rather than diversity.

To analyse data for the main explanatory variables (crop combination and plot density) we ran generalized linear models (GLM) or linear models (LM). For the response variable syrphid larvae abundance, GLM with quasi-Poisson distribution was used (overdispersed data) and for the RLER response variable, GLM with Poisson error distribution were used. For all other response variables, we ran LMs with normal error distribution, since these gave the optimal model fits.

2.7.3 Model description for data analysis

To analyse the effect of plot plant density and crop combination on all response variables (okra pests and their predators, okra plant height and biomass, okra yield (yield per plant and % marketable fruit per plot), soil CN ratio, RLER and economic profit), our models included block as a fixed effect, plot plant density (high/low) and crop combination as main explanatory variables, and the interaction between plot plant density and crop combination. The significance of our blocking factor in the analyses showed that there was significant spatial variation with higher invertebrate abundances in block 9 (next to a cassava field) and lower values in block 1 (next to a fallow field). By including block in all models, along with the randomized block design, we minimized any bias the spatial effect may have on our results. For the response variables soil CN ratio, *RLER* and economic profit we did not include any covariates in the model. For other response variables, we included suitable covariates mentioned below in each of the models to account for additional variation across our blocks.

For the response variables okra pests/predator (aphids, whiteflies, leaf beetles, spiders and syrphids) we included soil CN ratio, plant CN ratio, % crop cover, % weed cover and plant height. The abundances of different pests/predators were included as covariates when these were not the respective response variables.

For the response variables okra plant biomass, plant height and okra yield (okra yield per plant (Y) and percentage marketable fruit per plot (M_P)), we included soil CN ratio, % crop cover, % weed cover, and abundance of whiteflies, leaf beetles, aphids, spiders and syrphid larvae as covariates. Additionally, plant CN ratio, plant height and plant biomass were included as covariates only for okra yield response variables. M_P data were arcsine transformed before analysis.

We also conducted post hoc analysis using the Tukey HSD test to determine the effects of different crop treatments on response

© 2017 Society of Chemical Industry

Table 1. Effect of main experimental variables and covariates on okra invertebrates.

Explanatory variables and covariates	Response variables: Aphid abundance	Leaf beetle abundance	Whitefly abundance	Spider abundance	Syrphid larvae abundance
Block	$F_{8,58} = 3.02$, $P = 0.006$	$F_{8,55} = 2.63$, $P = 0.016$	$F_{8,58} = 4.74$, $P = 0.001$	$F_{8,58} = 1.18$, $P = 0.327$	$F_{8,54} = 20.14$, $P < 0.001$
Soil carbon–nitrogen ratio	×	×	×	×	$F_{1,54} = 6.39$, $P = 0.014$ (−0.35)
Crop cover (%)	×	×	$F_{1,58} = 8.79$, $P = 0.008$ (−0.13)	×	×
Plant height (cm)	×	$F_{1,55} = 9.29$, $P = 0.004$ (+0.03)	×	×	$F_{1,54} = 5.63$, $P = 0.021$ (+0.39)
Spider abundance	$F_{1,58} = 3.24$, $P = 0.077$ (−0.54)	×	×		×
Leaf beetle abundance	×		×	$F_{1,58} = 6.23$, $P = 0.015$ (+0.26)	×
Plot plant density	$F_{1,58} = 7.16$, $P = 0.009$	$F_{1,55} = 55.32$, $P < 0.001$	$F_{1,58} = 3.12$, $P = 0.049$	$F_{1,58} = 14.17$, $P = 0.003$	$F_{1,54} = 4.15$, $P = 0.046$
Crop combination	$F_{3,58} = 0.072$, $P = 0.975$	$F_{3,55} = 32.24$, $P < 0.001$	$F_{3,58} = 4.32$, $P = 0.008$	$F_{3,58} = 3.57$, $P = 0.019$	$F_{3,54} = 3.11$, $P = 0.033$
Density × Combination	×	$F_{3,55} = 7.87$, $P = 0.001$	×	×	$F_{3,54} = 3.90$, $P = 0.044$

Generalized linear models with quasi-Poisson distribution were used for syrphid larvae response variable. For all other response variables, linear models were used with normal error distributions. ×, value not significant in a model and removed from the final minimal model. Only those values that were kept in the final minimal model are shown. Covariates that were not significant for any of the response variables are not mentioned. Values in parentheses are coefficient values of the model for the respective explanatory variables. '+' indicates a positive association and '−' indicates a negative association between the response variables and the covariate.

variables. Correlation values reported in the result section were obtained using Pearson product–moment correlation method.

All data were analysed using R software version 3.2.2. We first fitted full models with all main effects and the interaction between the main explanatory variables, plus covariates. Then, all non-significant covariates were removed followed by the non-significant interaction, using step-wise analysis of variance (ANOVA) model fit comparisons.

3 RESULTS

3.1 Okra pests and their predators

Okra pests (aphids, leaf beetles and whiteflies) and their predators (spiders and syrphid larvae) started colonizing plants from the first observation week and were recorded in all plots throughout the experiment. Our field site was situated on a hill and different parts of the site were surrounded by cassava, plantain or set aside land. Hence, due to these spatial variations we recorded a strong effect of block on okra invertebrates and plants traits (Tables 1 and 2).

