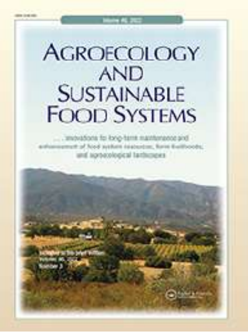

Agroecology and Sustainable Food Systems

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/wjsa21

Agroecological management with intra- and interspecific diversification as an alternative to conventional soil nutrient management in family maize farming

Yeimi D. Martínez-Camacho, Simoneta Negrete-Yankelevich, Ignacio E. Maldonado-Mendoza, Alejandra Núñez-de la Mora & Guadalupe Amescua-Villela

To cite this article: Yeimi D. Martínez-Camacho, Simoneta Negrete-Yankelevich, Ignacio E. Maldonado-Mendoza, Alejandra Núñez-de la Mora & Guadalupe Amescua-Villela (2022) Agroecological management with intra- and interspecific diversification as an alternative to conventional soil nutrient management in family maize farming, Agroecology and Sustainable Food Systems, 46:3, 364-391, DOI: 10.1080/21683565.2021.2015736

To link to this article: https://doi.org/10.1080/21683565.2021.2015736

AGROECOLOGY AND SUSTAINABLE FOOD SYSTEMS
2022, VOL. 46, NO. 3, 364–391
https://doi.org/10.1080/21683565.2021.2015736

Taylor & Francis
Taylor & Francis Group

Agroecological management with intra- and interspecific diversification as an alternative to conventional soil nutrient management in family maize farming

Yeimi D. Martínez-Camacho[a], Simoneta Negrete-Yankelevich[a], Ignacio E. Maldonado-Mendoza[b], Alejandra Núñez-de la Mora[c], and Guadalupe Amescua-Villela[d]

[a]Red de Ecología Funcional Instituto de Ecología A C, Xalapa, México; [b]Instituto Politécnico Nacional. CIIDIR - Unidad Sinaloa, Guasave, México; [c]Instituto de Investigaciones Psicológicas, Universidad Veracruzana, Xalapa, México; [d]Centro de Estudios E Investigación Gestálticos, Xalapa, México

ABSTRACT

In traditional polycultures such as *milpas*, soil degradation and the loss of agrodiversity, threaten rural food security. Although agroecological management using crop functional and genetic diversity could improve soil fertility and family nutrition, experimental evidence is scarce. We conducted a field experiment in which conventional agricultural management (CON) was compared to an agroecological alternative (AGR), with interspecific and intraspecific diversification factors. We hypothesized that: (1) the higher input of organic matter and the suspension of tillage in AGR plots would improve soil conditions, nutrient content and productivity in maize, and intra-root colonization by mycorrhizal fungi as compared to CON plots; and that (2) these conditions would further improve in AGR management with increased intra- and interspecific diversity, since a diverse plant community in the rhizosphere should enhance microbial activity. AGR increased pH, the soil availability of K, Ca and Mg, K in leaves, and mycorrhizal colonization. Within AGR, diversified treatments temporarily increased NO_3^- in the soil. The fixation of nitrogen by additional legumes could have produced this result. We conclude that AGR with interspecific diversification is a viable alternative to CON, since a variety of additional edible plants became available concomitantly with the improvement of mycorrhizal relationships and soil conditions.

KEYWORDS
Agrodiversity; legumes; milpa; soil nutrients; arbuscular mycorrhiza

Introduction

The product of accumulated cultural knowledge, traditional farming systems tend to be inter- and intraspecifically diverse and characterized by the concurrence of domesticated crops and animals (Altieri and Toledo 2011). These farming systems are utilized by approximately 50% of the world's farmers, and their crop genetic diversity plays a fundamental role in securing the long-term global food supply (Isakson 2009). In Mexico, a distinct polyculture dating

CONTACT Simoneta Negrete-Yankelevich simoneta.negrete@inecol.mx Red de Ecología Funcional Instituto de Ecología A C, Xalapa, México

from Mesoamerican civilization called *milpa* has been preserved, which mostly consists of maize, bean, and squash plus other secondary or wild crops with different ecological and nutritional functions (Zizumbo-Villarreal, Flores-Silva, and Colunga-García 2012). Archeological (Piperno and Flannery 2001), molecular (Matsuoka et al. 2002) and paleobiolinguistic (Brown et al. 2014) reports suggest that the Mexican *milpa* was central to the origin, domestication and diversification of maize. Unfortunately, the introduction of technology packages (i.e. improved seeds, inorganic fertilizers and pesticides) by government policies aimed at commodifying production has led to losses of species richness in edible crops and soil fertility in *milpas* (Groenewald and Van Den Berg 2012; Negrete-Yankelevich et al. 2013b). These consequences and the rising cost of external supplies required for the productivity of an already simplified agroecosystem put at risk the food and nutritional security of rural families, whose main livelihood is the *milpa*. To address this problem, agroecological management has been proposed as an alternative to achieve a sustainable agriculture in which food production is maintained over time without harming the environment and focus is placed on the economic viability of farms (Wezel et al. 2014). Practices commonly implemented in agroecological systems include organic fertilization, zero or minimal tillage, manual weeding, and crop diversification through rotation or intercropping, particularly with leguminous plants (Gliessman 2014).

The use of fertilizers rich in organic matter (stubble, manure and compost) is a sustainable practice that returns organic carbon (C) to the soil, extends the availability of nutrients over time, and improves the structure and biological properties of the soil by increasing soil microbial activity, favoring water storage and limiting nutrient leaching and runoff (Rosen and Allan 2007; Tamburini et al. 2020). It has been reported that tillage and inorganic fertilization can weaken plant root colonization by arbuscular mycorrhizal (AM) fungi, microbial symbionts that improve plant nutrition when conditions are limiting (Helgason, Walley, and Germida 2010; Kabir et al. 1998; Reicosky 2015). In contrast, zero or minimal tillage protects soil organo-mineral aggregates, reduces the loss of organic C to the atmosphere, and maintains edaphic biota communities, especially in the mycelial networks of AM fungi (Galvez et al. 2001; Ryan and Graham 2018).

Spatial inter- and intraspecific diversification of crops is thought to be a key practice in agroecological management, since it takes advantage of the differential occupation of ecological niches between plant species and varieties (Tooker, Frank, and Steffan-Dewenter 2012) and enhances multiple ecosystem services including pest control, nutrient cycling, and water regulation (Tamburini et al. 2020). Diversification with edible legumes is an attractive way to simultaneously increase N availability in the soil and in seeds that offer high protein value for human nutrition (Fustec et al. 2010; Ryan and Graham 2018). These plants provide a source of nitrogen for non-legume crops by fixing atmospheric N through their association with rhizobial bacteria (particularly the genus *Rhizobium*) in root nodules (Fustec et al. 2010). For example, the association of maize, fruit trees and squash with beans has been found to improve grain and fruit yield, as opposed to monocultures with and without trees (Molina-Anzures et al. 2016).

Intra- and interspecific diversification of crops could also favor AM fungi symbiosis, facilitating plant nutrition and reducing the need for inorganic fertilizers (Rillig et al. 2019). However, plant-AM fungi interactions vary considerably and are not always beneficial, depending on the species and environmental conditions involved (Montesinos-Navarro, Valiente-Banuet, and Verdú 2019). Negrete-Yankelevich et al. (2013a) observed in mountain *milpas* that crop-specific richness is positively correlated with the percentage of mycorrhizal colonization in maize roots and the concentration of P in maize leaves. AM fungi can help plants absorb more mineral nutrients and water from the soil in exchange for photosynthetically fixed carbon. In particular, the increased acquisition of P is widely documented to be a benefit of mycorrhization (Ferrol, Azcón-Aguilar, and Pérez-Tienda 2018). Thus, the biological function of AM fungi could be important in agroecosystems with volcanic soils, where pH is low and P is easily adsorbed by iron (Fe) and aluminum (Al) oxyhydroxides (Weng, Vega, and Van Riemsdijk 2011), such as in the tropical mountainous soils of Mexico. AM fungi can also contribute to the sequestration of organic C and N as well as the formation of soil aggregates, through the entanglement of their hyphal networks and the excretion of glomalin, a hydrophobic glycoprotein (Hodge and Fitter 2010; Singh, Singh, and Tripathi 2013).