3.1.1 Effect of plant density and crop combination on okra pests and their predators

Plant density of plots affected all invertebrates; specifically, a strong effect was observed for leaf beetles, aphids and spiders (Table 1). Overall, the abundances of leaf beetles, whiteflies, spiders and syrphid larvae per plant were reduced in HD plots, whereas aphid abundance increased in these plots (Table 3 and Fig. 1). Crop combination explained a significant amount of variation for all invertebrates, except aphids (Table 1). This suggests that crop identity is crucial in determining pest and predator abundances. Spider abundance differed between okra monoculture and okra–bean plots ($t = 2.67$, $P = 0.043$) and was highest in okra monocultures (Fig. 1). Spider abundance also increased in three-species combination plots (Fig. 1). Whitefly abundance was significantly lower in okra–maize than in okra–bean plots ($t = 2.72$, $P = 0.040$) and increased in okra monoculture plots (Fig. 1). We found that the effect of plant density on the abundance of leaf beetles and syrphid larvae varied across crop combinations (significant two-way interaction; Table 1). In comparison with LD plots, syrphid abundance was recorded to be lower in all HD plots except in okra–bean HD plots, suggesting an attraction of syrphids to bean plants (Fig. 1). Leaf beetle abundance did not differ between HD and LD okra monoculture plots ($t = 1.62$, $P = 0.732$), but it was lower in other intercropped HD plots in comparison with LD plots (Fig. 1).

There was no association between syrphids and any of the okra pests, but we did observe a marginal negative association between spider and aphid abundances (Table 1). Spider abundance was also higher in plots with higher leaf beetle abundance (Table 1). Whitefly abundance was lower in plots with higher percentage of crop cover (Table 1) and taller plants had a higher abundance of both leaf beetles and syrphid larvae (Table 1). Syrphid larvae abundance also decreased with higher soil CN ratio (Table 1).

3.2 Okra plant traits and yield

Okra plants started to produce fruits by week 8 and peak fruit production weeks were 9, 10 and 11, after which most plants had completed their life cycle and fruit production decreased

 © 2017 Society of Chemical Industry

Table 2. Effect of main experimental variables and covariates on okra plant traits.

Explanatory variables and covariates	Response variables			
	Plant biomass	Plant height	Yield per plant	% marketable fruits
Block	$F_{8,58} = 5.39$, $P = 0.001$	$F_{8,53} = 2.23$, $P = 0.039$	$F_{8,56} = 12.89$, $P < 0.001$	$F_{8,55} = 0.99$, $P = 0.452$
Crop cover (%)	×	$F_{1,53} = 9.61$, $P = 0.003$ (+0.29)	$F_{1,56} = 11.66$, $P = 0.001$ (+0.03)	×
Soil carbon–nitrogen ratio	×	$F_{1,53} = 4.09$, $P = 0.048$ (+1.45)	×	×
Plant height	×		$F_{1,56} = 11.24$, $P = 0.001$ (+0.04)	
Plant biomass			$F_{1,56} = 23.24$, $P < 0.001$ (+0.03)	×
Leaf beetle abundance	$F_{1,58} = 25.79$, $P < 0.001$ (+0.08)	$F_{1,53} = 8.73$, $P = 0.005$ (+0.79)	×	$F_{1,55} = 11.35$, $P = 0.001$ (−2.05)
Plot plant density	$F_{1,58} = 33.41$, $P < 0.001$	$F_{1,53} = 3.04$, $P = 0.037$	$F_{1,56} = 12.89$, $P = 0.006$	$F_{1,55} = 9.49$, $P = 0.003$
Crop combination	$F_{3,58} = 28.15$, $P < 0.001$	$F_{3,53} = 2.59$, $P = 0.062$	$F_{3,56} = 17.44$, $P < 0.001$	$F_{3,55} = 1.33$, $P = 0.273$
Density × Combination	×	$F_{3,53} = 3.89$, $P = 0.014$	×	$F_{3,55} = 2.07$, $P = 0.115$

Linear models were used with normal error distributions. ×, value was not significant in a model and was removed from the final minimal model. Only values that were kept in the final minimal model are shown. Covariates that were not significant for any of the response variables are not mentioned. Values in parentheses are coefficient values of the model for the respective explanatory variables. '+' indicates a positive association and '−' indicates a negative association between the response variables and the covariate.

Table 3. Measure of different variables per plot at low and high plant density.

Variables	Low plant density	High plant density
Plot variables		
Crop cover (%)	53.1 ± 1.42	84.9 ± 1.81
Weed cover (%)	46.7 ± 2.75	37.8 ± 2.90
Soil carbon–nitrogen ratio	12.2 ± 0.14	11.8 ± 0.18
Total okra fruit number	74.1 ± 6.33	105.4 ± 11.62
Invertebrates		
Aphid abundance	45.2 ± 5.66	67.2 ± 7.13
Leaf beetle abundance	16.5 ± 0.90	10.9 ± 0.92
Whitefly abundance	4.8 ± 0.53	3.9 ± 0.41
Spider abundance	1.2 ± 0.07	0.5 ± 0.06
Syrphid larvae abundance	0.8 ± 0.14	0.5 ± 0.08
Plant traits		
Okra plant height (cm)	47.2 ± 1.02	52.8 ± 1.37
Okra plant biomass (g)	9.6 ± 0.87	6.3 ± 0.72
Marketable fruits (%)	69.7 ± 3.23	55.9 ± 4.40

Values are given as mean ± 1 SE.

(total okra fruits harvested: week 9 = 3096, week 10 = 2351, week 11 = 1818, week 12 = 702). Bean plants flowered the earliest (week 5), followed by okra (week 6) and maize plants (week 8).

3.2.1 *Effect of plant density and crop combination on okra plant traits*

Plant density significantly affected okra plants and their yield (Table 2). Despite higher pest abundances in LD plots, okra plant biomass, yield per plant (Fig. 2) and % marketable fruits were all greater in LD than HD plots (Table 3), indicating some negative effects of high density. Higher yield per plant was also recorded in plots with a lower crop cover (Table 2), and crop cover was lower in LD plots (Table 3).

Crop combination also affected plant biomass and yield per plant (Table 2). Individual okra plant biomass mean was highest in okra monoculture (11.2 ± 0.94 g), followed by okra–bean (8.5 ± 0.93 g), okra–bean–maize (7.1 ± 0.91 g) and lowest in okra–maize (4.8 ± 1.25 g) plots. Plant biomass in okra–maize plots differed from other crop combinations (okra: $t = 6.44$, $P < 0.001$; okra–bean: $t = 4.62$, $P = 0.001$; okra–bean–maize: $t = 3.16$, $P = 0.012$). Plants with higher biomass also had a higher yield per plant (Table 1). Yield per plant was therefore also lowest in okra–maize plots and higher in okra monoculture and okra–bean plots (Fig. 2). Thus, there seems to be some negative effect of intercropping with maize on okra plants. However, this negative effect of maize on okra was reduced to some extent by the presence of bean. This was evident in our three-species plots where okra yield per plant was higher (1.9 ± 0.22) than in the two-species okra–maize plots (1.4 ± 0.16; Fig. 2). Further, the increase in okra yield per plant from okra–maize to okra–bean–maize plots (despite no significant interaction), was higher in LD than in HD plots (Fig. 2).

Unlike plant biomass and yield, plant height was greater in HD plots (Table 3) and we recorded a significant two-way interaction between density and combination on plant height (Table 2). Here, plant height showed no difference between LD and HD okra monocultures plots; however, it was higher in other HD than LD intercropped plots (Fig. S2). We also recorded that plant height increased with an increase in crop cover and with an increase in soil CN ratio (Table 2). Soil CN ratio was also higher in LD plots ($F_{1,59} = 4.87$, $P = 0.031$; Table 3) but was not affected by crop combination ($F_{3,59} = 1.82$, $P = 0.153$).

Crop combination had no effect on % of marketable fruits. Among the invertebrates, only leaf beetles were associated with okra plant biomass and % marketable fruits (Table 2), and we

© 2017 Society of Chemical Industry

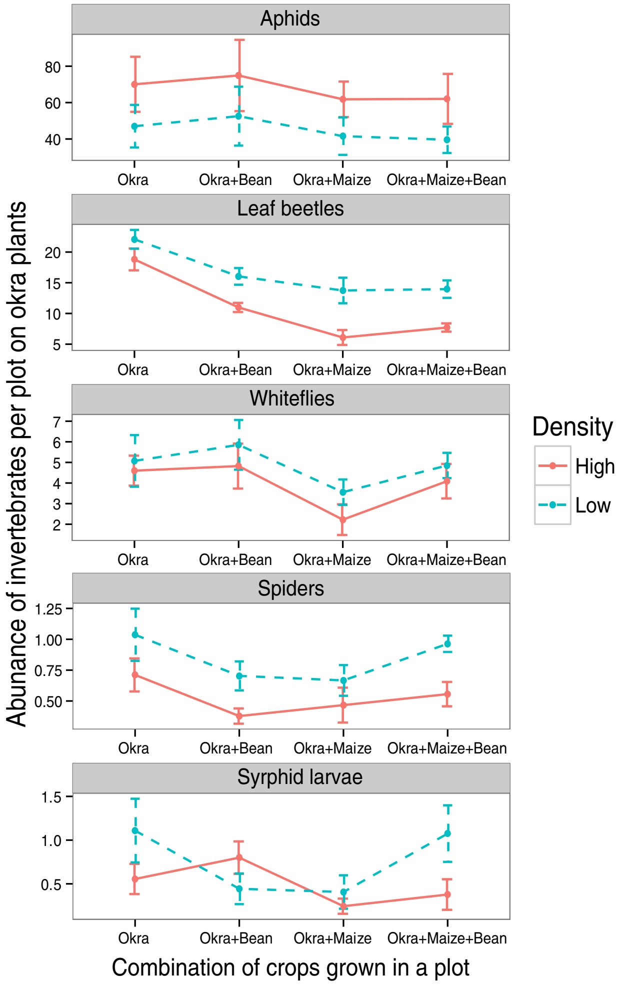

Figure 1. Cumulative average abundance of okra pests (aphids, whiteflies and leaf beetles) and predators (spiders and syrphid larvae) across the different combinations of crop plants grown in a plot, at the two different plant densities. Error bars represent ±1 SE.

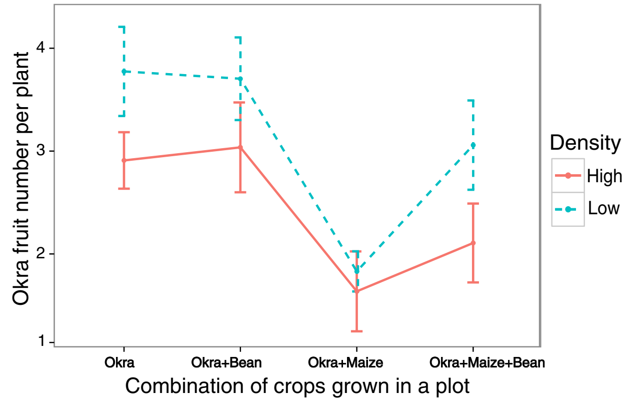

Figure 2. Okra fruit number per plant across the different combinations of crop plants grown in a plot, at the two different plant densities. Error bars represent ±1 SE.