The combination of leguminous plants with cereals could boost AM symbiosis. Legumes can solubilize P in the soil and increase its bioavailability for intercropped species (Hinsinger et al. 2011). Furthermore, N and P can be transferred from legumes to cereals (and vice versa) via AM fungi; specifically, the transfer to cereal can increase when the legume's root system is decaying (Johansen and Jensen 1996; van Kessel, Singleton, and Hoben 1985). Indeed, mycorrhizal colonization, P acquisition, and the quantity of AM propagules in the soil are all higher in interspersed maize and soybean (legume) crops than in monocultures of one or the other (Harinikumar, Bagyaraj, and Mallesha 1990).

Intraspecific diversification could also be an important strategy to achieve sustainable production in agroecological systems. In particular, the use of native seeds with a long history of local domestication and diversification, such as with maize in Mexico, allows the conservation of genetic diversity and supports continuing production under changing climatic or spatially heterogeneous conditions (Ureta et al. 2012). Indeed, it has been documented that traditional farmers simultaneously grow maize varieties with different periods of maturation and resistance to environmental stress in order to maximize harvest security (Clawson 1985; Moreno-Calles et al. 2012). The simultaneous sowing of different maize morphotypes could also enhance the richness of associated AM fungi, since their identity varies with host genotype (Sangabriel-Conde et al. 2015). Although a high diversity of AM fungi is no guarantee of increased crop productivity, it can offer protection from soil pathogens, increase the plant uptake of nutrients, and reduce P leaching (Maherali and Klironomos 2007; Ryan and Graham 2018). For instance, Tian et al. (2013) documented that the high richness of AM fungi in maize roots was related to a greater acquisition of P. However, the field experiment data combining crop intra- and interspecific diversification with management alternatives needed to understand the mechanisms that associate AM fungi colonization level and crop yield are notably lacking (Ryan and Graham 2018).

Therefore, in this work, we conducted an incomplete factorial experiment in the field to test whether interspecific (i.e. the addition of legumes and leafy greens to the basic maize-bean-squash triad) and intraspecific diversification (i.e. the mixture of different maize morphotypes) integrated into the agroecological management of *milpas* can promote a higher density of AM fungi in the rhizosphere, to improve nutrient availability, plant nutrition, and maize yield. We hypothesized that: (1) soil moisture, nutrient availability, maize nutrition, maize dry biomass (stover and grain), mycorrhizal colonization in maize roots, and the soil concentration of AM fungi propagules would all be higher in plots with agroecological versus conventional management; and (2) within plots under agroecological management, these properties should increase in response to inter- and intraspecific diversification.

Materials and methods

Study site

The study was conducted in the community of Ocotepec (Veracruz, Mexico), located on the southwest slope of the Cofre de Perote mountain (19° 21′ 44” N and 97° 09′ 30” W) at 2,000–2,300 m.a.s.l. During the experimental years , the average annual temperature was 12.5°C with a relative humidity of 79%. The annual rainfall was 419 mm in 2016 and 315 mm in 2017 (CONAGUA). The rainfall pattern in 2017 was very unusual due to the incidence of Hurricane Katia in the Gulf of Mexico. That year, the third part of the annual precipitation (109 mm) was concentrated in September, which substantially affected the productivity of the *milpas*. Each farmer within the study area typically has 3–5 pieces of land spread within the town’s farming area. In these lands, *milpas* are sown exclusively for family feeding, and the maize grain yield reaches approximately 2,300 kg·ha^{-1}. The agricultural cycle runs from March to October and maize is only harvested once per year. Our experimental study covered the 2016 and 2017 cycles. In contrast with other regions of Mexico, farmers here distinguish their maize morphotypes solely by their color: black and white are the most commonly used colors, while red and yellow are planted less frequently. All maize morphotypes in this region belong to the Cónico race with influences of other races (Arrocillo, Chalqueño and Coscomatepec; Leyva-Madrigal et al. 2020). The *milpa* soils are andosols (WRB 2019) with medium-low clay content (20–26%), low apparent density (0.5 g·cm^{-3}), a high capacity for water retention, acidic pH (<5), and a very low availability of P (<6 mg·kg^{-1}; see Supplementary Material).

Experimental design

Our field experiment used an incomplete factorial design (Byar, Herzberg, and Tan 1993), meaning that a second and third factor were only tested within one level of the first factor. We tested the effect of management type (agroecological management (AGR) and conventional management (CON) levels) on *milpa* soil and plant response variables. The effects of interspecific diversification (t: maize-bean-squash, tl: t + additional legumes, and tlh: tl + additional leafy greens) and intraspecific diversification (five levels: four maize colors and a mixture of all colors) were only tested within AGR. For AGR, we used a split-plot design with nesting of intraspecific diversification within interspecific diversification (Figure 1). The split-plot design was used to compare the effect of each maize color with the mixture of all colors. This design provided us with an efficient way to compare the intra- and interspecific diversification strategies that can be part of AGR with the CON strategy, which is widespread in the region and has no intra- or interspecific variability (see description below).

In the middle of eighteen separate pieces of land, we delimited twelve 10 × 20 m experimental plots (divided into subplots of 10 × 10 m) for AGR and six 10 × 10 m plots for CON (no split-plots were required, hence their smaller size; Figure 1a). All pieces of land were owned by different producers and contained one plot each. The plots were dispersed within the productive region of the community, had at least five years of continuous management as a *milpa*, and displayed similar topographies (i.e. a homogenous slope of < 30 degrees). Plot selection was conducted in collaboration with producers that volunteered with the DeMano project, which is aimed at improving food production sustainability for rural families in the region. Participants were informed of the required characteristics and they volunteered pieces of land where plots could be installed. AGR and CON plots where randomly assigned to the selected lands. Prior to the experiment, all plots were managed by farmers in the conventional manner (equivalent to CON), which consists of pre-planting tillage via a plow pulled by horses, along with the application of sheep manure during triad planting and inorganic fertilizers during *aterrada* (see below). No tillage was performed in AGR plots during the experiment and fertilization was entirely organic, with a bokashi fermented fertilizer prepared

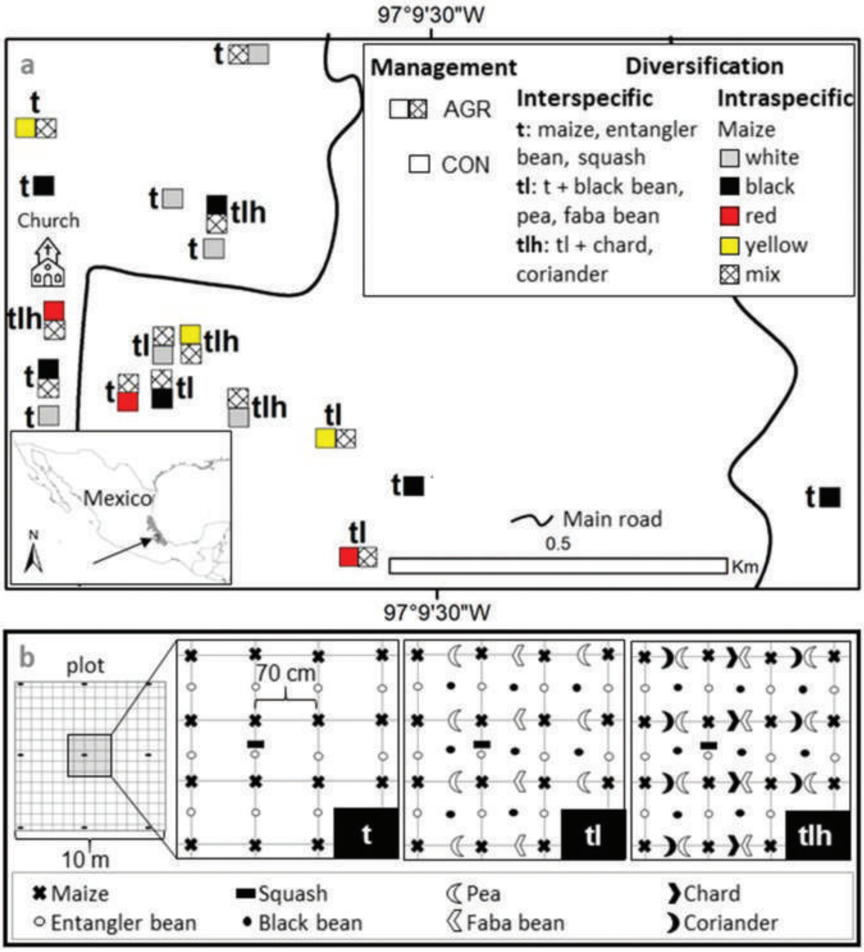

Figure 1. Experimental setting in the field. (a) Distribution of experimental plots and treatments under an incomplete factorial design. Agroecological management (AGR) split-plots are represented by two contiguous squares. Conventional management (CON) plots are represented by squares. The inter- and intraspecific diversification treatments were only tested under AGR. Letters next to plots indicate the interspecific diversification treatment (t: maize-bean-squash; tl: t + additional legumes; and tlh: tl + additional leafy greens) and the symbol's color corresponds to the intraspecific diversification treatment (color of maize morphotype or hashed symbols for the mix of all morphotypes). CON plots were kept with the traditional triad (t) interspecific diversity and sown with white or black maize, the two most commonly planted colors in the region. (b) Distribution of crops in diversification treatments (t, tl and tlh) within AGR split-plots.