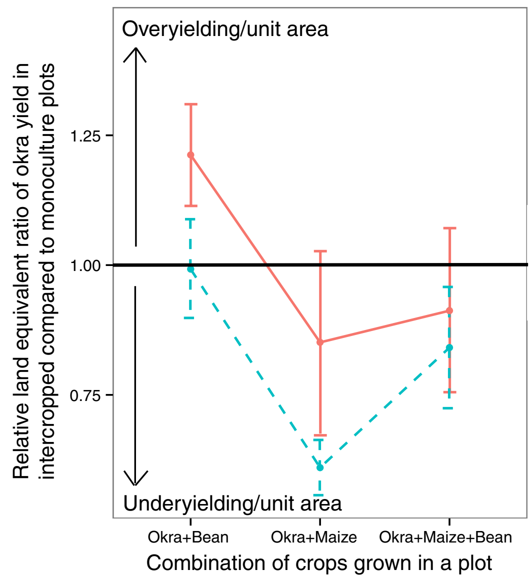

Figure 3. Relative land equivalent ratio (RLER) of intercropped plots at low and high plant density. This was calculated by dividing okra yield per m^2 in an intercropped plot with okra yield per m^2 in a monoculture plot. Error bars represent ±1 SE.

recorded no association between other invertebrates and okra plant biomass, yield per plant or % marketable fruits. Percentage marketable fruits reduced with an increase in leaf beetle abundance (Table 2). However, plant biomass was higher in plots with higher abundance of leaf beetles (Table 2). This might have occurred because leaf beetle abundance was positively correlated with leaf numbers ($r = +0.77$, df = 70, $P < 0.001$), which in turn was positively correlated with plant biomass ($r = +0.88$, df = 70, $P < 0.001$), suggesting that leaf beetles colonized plants with more leaves, rather than leaf beetles positively affecting plant biomass.

Plant carbon–nitrogen ratio showed no relationship with any invertebrate abundance or with okra plants.

3.2.2 *Relative land equivalent ratio, overall yield and resultant profit*

RLER >1 indicates over-yielding and RLER <1 indicates under-yielding by an intercropped plot. Okra RLER varied significantly across crop combinations ($X^2 = 142.85$, df = 2, $P < 0.001$), and was affected by plot plant density ($X^2 = 22.09$, df = 1, $P < 0.001$). Okra RLER was higher in HD than in LD plots (Fig. 3). RLER differed between okra–maize and okra–bean plots ($z = 37.35$, $P < 0.001$) and was >1 in the presence of bean alone; in the presence of maize alone it was <1 at both densities (Fig. 3).

We also recorded a two-way interaction between crop combination and density on RLER ($X^2 = 13.30$, df = 2, $P = 0.002$); in the three-crop combination bean reduced the negative effect of maize on okra to some extent, but only in LD plots (HD okra–bean–maize: LD okra–bean–maize $z = 39.11$, $P < 0.001$) (Fig. 3).

The resultant profit (total selling price – total input cost) to be gained varied significantly across crop combinations ($F_{3,59} = 8.32$, $P < 0.001$) and marginally by plot density ($F_{1,59} = 2.90$, $P = 0.093$), it was highest in okra–bean plots and lowest in okra–maize plots (Fig. 4). Although there was no overall significant interaction between combination and plant density ($F_{3,64} = 0.51$, $P = 0.674$), profit appeared higher in HD than in LD okra–bean plots (Fig. 4). Further, fertilizer usage (added per plant) was lowest in okra–bean (no fertilizer added to beans) and highest in HD okra monoculture plots (highest number of okra plants) (Table S2). Weed cover was also lower in HD than in LD plots and it was highest in okra monoculture plots (Fig. S3). The most profitable design in our study was okra–bean grown at high plant density, whereas, okra–maize grown at low plant density was the least profitable (Fig. 4).

 © 2017 Society of Chemical Industry

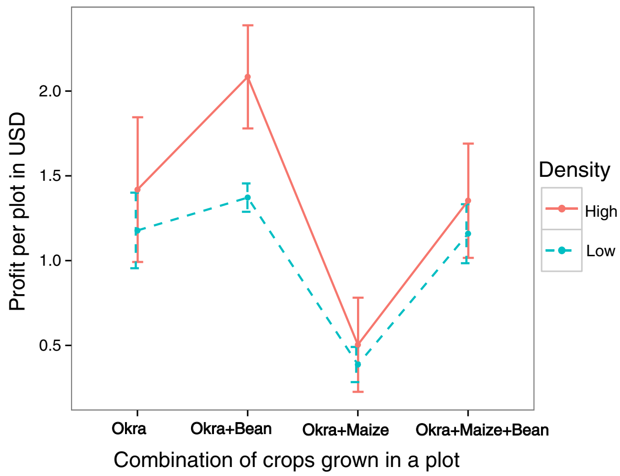

Figure 4. Economic profit per plot in USD across the different combinations of crop plants grown in a plot, at the two different plant densities. Profit was calculated by subtracting the total selling price obtained from all crops per plot with cost of total inputs (seeds and fertilizers) used per plot. Error bars represent ±1 SE.

4 DISCUSSION

Overall, we found that crop identity was important in our system with bean plants benefiting the production of okra, and maize having a strong negative effect. Crop identity also had varying effects on different okra-associated invertebrate species with low abundance of okra pests and their predators in the presence of maize alone. Additionally, plant density within a plot, which is often ignored in intercropping studies, significantly affected not only plant traits but also leaf beetles and whitefly pest species, which were reduced in plots with high plant density. In addition, it was crop combination and plot plant density, but not pest or predator abundances which influenced okra biomass and yield. The optimal strategy in our study for highest resultant profit, lowest fertilizer input and over-yielding (RLER >1) was to grow okra at high plant density in combination with bean plants. From additive studies, it is well-established for intercropping that per unit yield of primary crops is increased most when legumes are the secondary crop; in such systems, the polyculture yield often exceeds the monoculture yield.[45]

Unlike crop identity and density, we did not observe an effect of crop diversity on any invertebrate species except leaf beetles. A myriad of factors can affect invertebrate abundance, such as vegetation structure,[59,60] visual cues of plant species,[27,29,61] feeding range and host-specificity of pest and predator species,[9,62,63] and the presence of floral structures,[64,65] all of which are dependent on the identity of the plants present rather than plant diversity. Further, even studies showing positive effects of diversity on predator abundances have shown that this effect can vary at different trophic levels or due to factors such as intraguild predation, and that these can also be species-specific.[7,66,67] Hence, additional factors may override the effects of diversity and simply increasing diversity in agroecosystems does not automatically reduce pests and enhance their predators.[24]

Variation in pest abundances across our different crop combinations was species-specific and could potentially be explained by their plant host-specificity and feeding range. Whitefly abundance was highest in okra monoculture plots and in the presence of bean, possibly as both bean and okra are their major host plants.[68,69] Whereas, leaf beetles (*N. uniformis*) were most abundant in okra monoculture plots. These leaf beetles are oligophagous pests with a small host range, feeding predominantly on okra.[70] In accordance with the 'resource concentration' hypothesis, this smaller host–plant range could have led to the highest leaf beetle abundance being observed in okra monocultures.[9] On the contrary, the abundance of the highly polyphagous cotton aphids was not influenced by crop combinations because they feed on maize, bean and okra.[71] Further, reduction of leaf beetles and whiteflies in plots with maize could also be attributed to it being an effective barrier plant. Maize is taller and has a larger canopy than both okra and bean, possibly hindering pest host search and ultimately their abundance.[72]

We allowed natural colonization of predators in this experiment, and the main species were syrphid larvae and spiders. Syrphid abundance was higher in HD than LD okra and bean plots. As okra and bean plants flowered earlier than maize, higher attraction of syrphid flies to HD okra–bean plots may have occurred due to high abundance of floral resources in these plots.[64] We observed more spiders in plots with higher leaf beetle abundance, indicating that they perhaps share a similar habitat preference (e.g. okra monocultures) or that leaf beetles attracted spiders as a prey source. Spider abundance was also higher in three-species plots probably due to increased habitat complexity, which in turn has been known to attract more invertebrates.[59] Thus, we can state that the response of natural predators to intercropping can also be predator and plant species-specific.[18,19,24]

There was no strong association between predators and any of the pest species or okra yield, which can be attributed to low numbers of predators that we observed (Table 3). However, spiders did show a marginal negative association with aphids. Previous studies also found that spiders reduce aphids by only a small percentage,[73,74] and this may occur because, as generalists, spiders have wide-host range meaning they also consume alternative (non-target pest) prey species.

Plant density, leading to variation in the plant–soil contrast and plant structure had a strong effect on the invertebrates. Both, leaf beetles and syrphid flies (flying species), were attracted to taller okra plants, which would have been more visible and accessible than shorter plants.[60,75] Whitefly abundances decreased in HD plots (more resources) and with an increase in crop cover. In HD plots, there was higher percentage of crop cover, which could have hindered host-searching of whiteflies as these are flying species, particularly if they rely on the plant–soil contrast as a cue. The plant–soil contrast may also explain low abundances of leaf beetles in HD plots, as some species are more attracted to green than brown backgrounds.[27,29] Finch and Collier[28] illustrated this further in a study in which they intercropped cabbage with green and brown clover. They found that the eggs laid by cabbage pest species decreased only when the surrounding clover was green and not when it was brown. In LD intercropped plots okra rows were replaced by additional crops, whereas, in HD intercropped plots the bare soil was replaced with secondary crops (additional green surfaces). Hence, in HD intercropped plots, leaf beetles possibly landed more on the additional green surfaces, resulting in their reduced numbers on okra. In HD okra monocultures, the additional green surfaces were okra plants and thus leaf beetle numbers decreased only slightly in these plots in comparison with other HD plots. The importance of visual contrasts on beetles has been shown by previous studies.[30,31] By contrast to leaf beetles and whiteflies, aphid abundance increased in HD plots. Although aphid abundance has been shown to be affected by visual contrasts,[26,29] the cotton aphid feeds on all plants used in our study; hence, their higher abundance in HD plots probably occurred as it was easier

© 2017 Society of Chemical Industry

for them to search for their host plants and they remained in plots with higher resources.[33,34,42]

Leaf beetles were the only pests that affected okra yield by reducing the number of marketable fruits, but this did not lead to leaf beetles reducing okra yield per plant. Instead yield per plant was influenced more by crop combination. It has been suggested that factors other than pests, e.g. competitive or facilitative interactions amongst crops strongly affect yield.[24] For example, in HD plots with beans there was likely a higher availability of plant resources as beans can fix soil nitrogen,[44] facilitating greater okra yield even in the absence of additional fertilizer to the bean plants. By contrast, maize requires large amount of nutrients[51] and is a tall plant with a wide canopy, leading to reduced sunlight for okra plants (crop cover was ∼60% in LD and ∼95% in HD okra–maize plots). Beans did not cover okra plants. Therefore, when okra was grown alone with maize, competition for nutrient and light resources was higher, resulting in reduced okra yield. However, the competitive effect of maize on okra was reduced in the presence of bean because okra yield increased when bean was grown along with okra and maize (three-species plots). Nevertheless, this positive effect of bean was stronger in LD plots, possibly due to even greater competition for resources (more abiotic stress) with higher maize plant numbers in three-species HD plots.[76,77]

Reduced sunlight due to maize might also explain why okra plant height was seen to increase in the presence of maize in HD plots and with an increase in crop cover. Increase in stem elongation in dense vegetation is generally believed to be induced by canopy shading as plants grow tall to obtain sufficient light[78] and allocate more resources to the stem than to other parts.[79] We did not record significant variation in soil CN across crop combinations likely because samples were taken only once at the end of the season, potentially after the main facilitation time point. However, N-fixing by beans, high nutrient requirements and large canopy cover of maize are all well-established mechanisms, so their potential effect on the okra plants cannot be ruled out.