in situ (see below). In each AGR plot, one of three levels of interspecific diversification was sown at random. The three levels included: t, a basic triad comprising maize, entangler bean (*Phaseolus dumosus* Macfady), and squash (*Cucurbita ficifolia* Bouché); tl, a basic triad with additional legumes comprising black bean (*Phaseolus vulgaris* L.), pea (*Pisum sativum* L.), and faba bean (*Vicia faba* L.); and tlh, a basic triad with legumes and additional leafy greens comprising tl + chard (*Beta vulgaris* L. var. *cicla*) and coriander (*Coriandrum* *sativum* L.) (Figure 1b). This resulted in four replicate plots per interspecific diversification treatment. A maize morphotype (red, yellow, white or black) was sown on a randomly selected AGR subplot and the mixture of all colors was planted on the adjacent subplot (Figure 1a), resulting in three subplots per maize color and twelve multicolored replicates. All six CON plots maintained the conventional triad interspecific diversity (corresponding to the t treatment described above). Three randomly selected CON plots were sown with white maize and three with black maize. Presently, yellow and red maize are rare in the region, and the mixing of maize colors is not a custom. Therefore, only black and white mono-color plots were established for the CON plots (hence their 10 × 10 m size). The experiment was conducted during the 2016 and 2017 crop cycles.

Sowing and fertilization

On March 10 of 2016 and 2017, triads were sown in CON and AGR plots with traditional row spacing (every 70 cm) and in holes made with hoes. Maize (three seeds per hole), entangler bean (two seeds per hole), and squash (two seeds per hole, in a 4.2-m grid) were sown in the same row (Figure 1b). In order to keep the agroecological alternative as culturally relevant as possible for the AGR interspecific diversification treatments, the choice of crops to add to the triad and their dates and modes of planting were based on the local management of backyard cultivation that some farmers practice in the region. All seeds were locally obtained from farmers. The additional crops were sown between rows of the triad. For the tl and tlh plots, the black beans were sown (three seeds per hole) at the same time as the triad, in intermediate rows. On May 4, the faba beans (two seeds per hole) and peas (three seeds per hole) were alternately sown in the same intermediate rows, in between black beans (Figure 1b). Additionally, in tlh plots, chard (two seeds per hole) and coriander (three seeds per hole) were sown between maize and faba beans and between maize and peas, respectively (Figure 1b). Three weeks before planting, farmers with AGR plots prepared on-site a bokashi fermented fertilizer with stubble, sheep manure, ash, pulque (locally fermented agave drink as a source of microorganisms), soil and unrefined brown sugar. This fertilizer was instituted with the intent of adding nutrients in different degrees of fermentation, so as to release nutrients gradually and avoid loss by leaching and over-fertilization. During the sowing of the triad, 50 kg of bokashi fertilizer were applied per 10 × 10 m AGR subplot, equally distributed among all holes and on the seeds. Six weeks after the triad planting, bokashi fertilization was repeated, placing the same amount of fertilizer at the base of maize plants and then making a mound of soil around the adventitious roots. Local farmers call this practice *aterrada*. Subsequently, all sowings were superficially covered with a thin padding of dried and chopped straw to prevent soil loss, decrease soil water

Table 1. Mean nutrient input ± standard error per year for each type of management (AGR: agroecological management; CON: conventional management). Estimations per ha of inorganic fertilization were calculated based on the inputs for the entire piece of land reported by CON plot producers in interviews (n = 4), the reported content of nutrients per kg in the packaging of the used fertilizers, and the area of land (calculated with a GIS). Bokashi nutrient inputs were estimated from laboratory analyses of the bokashis, prepared by AGR plot owners (n = 12) who formulated them with maize stubble, sheep manure, ash, *pulque*, soil, and unrefined brown sugar.

	AGR	CON	
Nutrient	bokashi	Sheep manure	Inorganic fertilization
N-NH$_4^+$ (kg·ha^{-1}·yr^{-1})	0.72 ± 0.11	6.65 ± 1.11	427 ± 45.32†
N-NO$_3^-$ (kg·ha^{-1}·yr^{-1})	1.09 ± 0.20	24.88 ± 4.07	‡
P (kg·ha^{-1}·yr^{-1})	4.50 ± 0.41	19.66 ± 3.22	68.33 ± 24.88
K (kg·ha^{-1}·yr^{-1})	127.97 ± 5.40	342.20 ± 56.03	‡
Ca (kg·ha^{-1}·yr^{-1})	42.80 ± 1.70	11.42 ± 1.86	-
Mg (kg·ha^{-1}·yr^{-1})	27.49 ± 1.57	29.57 ± 4.83	-
OM (kg·ha^{-1}·yr^{-1})	3792.87 ± 127.08	6461.08 ± 1057.89	–
Org. C (kg·ha^{-1}·yr^{-1})	2200.04 ± 73.72	3746.90 ± 613.49	
Total C (kg·ha^{-1}·yr^{-1})	2302.12 ± 76.35	3839.95 ± 628.72	-
Total N (kg·ha^{-1}·yr^{-1})	130.75 ± 3.75	337.44 ± 61.80	-

OM: organic matter.
† In the form of ammoniacal nitrogen and urea.
‡Only one reported value (N-NO$_3^-$: 48.63 kg·ha^{-1}·yr^{-1}, K: 50.31 kg·ha^{-1}·yr^{-1}).

evaporation, and prevent weed germination (Stavi, Bel, and Zaady 2016). The usual application of sheep manure at the time of triad planting (approximately 87.73 kg per 10 × 10 m plot) and inorganic fertilizers during *aterrada* (approximately 4 kg N and 1.56 kg P per plot; Table 1) was maintained in CON plots. Both CON and AGR plot management was performed by plot owners in collaboration with the research team, who made weekly visits during the experiment.

To estimate nutrient contribution per hectare for each type of management, we performed chemical analyses on a compound sample of sheep manure provided by several producers, and on each of the twelve bokashi fertilizers applied during 2016 to the AGR plots (Table 1). Additionally, interviews of the owners of the CON plots provided us with information about the amount of sheep manure and the brand and amount of chemical fertilizer used by each producer for each plot. We then estimated the rate of application per hectare per AGR and CON plot for each nutrient, taking into account the manure and bokashi chemical analyses and application rates, the concentration of nutrients reported by each brand of fertilizer, and the reported chemical fertilizer input (Table 1).

Soil analysis

On three different sampling dates (October 21, 2016: Harvest I; January 12, 2017: Interharvest; and September 14, 2017: Harvest II), a soil sample was taken in the middle of each AGR subplot and CON plot with a 5 × 5 cm (diameter x height) PVC cylinder to determine the apparent density, and three large soil samples (500 g) were removed for chemical analyses. The large soil samples were taken with a shovel at a depth no greater than 15 cm, at maximum equidistant points from the soil density sample (avoiding a 2-m border strip) in order to form a composite soil sample. The following soil parameters were analyzed for each composite sample at each sampling time: (1) soil moisture; (2) pH (1:2 H_2O); (3) organic matter content, using the Walkley and Black method; (4) N-NO_3^- and N-NH_4^+ content, determined by KCl extraction distillation and titration (Anderson and Ingram 1993); (5) total C and N, using a Perkin Elmer analyzer (model 2400) for pyrolysis and infrared detection; (6) available P, using the Bray and Kurtz method; and (7) Ca, Mg and K exchange, using the ammonium acetate extraction method at pH 7 (Chapman 1965), followed by Ca and Mg quantification in a Varian atomic absorption spectrophotometer (model 240FS) and K quantification in a flame photometer (Corning model 410). Due to problems during the transfer of samples to the laboratory, the Harvest I soil samples were improperly stored at room temperature for 81 days. As a result, data on N-NO_3^- content for that sampling date were discarded.

Maize biomass and nutrient content in maize leaves

Harvest I took place on October 22, 2016 and Harvest II on September 8, 2017. In both harvests, three whole maize plants (except the roots) were collected from each CON plot and AGR subplot in a zig-zag pattern (Ion et al. 2014). The plant material was dried at 70°C for 72 hours, and the total dry weight of stover and grain were separately determined and averaged for the three plants. Grain yield and maize plant biomass per ha were estimated in order to compare productivity with other studies. The extrapolation was based on the fact that each maize plant and its surrounding space covers 1.5 m^2 (i.e. 1.5% of an AGR sampling plot or CON subplot). On average, the coefficient of variation (CV) between the biomasses of the three sampled plants per plot/subplot per sampling date was 60% for grain and 40% for stover. Plant nutrient analyses were carried out on a homogenized mixture of all maize leaves (including stalk-emerging and ear-covering leaves) from the three plants per plot or subplot. The mixture was pulverized prior to digestion with 65% nitric acid and 70% perchloric acid (Allan 1971). P was quantified by colorimetry with vanado-molybdate, and quantification of C, N, Ca and Mg was performed with the same procedures as used for soil.

Mycorrhizal colonization in maize roots

The roots of five plants were collected for treatment in both harvests (Cervantes-Gámez et al. 2021), with the exception of subplots containing the maize mixture, since it was not possible to determine the maize morphotype of these roots. The roots were immediately stored in 50% ethyl alcohol. In the laboratory, the roots were cut into 2-cm segments and then treated with 10% potassium hydroxide at 120°C for 15 minutes, according to the method from Phillips and Hayman (1970). Subsequently, the roots were rinsed three times with distilled water, placed in 1% hydrochloric acid for one minute to clarify them, and transferred to 0.05% trypan blue solution (diluted in lactoglycerol) for 3.5 hours. Mycorrhizal colonization was estimated by the quadrant intersection method (Giovannetti and Mose 1980), using approximately 50 root segments per plant (for a total of 250 root segments per treatment) and a Leica EZ4 D stereoscopic microscope.

Soil concentration of infective AM fungi propagules

The concentration of infective AM fungi propagules in soils was estimated using the Most Probable Number method (MPN; using a method from Porter (1979) and modified by Bagyaraj and Stürmer 2008). The tl diversification treatment was excluded from this analysis in order to reduce costs and greenhouse space. During the Interharvest period (April 6, 2017), three large soil samples (similar to those taken for chemical analyses) were collected at equidistant points from each CON plot and AGR subplot. Subsequently, soil mixtures were formed with the three samples, sieved with a 2-mm^2 mesh opening, and dried at room temperature. For each soil mixture, four dilutions were used (from 10^{-1} to 10^{-4}), with a 1:9 dilution ratio of sand and sterile vermiculite (1:1). In this experiment, we used local white maize seeds (obtained from 12 local producers and mixed together) with an average viability of 97%. The seeds were disinfected with 10% sodium hypochlorite for 10 minutes and rinsed three times with distilled water. For each dilution level, five replicates were established in polypropylene rhizocones (220 cm^3) with 100 g of the corresponding dilution. Two seeds were sown per rhizocone, and thinning was performed when the plants reached a height of 10 cm so as to leave one plant per rhizocone. Replicates were randomly distributed on tables and randomly repositioned every two weeks in a greenhouse whose temperature fluctuated between 25 and 45°C. Every third day, irrigation was performed with distilled water under a field capacity of approximately 60%. From the second to the fifth week, plants were treated with 30 mL of Long Asthon nutrient solution (Hewitt 1966) adjusted to pH 6 and modified for a P concentration of 10 $\mu g \cdot mL^{-1}$. After six weeks, the roots were harvested and preserved in 50% ethyl alcohol so as to follow the same clarification and staining method described for mycorrhizal colonization. In this case, the magnified intersection method (McGonigle et al. 1990) was performed on 10 root segments to record the presence or absence of fungal structures (hyphae, arbuscules or spores) in each plant. Fifty fields per individual were observed with the 10X objective of a light microscope (Leica LAS EZ4). The MPN per gram of soil was determined using the spreadsheet system from the US Food and Drug Administration (FDA. Food and Drug Administration 2010), which takes into account the imbalance in the number of replicates at the end of the experiment resulting from any plant senescence.

Statistical analyses

We used mixed linear models to test the effects of experimental treatments on soil properties, the chemical composition of leaves, stover and grain dry biomass of maize, mycorrhizal colonization and MPN. The fixed factors were: 1) period (Harvest I and Harvest II, except for soil properties where Interharvest was also included); 2) management type (AGR or CON); 3) interspecific diversification (t, tl and tlh); and 4) intraspecific diversity (red, white, yellow, black and mixed maize). The random factors were subplots nested within plots. Only second-order interactions were tested. Given the incomplete factorial design, the interaction between management type and diversification treatments was not available. Soil nutrient values (Ca, Mg, K, NO_3 and P) were square root-transformed to achieve normality of the residuals. The models were adjusted using maximum likelihood, and the saturated model was simplified using a "both ways" strategy, in which the models with and without each factor were compared using an analysis of variance, and if the variance explained by the simplified model was not significantly lower, the factor was removed from the model. Finally, only models whose Akaike Information Coefficient (ΔAIC) differed from the null model (i.e. the variable explained by its mean) by less than −5 were considered plausible (Richards 2015). A Likelihood ratio test was performed on the chosen model using maximum likelihood and then readjusted with restricted maximum likelihood to estimate parameters and confidence intervals (Bolker 2015). Treatment contrasts were used in order to detect differences between levels of the factors included in the model (Crawley 2013). All analyses were performed in the R 3.4.2 environment (R Core Team, Viena, Austria) with the nlme package (Pinheiro et al. 2017). The intraspecific diversification factor is not shown in the statistical results (Table 2) since it was not retained in the final models after stepwise simplification, as a result of its low explanatory power.

Results

The soil pH in the AGR plots was greater than 5 in the three sampling periods, while in the CON plots the pH was greater than 5 only during the Interharvest (Table 2, Figure 2a). The concentrations of K, Ca and Mg increased respectively by 132%, 188% and 138% in the soil of AGR plots as compared to the CON plots (Table 2, Figure 2b-d), whose Interharvest soil conditions were equivalent to AGR plots prior to the experiment (Supplementary Material). Within CON, the concentration of N in maize leaves rose by 26% between

Table 2. Summary of mixed linear models.

Dependent variable	Random conditional modes	Period F-value	Management F-value	InterD F-value	Period×Manag F-value	Period×InterD F-value	Δ AIC	L-Ratio
Soil								
Moisture	σ_a^2: 2.99 σ^2: 149.33	$F_{(2,58)}$: 18.97***	ni	ni	ni	ni	−27.02	31.02***
Bulk density	σ_a^2: 0.0009 σ^2: 0.0049	$F_{(2,58)}$: 4.89*	ni	ni	ni	ni	−5.35	9.35**
pH	σ_a^2: 0.18 σ^2: 0.18	$F_{(2,56)}$: 33.608***	$F_{(1,16)}$: 6.52*	ni	$F_{(2,56)}$: 3.427*	ni	−46.77	56.77***
P	σ_a^2: 2.47×10^{-10} σ^2: 0.3249	$F_{(2,58)}$: 17.17***	ni	ni	ni	ni	−24.73	28.73***
K	σ_a^2: 6.22×10^{-12} σ^2: 0.0196	$F_{(2,58)}$: 10.98***	$F_{(1,16)}$: 7.85*	ni	ni	ni	−20.83	26.83***
Ca	σ_a^2: 0.1225 σ^2: 0.1296	ni	$F_{(1,16)}$: 4.56*	ni	ni	ni	−2.53	4.53*
Mg	σ_a^2: 0.0049 σ^2: 0.0324	ni	$F_{(1,16)}$: 5.84*	ni	ni	ni	−3.62	5.62*
NO_3^-	σ_a^2: 8.48×10^{-5} σ^2: 1.2978	$F_{(1,27)}$: 51.44***	ni	$F_{(2,15)}$: 2.75	ni	$F_{(2,27)}$: 7.94**	−38.30	48.30***
Chemical composition of maize leaves								
C	σ_a^2: 2.4649 σ^2: 146256612	$F_{(1,29)}$: 21.41***	ni	ni	ni	ni	−15.88	17.88***
N	σ_a^2: 125103.69 σ^2: 3031255.1	$F_{(1,29)}$: 10.04**	$F_{(1,14)}$: 2.59	$F_{(2,14)}$: 2.46	$F_{(1,26)}$: 5.04*	$F_{(2,26)}$: 7.35**	−17.81	31.81***
P	σ_a^2: 18060.67 σ^2: 213767.52	$F_{(1,29)}$: 9.78**	ni	ni	ni	ni	−6.76	8.76**
K	σ_a^2: 1.3456 σ^2: 3461720.72	$F_{(1,29)}$: 290.41***	$F_{(1,16)}$: 5.02*	ni	ni	ni	−93.60	97.60***
Ca	σ_a^2: 0.0064 σ^2: 1140324.98	$F_{(1,29)}$: 29.73***	$F_{(1,16)}$: 6.51*	ni	ni	ni	−24.68	28.68***
Mg	σ_a^2: 0.0049 σ^2: 96180.62	$F_{(1,29)}$: 9.23**	ni	ni	ni	ni	−6.52	8.52**
Maize productivity								
Stover biomass	σ_a^2: 2.59×10^{-14} σ^2: 0.0144	$F_{(1,29)}$: 9.86**	ni	ni	ni	ni	−7.15	9.15**

(*Continued*)

Table 2. (Continued).