We obtained highest total yield and economic profit from HD plots, and even over-yielding (RLER >1) from HD okra–bean plots. Weed cover was also lower in HD and intercropped plots, which would further reduce labour cost and competition for the harvested crops. Hence, we suggest that okra–bean grown at high plant density is the most efficient design in our system.

Overall, our study focuses on the importance of crop identity and plant density when designing intercropped fields. Traits of secondary crop species such as nitrogen fixation and canopy cover should be screened to determine key elements that affect pest and predator abundances and ultimately result in improved yield.[80] Furthermore, we also show how plant density affects pests, predators and even mediates the effect of crop identity. With an ever-growing human population and continually exploiting natural resources, it is crucial to design sustainable cropping systems with an aim to achieve the maximum yield from available land. Legumes such as beans can be included in designs when nutrient limitation is the major obstacle and barrier crops such as maize can be included in designs when pests are the major obstacle in crop production. A system such as ours built on traditional practices would be more acceptable to subsistence farmers and meet their socio-economic needs.

ACKNOWLEDGEMENTS

We sincerely thank the reviewers for their comments. We also thank Thomas Mendouga of IITA for his support in arranging material and labour needed for the experiment and Rose Ndango for carrying out the carbon and nitrogen analysis. This work was supported by the German Federal Ministry for Economic Cooperation and Development (BMZ) (through IITA).

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

REFERENCES

1 Kissinger G, *Herold M and De Sy V*, *Drivers of Deforestation and Forest Degradation:* A Synthesis Report for REDD+ policymakers. Lexeme Consulting, Vancouver, Canada (2012).
2 Food and Agriculture Organization of the United Nations (FAO), *Global Agriculture Towards 2050*. FAO, Rome, Italy (2009). Available: http://www.fao.org/fileadmin/templates/wsfs/docs/Issues_papers/HLEF2050_Global_Agriculture.pdf
3 Foley JA, Ramankutty N, Brauman KA, Cassidy ES, Gerber JS, Johnston M *et al.*, Solutions for a cultivated planet. *Nature* **478**:337–342 (2011).
4 Vandermeer JH, *The Ecology of Intercropping*. Cambridge University Press, Cambridge, UK (1992).
5 Altieri MA and Koohafkan P, *Enduring Farms: Climate Change, Smallholders and Traditional Farming Communities*. Third World Network, Penang, Malaysia (2008).
6 Naeem S, Duffy JE and Zavaleta E, The functions of biological diversity in an age of extinction. *Science* **336**:1401–1406 (2012).
7 Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M *et al.*, Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* **468**:553–556 (2010).
8 Weigelt A, Weisser WW, Buchmann N and Scherer-Lorenzen M, Biodiversity for multifunctional grasslands: equal productivity in high-diversity low-input and low-diversity high-input systems. *Biogeosciences* **6**:1695–1706 (2009).
9 Root RB, Organization of a plant–arthropod association in simple and diverse habitats: the fauna of Collards (*Brassica oleracea*). *Ecol Monogr* **43**:95–124 (1973).
10 Letourneau DK, Armbrecht I, Rivera BS, Lerma JM, Carmona EJ, Daza MC *et al.*, Does plant diversity benefit agroecosystems? *A synthetic review*. *Ecol Appl* **21**:9–21 (2010).
11 Perrin RM and Phillips ML, Some effects of mixed cropping on the population dynamics of insect pests. *Entomol Exp Appl* **24**:585–593 (1978).
12 Khan ZR, Ampong-Nyarko K, Chiliswa P, Hassanali A, Kimani S, Lwande W *et al.*, Intercropping increases parasitism of pests. *Nature* **388**:631–632 (1997).
13 Cook SM, Khan ZR and Pickett JA, The use of push–pull strategies in integrated pest management. *Annu Rev Entomol* **52**:375–400 (2007).
14 Moore L and Watson TF, Trap crop effectiveness in community boll weevil control programs. *Cott A Coll Agric Rep* (1991).
15 Badenes-Perez FR, Shelton AM and Nault BA, Evaluating trap crops for diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *J Econ Entomol* **97**:1365–1372 (2004).
16 Smith HA and McSorley R, Intercropping and pest management: a review of major concepts. *Am Entomol* **46**:154–161 (2000).
17 Risch SJ, Andow D and Altieri MA, Agroecosystem diversity and pest control: data, tentative conclusions, and new research directions. *Environ Entomol* **12**:625–629 (1983).
18 Altieri MA and Nicholls CI, *Biodiversity and Pest Management in Agroecosystems*. Food Products Press, New York, USA (2004).
19 Ratnadass A, Fernandes P, Avelino J and Habib R, Plant species diversity for sustainable management of crop pests and diseases in agroecosystems: a review. *Agron Sustain Dev* **32**:273–303 (2012).
20 Gols R, Bukovinszky T, Hemerik L, Harvey JA, Van Lenteren JC and Vet LEM, Reduced foraging efficiency of a parasitoid under habitat complexity: implications for population stability and species coexistence. *J Anim Ecol* **74**:1059–1068 (2005).
21 Kruidhof HM, Roberts AL, Magdaraog P, Muñoz D, Gols R, Vet LEM *et al.*, Habitat complexity reduces parasitoid foraging efficiency, but does not prevent orientation towards learned host plant odours. *Oecologia* **179**:353–361 (2015).
22 Perfecto I and Vet LEM, Effect of a nonhost plant on the location behavior of two parasitoids: the tritrophic system of *Cotesia*