Dependent variable	Random conditional modes	Period F-value	Management F-value	InterD F-value	Period×Manag F-value	Period×InterD F-value	Δ AIC	L-Ratio
Grain biomass	σ_a^2: 0.000036 σ^2: 0.0016	$F_{(1,27)}$: 41.39***	ni	ni	ni	ni	−29.61	31.61***
Arbuscular mycorrhizal fungi								
Colonization	σ_a^2: 12.1801 σ^2: 108.5764	$F_{(1,17)}$: 47.31***	$F_{(1,16)}$: 7.70*	ni	ni	ni	−29.80	33.80***
MPN	σ_a^2: 0.00006724 σ^2: 20724.4816	na	$F_{(1,11)}$: 1.53	$F_{(1,11)}$: 0.02	na	na	-	-

InterD: interspecific diversification; Manag: management (AGR and CON levels).

'Random conditional modes' represents the variance estimates between and within the random factor levels in mixed models (σ^2_a: variance between plots, σ^2: variance within plots).

F-values are presented with their level of significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

L-ratio: Likelihood ratio.

ni: not included in the model after stepwise simplification; na: not applicable.

Period factor had three levels (Harvest I, Interharvest and Harvest II) for soil variables, and two levels (Harvest I and Harvest II) for chemical composition of maize leaves, maize productivity, and arbuscular mycorrhizal fungi.

The Intraspecific diversification factor is not presented since it was never included in the final model after stepwise simplification.

Harvest I and II, so that it was 17% higher under this management than in AGR, which remained unchanged between harvests (Table 2, Figure 2e). The K concentration in maize leaves was 22% higher under AGR than under CON (Table 2, Figure 2f). Conversely, the Ca concentration in leaves was 23% higher under CON than in AGR (Table 2, Figure 2g). The AM fungi

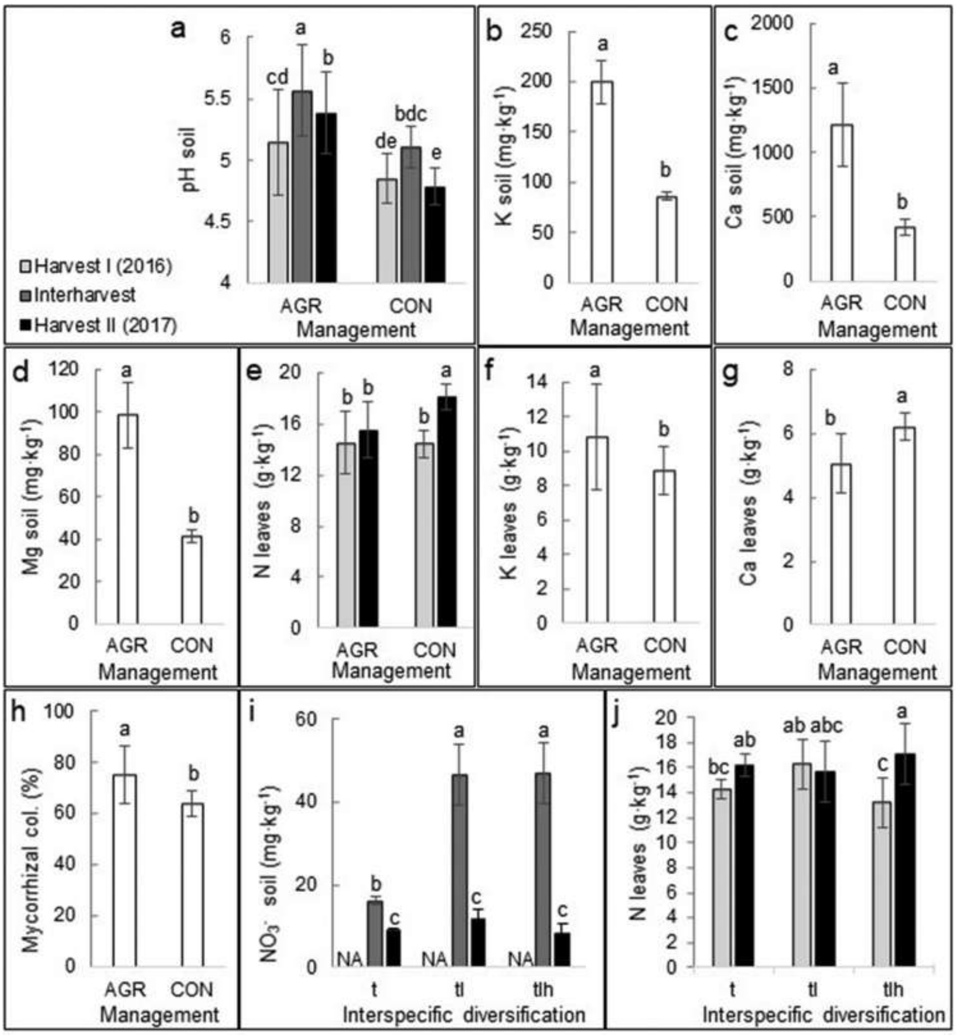

Figure 2. Responses of soil characteristics (a-d and i), mycorrhizal colonization of maize roots (h), and nutrient content in maize leaves (e-g and j) to the different experimental treatments. Data are presented as mean ± standard error. AGR: agroecological management; CON: conventional management; t: maize, entangler bean and squash; tl: t + black bean, faba bean and pea; and tlh: tl + chard and coriander. Different letters denote significant differences according to *treatment contrasts* (see section 2.8). a, e, i and j show the simultaneous effects of sampling date and management or interspecific diversification factors, since these factors had significant interactive effects (see Table 2). NA: not available.

colonization in maize roots was 11% higher under AGR than in CON (Table 2, Figure 2h). However, MPN and maize productivity (grain and stover biomass) did not differ significantly between management strategies (Table 2).

Within AGR, soil availability of NO_3- benefited from interspecific diversification. During Interharvest, the concentration of NO_3^- was 188% higher in tl than in t, and 189% higher in tlh than in t. In contrast, before the experiment started (Supplementary Material) and in Harvest II, no significant differences were found between AGR plots (Table 2, Figure 2i). The concentration of N in maize leaves was also temporarily affected by interspecific diversification. In Harvest I, the N concentration was 23% higher in tl than in tlh, whereas this concentration was similar between the three treatments in Harvest II (Table 2, Figure 2j). On the other hand, within tlh, this concentration was 30% higher in Harvest II than in Harvest I (Figure 2j).

Intraspecific diversification was not included in any of the final models due to its limited explanatory power (i.e. models that included it as a factor were eliminated in the stepwise simplification process). Maize productivity (grain and stover biomass) and MPN did not differ between interspecific diversification treatments (Table 2). During the experiment, some soil and plant variables only showed significant differences between sampling dates. Finally, whereas moisture, soil P availability, and the concentrations of C, P and Mg in maize leaves increased with sampling date, soil bulk density and maize productivity (stover and grain) decreased (Tables 2 and 3).

Discussion

Effect of agroecological management

This study demonstrates that within a two-year time frame, AGR implementation can improve pH, the soil availability of K, Ca and Mg, the content of K in leaves, and mycorrhizal colonization in maize roots as compared to CON plots. Before our study, we predicted that AGR would also improve the physical properties of the soil. However, the percentage of moisture and bulk density were similar between the two management types. Changes in these properties may require the accumulation of organic matter in the soil, which did not take place in our plots; in contrast, this has been reported in farms with at least three years of organic management (Celik, Ortas, and Kilic 2004; Thomazini et al. 2015).

Mountainous soils tend to have naturally low pH, which limits nutrient availability to plants through the adhesion of exchange cations (Ca^{2+}, K^+, Mg^{2+}) to the surface of clays and organic matter by protons (H^+) in the soil solution (Masood and Bano 2016). The transformation of our experimental plots to AGR increased the pH on average by 0.2 units for the first harvest (from pH 4.9 to 5.1), and by 0.6 units for the second harvest (from pH 4.8 to

Table 3. Mean ± standard error of the variables affected by the period. All plots are averaged regardless of the management treatment implemented.

Criteria	Variable	Harvest I	Interharvest	Harvest II
Soil	Moisture (%)	74.03 ± 3.37b[†]	76.55 ± 6.59b	91.99 ± 6.59a
	Bulk density (g·cm^{-3})	0.67 ± 0.02a	0.61 ± 0.03b	0.65 ± 0.03ab
	pH	5.04 ± 0.1 c	5.42 ± 0.15a	5.22 ± 0.15b
	P (mg·kg^{-1})	1.28 ± 0.07b	1.58 ± 0.23b	3.76 ± 0.23a
	K (mg·kg^{-1})	125.12 ± 3.91b	211.14 ± 7.82a	144.67 ± 7.82b
	NO_3^- (mg·kg^{-1})	121.46 ± 0.84a	29.29 ± 2.76b	9.05 ± 2.76 c
Chemical composition of maize leaves	C (g·kg^{-1})	421.37 ± 2.49b	-	435.82 ± 5.75a
	N (g·kg^{-1})	14.55 ± 0.50b	-	16.08 ± 1.09a
	P (g·kg^{-1})	1.79 ± 0.15b	-	2.16 ± 0.28a
	K (g·kg^{-1})	6.22 ± 0.52b	-	14.41 ± 1.02a
	Ca (g·kg^{-1})	6.12 ± 0.28a	-	4.62 ± 0.57b
	Mg (g·kg^{-1})	1.95 ± 0.07b	-	2.19 ± 0.15a
Maize productivity	Stover biomass (g·plant^{-1})	390 ± 20a	-	300 ± 50b
	Grain biomass (g·plant^{-1})	120 ± 10a	-	50 ± 20b
AM fungi	Colonization (%)	83.27 ± 3.07a	-	59.38 ± 6.81b

-: Interharvest period was only available for soil properties since plots at that time had no growing maize plants.
†Different letters denote significant differences according to *treatment contrasts* (see section 2.8).

5.4). Reyna-Ramírez et al. (2018) found the same increase in pH (0.6 units) after two years of organic fertilization in *milpas*. Experiments with at least five years of organic fertilization show that the increase in pH and nutrients correlates with the accumulation of available organic matter (Clark et al. 1998; García et al. 1989). In our case, there were no differences in the amount of organic matter in the soil, so it is more likely that the increase in pH observed in AGR plots was the result of the nearly fourfold contribution of Ca by bokashi as compared to sheep manure, the sole external source of Ca in CON. This high Ca input could also explain the increased availability of this particular nutrient in the soil, which could have had a buffering effect similar to that achieved by liming (Hargreaves, Adl., and Warman 2008; Rowley, Grand, and Verrecchia 2018). Increasing the pH in acidic soils is usually favorable as it improves conditions for microbial decomposition (Rowley, Grand, and Verrecchia 2018). Furthermore, the essential plant nutrients are known to have an acceptable availability between pH 5.5 and 6.5 (Taiz and Zeiger 2010). As expected, the pH increase observed in our AGR plots was accompanied by an increase in the availability of K, Ca and Mg. Although there was generally a greater nutrient input in CON plots as compared to AGR plots, the increased availability of K, Ca and Mg in AGR plots points to the efficiency of bokashi as a fertilizer. Indeed, bokashi probably added nutrients in different degrees of decomposition by releasing nutrients more gradually, thereby avoiding losses by leaching. In particular, sustained long-term Ca release is important because it contributes to the stabilization of soil organic carbon by aggregating small organic matter molecules (Iskrenova-Tchoukova, Kalinichev, and Kirkpatrick 2010). However, the expected accumulation of organic matter necessary to promote the release of P is likely to require more than two years of agroecological management (Yang, Chen, and Yang 2019).

By increasing the availability of nutrients in the soil of AGR plots, we expected the concentration of maize leaves to increase as well. However, this only occurred with K. It is possible that the plants favored the absorption of K when its availability increased in the soil, since plants have a greater requirement for K than Ca or Mg. For example, the optimal range of K in maize leaves at initial silking is [19.0–25.0 g·kg^{-1}], as compared to [2.1–10.0 g·kg^{-1}] for Ca and [1.6–6.0 g·kg^{-1}] for Mg (Rogovska et al. 2014). When K is deficient, plants absorb more Ca in order to maintain their osmotic balance (Conn and Gilliham 2010). For this reason, the plants in our study may have absorbed more K than Ca, despite the increase of both in AGR. Followed by N and P, K is considered to be one of the most limiting nutrients for plant growth (Wang et al. 2013). Since K ions reduce the formation of reactive oxygen species that cause cell damage under stressful conditions (Cakmak 2005), the improved K absorption under AGR could be important for counteracting the adverse effects of biotic and abiotic stresses.

The increased N concentration in Harvest II maize leaves could be due to the high inorganic N input of CON (Altieri, Ponti, and Nicholls 2012). Morales, Perfecto, and Ferguson (2001) found an 11% difference between leaves with organic and inorganic fertilization, two months after maize planting (i.e. an increase from 26.7 to 29.7 g·kg^{-1}). In our case, we observed a 16% difference (from 15.5 to 18.1 g·kg^{-1}). However, no correlation with grain yield was found in either case.

Contrary to what we expected, maize productivity was not higher with AGR management. We found that the annual amount of inorganic N entering our study site through CON is very high (427 kg N·ha^{-1}) as compared to the amount used in *milpas* from other regions (Morales, Perfecto, and Ferguson 2001, 243 kg N·ha^{-1}; Flores-Sánchez et al. 2011 , 121 kg N·ha^{-1}; Reyna-Ramírez et al. 2018, 186 kg N·ha^{-1}). Fertilization levels in Ocotepec were similar to those reported in maize crops with wheat in the irrigated area of northwest China (450 kg N·ha^{-1} per year), where water contamination from nitrate leaching has been reported (Zhang and Li 2003). Considering that productivity was equivalent between CON and AGR despite the higher N input in CON, a considerable proportion of inorganic N was likely lost through nitrate leaching. It has already been reported that the use of inorganic fertilizers in mountains with high precipitation does not raise productivity, since the nutrients are lost through leaching and surface runoff (Koerselman and Meuleman 1996). Therefore, organic nitrogen sources are convenient for these ecosystems since they release N more slowly. It is thus possible that nitrogen fixation by leguminous crops in the tl and tlh treatments contributed to the delayed input of this nutrient, as NO_3^- was higher in the Interharvest soil of these interspecific diversification treatments, possibly sustaining its availability for plants in the following cycle. The lack of difference in maize productivity between AGR and CON could have also resulted from a deficiency in other nutrients besides N in the two management strategies. In particular, the P content in the soils of Ocotepec plots (≈2-8 $mg{\cdot}kg^{-1}$) was less than half of the reported value for other *milpas* (≈16-190 $mg{\cdot}kg^{-1}$; Aguirre-von-wobeser et al. 2018; Lambert and Arnason 1986; Moreno-Espíndola et al. 2018). Productivity in these other *milpas* was also higher (≈2,500–10,000 $kg{\cdot}ha^{-1}$) as compared to Ocotepec (≈2,300 $kg{\cdot}ha^{-1}$). It is possible then that after two years, AGR plots were as *P*-deficient as CON plots, therefore keeping maize productivity low.

Our prediction that the potential for mycorrhizal inoculum would be greater in AGR was supported by an 11% increase in mycorrhizal colonization in maize roots, but not by MPN. Bilalis and Karamanos (2010) also found in a two-year experiment that zero tillage and organic fertilization increased mycorrhizal colonization by 19%. However, given that MPN did not change in the 13 months after the introduction of AGR (suggesting that soil inoculum is not affected by changes in short-term management practices), it is likely that mycorrhizal colonization was strengthened by the gradual release of bokashi nutrients and the cessation of tillage. Even in the absence of any yield increase, AM fungi may have contributed to the reduced nutrient losses and the increased K acquisition by maize plants in AGR (Rillig et al. 2019).