 © 2017 Society of Chemical Industry

spp.(Hymenoptera: Braconidae), *Pieris rapae* (Lepidoptera: Pieridae), and *Brassica oleraceae*. *Environ Entomol* **32**:163–174 (2003).
23 Room PM and Smith ESC, Relative abundance and distribution of insect pests, ants and other components of the cocoa ecosystem in Papua New Guinea. *J Appl Ecol* **12**: 31–46 (1975).
24 Poveda K, Gómez MI and Martínez E, Diversification practices: their effect on pest regulation and production. *Rev Colomb Entomol* **34**:131–144 (2008).
25 Cates RG, Feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores: the effect of resource abundance and plant chemistry. *Oecologia* **46**:22–31 (1980).
26 Kennedy JS, Booth CO and Kershaw WJS, Host finding by aphids in the field. *Ann Appl Biol* **49**:1–21 (1961).
27 Smith JG, Influence of crop background on aphids and other phytophagous insects on Brussels sprouts. *Ann Appl Biol* **83**:1–13 (1976).
28 Finch S and Collier RH, Host–plant selection by insects – a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. *Entomol Exp Appl* **96**:91–102 (2000).
29 Döring TF, How aphids find their host plants, and how they don't. *Ann Appl Biol* **165**:3–26 (2014).
30 Kühnle A and Müller C, Relevance of visual and olfactory cues for host location in the mustard leaf beetle *Phaedon cochleariae*. *Physiol Entomol* **36**:68–76 (2011).
31 Stenberg JA and Ericson L, Visual cues override olfactory cues in the host-finding process of the monophagous leaf beetle *Altica engstroemi*. *Entomol Exp Appl* **125**:81–88 (2007).
32 Douwes P, Host selection and host finding in the egg-laying female *Cidaria albulata* L.(Lep. Geometridae). *Opusc Entomol* **33**:233–279 (1968).
33 Ralph CP, Effect of host plant density on populations of a specialzied, seed-sucking bug, *Oncopeltus fasciatus. Ecology* **58**: 799–809 (1977).
34 Obermaier E, Heisswolf A, Poethke HJ, Randlkofer B and Meiners T, Plant architecture and vegetation structure: two ways for insect herbivores to escape parasitism. *Eur J Entomol* **105**:233–240 (2008).
35 Morris JR, Vandermeer J and Perfecto I, A keystone ant species provides robust biological control of the coffee berry borer under varying pest densities. *PLoS One* **10**:e0142850 (2015).
36 Pearce S and Zalucki MP, Do predators aggregate in response to pest density in agroecosystems? *Assessing within-field spatial patterns. J Appl Ecol* **43**:128–140 (2006).
37 Gooding MJ, Kasyanova E, Ruske R, Hauggaard-Nielsen H, Jensen ES, Dahlmann C *et al.*, Intercropping with pulses to concentrate nitrogen and sulphur in wheat. *J Agric Sci* **145**:469–479 (2007).
38 Agegnehu G, Ghizaw A and Sinebo W, Yield performance and land-use efficiency of barley and faba bean mixed cropping in Ethiopian highlands. *Eur J Agron* **25**:202–207 (2006).
39 Bukovinszky T, Tréfás H, Van Lenteren JC, Vet LEM and Fremont J, Plant competition in pest-suppressive intercropping systems complicates evaluation of herbivore responses. *Agric Ecosyst Environ* **102**:185–196 (2004).
40 Ponti L, Altieri MA and Gutierrez AP, Effects of crop diversification levels and fertilization regimes on abundance of *Brevicoryne brassicae* (L.) and its parasitization by *Diaeretiella rapae* (M'Intosh) in broccoli. *Agric For Entomol* **9**:209–214 (2007).
41 Gianoli E, Ramos I, Alfaro-Tapia A, Valdéz Y, Echegaray ER and Yábar E, Benefits of a maize–bean–weeds mixed cropping system in Urubamba valley, *Peruvian Andes. Int J Pest Manag* **52**:283–289 (2006).
42 Bach CE, Effects of plant density and diversity on the population dynamics of a specialist herbivore, the striped cucumber beetle, *Acalymma vittata* (Fab). *Ecology* **61**:1515–1530 (1980).
43 Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G *et al.*, Facilitation in plant communities: the past, the present, and the future. *Func Ecol* **96**:18–34 (2008).
44 Brooker RW, Bennett AE, Cong W, Daniell TJ, George TS, Hallett PD *et al.*, Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology. *New Phytol* **206**:107–117 (2015).
45 Iverson AL, Marín LE, Ennis KK, Gonthier DJ, Connor-Barrie BT, Remfert JL *et al.,* Review: so polycultures promote win-wins or trade-offs in agricultural ecosystem services? *A meta-analysis. J Appl Ecol* **51**:1593–1602 (2014).
46 Food and Agriculture Organization of the United Nations (FAO), *Value of Production*. FAO, Rome, Italy. Available: http://www.fao.org/faostat/en/#home
47 Benchasri S, Okra (*Abelmoschus esculentus* (L.) Moench) as a valuable vegetable of the world. *Ratar Povrt* **49**:105–112 (2012).
48 Ibeawuchi II, Obiefuna JC and Ofoh MC, Effects of row spacing on yield and yield components of okra (*Abelmoschus esculentus*) and mixture groundnut (*Archis hypogaea*). *J Agron* **4**:304–307 (2005).
49 Splittstoesser WE, *Vegetable Growing Handbook: Organic and Traditional Methods*, 3rd edn. Springer, New York, USA (1990).
50 Hardacre AK and Turnbull HL, The growth and development of Maize (*Zea mays* L.) at five temperatures. *Ann Bot* **58**:779–787 (1986).
51 Roy RN, Finck A, Blair GJ and Tandon HLS, *Plant Nutrition for Food Security: A Guide for Integrated Nutrient Management*. FOA, Rome, Italy (2006).
52 Chabi-Olaye A, Nolte C, Schulthess F and Borgemeister C, Relationships of intercropped maize, stem borer damage to maize yield and land-use efficiency in the humid forest of Cameroon. *Bull Entomol Res* **95**:417–427 (2005).
53 CABI. *Invasive species compendium datasheet:* Zea mays *(maize)*. CABI, Wallingford, UK (2017). Available: http://www.cabi.org/isc/datasheet/57417
54 Food and Agriculture Organization of the United Nations (FAO), Crop water information: bean (2015). Available: http://www.fao.org/nr/water/cropinfo_bean.html
55 Heuze V, Tran G and Noziere P and Lebas F, *Common bean (*Phaseolus vulgaris*)*. Feedipedia, a programme by INRA, CIRAD, AFZ and FAO (2015). Available: http://feedipedia.org/node/266
56 Abate T and Ampofo JKO, Insect pests of beans in Africa: their ecology and management. *Annu Rev Entomol* **41**:45–73 (1996).
57 CABI. *Invasive species compendium datasheet:* Phaseolus vulgaris *(common bean)*. CABI, Wallingford, UK (2017). Available: http://www.cabi.org/isc/datasheet/40626
58 Mead R and Willey RW, The concept of a 'Land Equivalent Ratio' and advantages in yields from intercropping. *Exp Agric* **16**:217–228 (1980).
59 Langellotto GA and Denno RF, Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* **139**:1–10 (2004).
60 Castagneyrol B, Giffard B, Péré C and Jactel H, Plant apparency, an overlooked driver of associational resistance to insect herbivory. *Ecology* **101**:418–429 (2013).
61 Benelli G and Canale A, Learning of visual cues in the fruit fly parasitoid *Psyttalia concolor* (Szépligeti) (Hymenoptera: Braconidae). *BioControl* **57**:767–777 (2012).
62 Sheehan W, Response by specialist and generalist natural enemies to agroecosystem diversification: a selective review. *Environ Entomol* **15**:456–461 (1986).
63 Dassou AG and Tixier P, Response of pest control by generalist predators to local-scale plant diversity: a meta-analysis. *Ecol Evol* **6**:1143–1153 (2016).
64 Ramsden MW, Menéndez R, Leather SR and Wäckers F, Optimizing field margins for biocontrol services: the relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. *Agric Ecosyst Environ* **199**:94–104 (2015).
65 Lavandero B, Wratten SD, Didham RK and Gurr G, Increasing floral diversity for selective enhancement of biological control agents: a double-edged sward? *Basic Appl Ecol* **7**:236–243 (2006).
66 Straub CS, Finke DL and Snyder WE, Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biol Control* **45**:225–237 (2008).
67 Bianchi FJJ, Booij CJH and Tscharntke T, Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc R Soc London B Biol Sci* **273**:1715–1727 (2006).
68 Mansour SAA, Roff MNM, Khalid AS, Ismail A and Idris AG, Population abundance of whitefly, *Bemisia tabaci* (Genn.), on chilli and other vegetable crops under glasshouse conditions. *J Trop Agric Fd Sc* **41**:149–157 (2013).
69 CABI, Bemisia tabaci *(tobacco whitefly)*. CABI, Wallingford, UK (2015). Available: http://www.cabi.org/isc/datasheet/8927
70 Pitan OOR and Ekoja EE, Yield response of okra, *Abelmoschus esculentus* (L.) Moench to leaf damage by the flea beetle, *Podagrica uniforma* Jacoby (Coleoptera: Chrysomelidae). *Crop Prot* **30**:1346–1350 (2011).
71 Van Emden HF and Harrington R (eds), *Aphids as Crop Pests*. CABI, Wallingford, UK (2007).
72 Perrin RM, Pest management in multiple cropping systems. *Agro-Ecosystems* **3**:93–118 (1976).