Effects of intra- and interspecific diversification

Crop diversification, which is traditionally present in *milpas* and other polyculture systems, has been proposed as one of the key strategies needed to simultaneously achieve family food security and soil conservation (Lin 2011). However, experimental evidence supporting this link is scarce, particularly in the context of real farm conditions (Bowles et al. 2020; Hatt et al. 2018). Although we predicted that nutrient concentration would be positively associated with crop enrichment, only the NO_3^- concentration during Interharvest was increased by the addition of legumes (i.e. black beans, faba beans and peas). This suggests a higher nitrification rate associated with the decomposition of leguminous stubble in the tl and tlh treatments (Herridge, Peoples, and Boddey 2008; O'Connor et al. 2010). This pattern may not have been observed in Harvest II due to NO_3^- leaching, due to the occurrence of unusually heavy rains (Benoit et al. 2015). Although there was an interspecific diversification effect regarding the concentration of N in maize leaves, it was not expected according to the pattern of NO_3^-availability. In addition, there was a higher concentration of N in the leaves of the tl treatment as compared to the tlh treatment in Harvest I. This difference could be due to the initial competition for N between maize and additional leafy greens. However, the absence of this difference in Harvest II suggests that after one year the increase in soil NO_3^- by additional legumes reduced the competition for N absorption. The nutrient acquisition by primary crops can vary depending on the environmental conditions and functional attributes of the associated crops (Andersen et al. 2007). For example, using a legume species such as *Vicia villosa* Roth as a cover crop could increase the acquisition of N and P in maize more than cover consisting of a diverse group of crops (Njeru et al. 2014).

Although we initially predicted that interspecific diversification would promote mycorrhizal colonization, MPN and maize productivity, our results do not support this idea. Mycorrhizal colonization is a complex and seasonally dynamic process whose estimation in a phenological phase of the host plant could offer incomplete descriptions in comparison to phenological follow-up (Kabir et al. 1998; Tian et al. 2011). For example, Njeru et al. (2014) found that the use of legumes as cover crops can increase mycorrhizal colonization in roots of the juvenile phase of maize (~17-24 days old), but not in the maturation phase. In our study, the percentage of colonization corresponding to the maize fruiting phase was not affected by interspecific diversity, contrary to what has previously been reported in *milpas* (Negrete-Yankelevich et al. 2013a). The exposure time to diversification in our study may not have been sufficient to transform the mycorrhizal community and the infective propagule pool (MPN) in the soil. In contrast, the plots compared in Negrete-Yankelevich et al. (2013a) were managed with associated crops over a long time period, allowing for the establishment of a differentiated mycorrhizal community. It is also important to note that we chose diversification based on legumes and leafy greens grown in the area, in order to determine if their addition could improve food production for local consumption. However, crop identity can have a fundamental effect on soil conditions and the efficiency of the primary crop (Njeru et al. 2014), indicating that our inferences are restricted to the choice of such crops.

Interestingly, Sangabriel-Conde et al. (2014) reported differences in mycorrhizal colonization, P absorption, and biomass between traditional polycultures with different maize morphotypes. In contrast, none of the intraspecific diversification treatments in our work (i.e. maize identity or mixing of morphotypes) had enough explanatory power to be included in the final models. The recently discovered low-genetic differentiation between morphotypes from Ocotepec (Leyva-Madrigal et al. 2020) could possibly explain this unexpected homogeneity.

Sampling period effect

The differences in soil properties between the three periods, and in mycorrhizal colonization, maize biomass, and chemical composition of maize leaves between harvests, were likely caused by intra- and inter-annual climatic variation as well as a premature harvest in the second year, which occurred 37 days earlier than usual due to Hurricane Katia. The coincidence between rainy period and sampling period could explain the changes in soil moisture and P and NO_3^- concentrations, due to the flush effects of atypical rains favoring the disintegration and mineralization of the P organic fraction (Oehl et al. 2004) and nitrate runoff (Benoit et al. 2015; Reyna-Ramírez et al. 2018).

Limitations and future directions

Agrodiversity is essential for subsistence agroecosystems, since the consumption of different crops provides a nutritional advantage to poor rural families, given the diversification of their diet (Frison, Cherfas, and Hodgkin 2011). Moreover, a differentiated harvest of crops reduces seasonal food insecurity (Falkowski et al. 2019). We did not estimate the yield of companion crops or the rate of their consumption by farmers' families in this study. However, Lopez-Ridaura et al. (2021) reported an association between crop diversification in *milpas* and family consumption of a more diverse diet, which in turn has been shown to provide a nutritional advantage (Frison, Cherfas, and Hodgkin 2011; Oyarzun et al. 2013). In our study, the diversification of *milpas* probably promoted a win-win situation. Specifically, maize productivity was not diminished by the existence of additional crops and there was increased soil nutrient availability and mycorrhizal colonization, suggesting the efficient use of resources in the soils. Consequently, additional edible crops became available for consumption by the farmers. However, our estimation of maize yield was extrapolated for each plot or subplot from three plants (1.5% of the total), and there was substantial variability in grain ($\overline{CV} = 60\%$) and stover ($\overline{CV} = 40\%$) biomass among these plants. Therefore, the lack of statistical difference in productivity may have been influenced by the small sample size relative to the high variability. Nevertheless, our result is consistent with other studies that reported an equal or greater total yield in agroecosystems with two or three associated crops in comparison to monocultures under the same conditions (Li et al. 1999; Molina-Anzures et al. 2016; Reyna-Ramírez et al. 2018). Furthermore, one recent meta-analysis has shown that agricultural diversification also promotes ecosystem services (such as biodiversity conservation, pollination, pest control and nutrient cycling) without compromising crop yield (Tamburini et al. 2020).

Smallholder agriculture also plays a fundamental role in the conservation of crop genetic diversity for humanity. A large pool of germplasm enables domesticated plants to adapt to environmental change (Isakson 2009), thereby securing future food supplies. It has therefore been suggested that agricultural policies should be developed that prioritize the resilience of food systems, which involves valuing and protecting the most vulnerable smallholders and the diversity of their plant resources (Stratton, Kuhl, and Blesh 2020). In the case of Ocotepec families (and many others in Mexico), inorganic fertilizers are often supplied by local government programs or political organizations (personal observation), and are thus preferred by farmers since they don't incur costs. In particular when organic matter is not replenished, the subsidizing of urea is a problem for soil quality and health, because excessive N is introduced, provoking an unbalanced availability of nutrients (Flores-Sánchez et al. 2015). Our study shows that including interspecific diversification with AGR could be a more sustainable alternative for local governments and organizations to support, since it could improve the diversity of available food while improving soil conditions, even in the absence of inorganic fertilization. If farmers had to purchase all of the supplies needed to produce bokashi, then the monetary cost of organic fertilization would be 20% higher than the cost of conventional fertilization. However, if farmers used their own sheep manure to make bokashi, then the costs would be 58% lower than conventional fertilization, making this alternative more economically attractive for government programs as well as farmers.

Conclusion

This study provides evidence that AGR can be equally or more efficient in its use of soil resources than CON with a high addition of inorganic nitrogen. In just two years, agroecological management improved pH, the soil availability of K, Ca and Mg, K absorption, and mycorrhizal colonization in maize. The addition of legumes and leafy greens to AGR temporarily increased the availability of NO_3^- in the soil, a strategy that could potentially increase the availability of foods rich in protein and vitamins (black beans, faba beans, pea, chard and coriander) for *milpa*-producing families.