 © 2017 Society of Chemical Industry

73 Diehl E, Sereda E, Wolters V and Birkhofer K, Effects of predator specialization, host plant and climate on biological control of aphids by natural enemies: a meta-analysis. *J Appl Ecol* **50**:262–270 (2013).
74 Birkhofer K, Gavish-Regev E, Endlweber K, Lubin YD, Von Berg K, Wise DH *et al.*, Cursorial spiders retard initial aphid population growth at low densities in winter wheat. *Bull Entomol Res* **98**:249–255 (2008).
75 Lawton JH, Plant architecture and the diversity of phytophagous insects. *Annu Rev Entomol* **28**:23–39 (1983).
76 Bertness MD and Callaway R, Positive interactions in communities. *Trends Ecol Evol* **9**:191–193 (1994).
77 García-Cervigón AI, Gazol A, Sanz V, Camarero JJ and Olano JM, Intraspecific competition replaces interspecific facilitation as abiotic stress decreases: The shifting nature of plant–plant interactions. *Perspect Plant Ecol Evol Syst* **15**:226–236 (2013).
78 Anten NPR, Casado-Garcia R and Nagashima H, Effects of mechanical stress and plant density on mechanical characteristics, growth, and lifetime reproduction of tobacco plants. *Am Nat* **166**:650–660 (2005).
79 Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P and Mommer L, Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol* **193**:30–50 (2012).
80 Landis DA, Wratten SD and Gurr GM, Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu Rev Entomol* **45**:175–201 (2000).

© 2017 Society of Chemical Industry