Availability of Data and Material

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Acknowledgments

We would like to specially thank Frédérique Reverchon and Rocío Vega-Frutis who reviewed early versions of this manuscript, to Salvador González-Arroyo and Marisol González-Arroyo for field assistance, Alicia Fierro-Coronado, Sandra Rocha-Ortíz and Omar Lázaro-Castellanos for their laboratory assistance, to Emily J. Wolfe-Sherrie for the translation of the manuscript and to Ocotepec producers for their help and trust, because without them, this study would not have been possible. We are also grateful to two anonymous reviewers who's suggestions greatly improved this manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work is part of the DeMano Project supported by National Problems (CONACyT-80033) and Veracruzano Environmental Fund (Fondo Ambiental Veracruzano F.A.V./006/2016</#AWARD-ID;>). The work was part of a master's degree funded by a postgraduate scholarship from the National Council of Science and Technology of Mexico (CONACYT (CONACYT-450579);Consejo Nacional de Ciencia y Tecnología [450579,80033];

ORCID

Yeimi D. Martínez-Camacho http://orcid.org/0000-0002-1818-2397
Simoneta Negrete-Yankelevich http://orcid.org/0000-0002-4429-6662
Ignacio E. Maldonado-Mendoza http://orcid.org/0000-0001-9952-1508
Alejandra Núñez-de la Mora http://orcid.org/0000-0002-1609-0771
Guadalupe Amescua-Villela http://orcid.org/0000-0002-0984-2883

References

Aguirre-von-wobeser, E., J. Rocha-Estrada, L. R. Shapiro, M. de La Torre, and L. Brusetti. 2018. Enrichment of verrucomicrobia, actinobacteria and burkholderiales drives selection of bacterial community from soil by maize roots in a traditional milpa agroecosystem. *PLoS ONE* 13 (12):e0208852. doi:10.1371/journal.pone.0208852.

Allan, J. E. 1971. *The preparation of agricultural samples for analysis by atomic absorption spectroscopy*. California: Varian Techtron.

Altieri, M. A., L. Ponti, and C. I. Nicholls. 2012. Soil fertility, biodiversity and pest management. In *Biodiversity and insect pests: Key issues for sustainable management*, ed. G. M. Gurr, S. D. Wratten, E. Snyder, and D. M. Y. Read, 72–84. John Wiley & Sons, Ltd.

Altieri, M. A., and V. M. Toledo. 2011. The agroecological revolution in Latin America: Rescuing nature, ensuring food sovereignty and peasants. *The Journal of Peasant Studies* 28 (3):587–612. doi:10.1080/03066150.2011.582947.

Andersen, M. K., H. Hauggaard-Nielsen, J. Weiner, and E. S. Jensen. 2007. Competitive dynamics in two- and three- component intercrops. *Journal of Applied Ecology* 44 (3):545–51. doi:10.1111/j.1365-2664.2007.01289.x.

Anderson, J. M., and J. S. I. Ingram. 1993. *Tropical soil biology and fertility: A handbook of methods*. second ed ed. Wallingford: CAB International.

Bagyaraj, J. D., and S. L. Stürmer. 2008. Arbuscular mycorrhizal fungi (AMF). In *A handbook of tropical soil biology: Sampling and characterization of below-ground biodiversity*, ed. F. M. S. Moreira, E. J. Huising, and D. E. Bignell, 131–43. UK and USA: Earthscan.

Benoit, M., J. Garnier, G. Billen, J. Tournebize, E. Gréhan, and B. Mary. 2015. Nitrous oxide emissions and nitrate leaching in an organic and a conventional cropping system (Seine basin, France). *Agriculture Ecosystems and Environment* 213:131–41. doi:10.1016/j.agee.2015.07.030.

Bilalis, D. J., and A. J. Karamanos. 2010. Organic maize growth and mycorrhizal root colonization response to tillage and organic fertilization. *Journal of Sustainable Agriculture* 34 (8):836–49. doi:10.1080/10440046.2010.519197.

Bolker, B. M. 2015. Linear and generalized linear mixed models. In *Ecological statistics contemporary theory and application*, ed. G. A. Fox, S. Negrete-Yankelevich, and J. V. Sosa, 309–33. Oxford: Oxford University Press.

Bowles, T. M., M. Mosshammer, Y. Socolar, F. Calderón, M. A. Cavigelli, S. W. Culman, W. Deen, C. F. Drury, A. García, Y. García, et al. 2020. Long-term evidence shows that crop-rotation diversification increases agricultural resilience to adverse growing conditions in North America. *One Earth* 2 (3):284–93. doi:10.1016/j.oneear.2020.02.007.

Brown, C. H., C. R. Clement, P. Epps, E. Luedeling, and S. Wichmann. 2014. The paleobiolinguistics of maize (*Zea mays* L.). *Ethnobiology Letters* 5:52–64. doi:10.14237/ebl.5.2014.130.

Byar, D. P., A. M. Herzberg, and W. Y. Tan. 1993. Incomplete factorial designs for randomized clinical trials. *Statistics in Medicine* 12 (17):1629–41. doi:10.1002/sim.4780121708.

Cakmak, I. 2005. The role of potassium in alleviating detrimental effects of abiotic stresses in plants. *Journal of Plant Nutrition and Soil Science* 168 (4):521–30. doi:10.1002/jpln.200420485.

Celik, I., I. Ortas, and S. Kilic. 2004. Effects of compost, mycorrhiza, manure and fertilizer on some physical properties of a Chromoxerert soil. *Soil & Tillage Research* 78 (1):59–67. doi:10.1016/j.still.2004.02.012.

Cervantes-Gámez, R. G., O. Peñuelas-Rubio, N. Araujo-Benard, R. A. Fierro- Coronado, D. Trejo-Aguilar, I. E. Maldonado-Mendoza, and J. D. Cordero-Ramírez. 2021. Diversity of arbuscular mycorrhizal fungi associated to volunteer maize plants in transition soils: Natural ecosystem - agricultural use. *Scientia Fungorum* 51:e1330. doi:10.33885/sf.2021.51.1330.

Chapman, H. D. 1965. Cation exchange capacity. In *Methods of soil analysis. Part 2. agronomy monograph no. 9*, ed. C. A. Black, 891–901. Madison, Wisconsin: American Society of Agronomy.

Clark, M. S., W. R. Horwath, C. Shennan, and K. M. Scow. 1998. Changes in soil chemical properties resulting from organic and low-input farming practices. *Agronomy Journal* 90 (5):662–71. doi:10.2134/agronj1998.00021962009000050016x.

Clawson, D. L. 1985. Harvest security and intraspecific diversity in traditional tropical agriculture. *Economic Botany* 39 (1):56–67. doi:10.1007/BF02861175.

CONAGUA. Comisión nacional del agua. data (2016 and 2017) from Estación Meteorológica Automática de Perote.

Conn, S., and M. Gilliham. 2010. Comparative physiology of elemental distributions in plants. *Annals Botany* 105:1081–102. doi:10.1093/aob/mcq027.

Crawley, M. I. 2013. *The R book*. John Wiley & Sons, Ldt. United Kingdom.

Falkowski, T. B., A. Chankin, S. A. W. Diemont, and R. W. Pedian. 2019. More than just corn and calories: A comprehensive assessment of the yield and nutritional content of a traditional Lacandon Maya milpa. *Food Security* 11 (2):389–404. doi:10.1007/s12571-019-00901-6.

FDA. Food and Drug Administration, 2010. BAM Appendix 2: Most probable number from serial dilutions. https://www.fda.gov/Food/FoodScienceResearch/LaboratoryMethods/ucm109656.htm/ (accessed 12 February 2018).

Ferrol, N., C. Azcón-Aguilar, and J. Pérez-Tienda. 2018. Review: Arbuscular mycorrhizas as key players in sustainable plant phosphorus acquisition: An overview on the mechanisms involved. *Plant Science* 280:441–47. doi:10.1016/j.plantsci.2018.11.011.

Flores-Sánchez, D., J. C. J. Groot, E. A. Lantinga, M. J. Kropff, and W. A. H. Rossing. 2015. Options to improve family income, labor input and soil organic matter balances by soil management and maize–livestock interactions. Exploration of farm-specific options for a region in Southwest Mexico. *Renewable Agriculture and Food Systems* 30 (4):373–91. doi:10.1017/S1742170514000106.

Flores-Sanchez, D., J. K. Koerkamp-Rabelista, H. Navarro-Garza, E. A. Lantinga, J. C. J. Groot, M. J. Kropff, and W. A. H. Rossing. 2011. Diagnosis for ecological intensification of maize-based smallholder farming systems in the Costa Chica, Mexico. *Nutrient Cycling in Agroecosystems* 91 (185):185–205. doi:10.1007/s10705-011-9455-z.

Frison, E. A., J. Cherfas, and T. Hodgkin. 2011. Agricultural biodiversity is essential for a sustainable improvement in food and nutrition security. *Sustainability* 3 (1):238–53. doi:10.3390/su3010238.

Fustec, J., F. Lesuffleur, S. Mahieu, and J. B. Cliquet. 2010. Nitrogen rhizodeposition of legumes. *A Review. Agronomy for Sustainable Development* 30 (1):57–66. doi:10.1051/agro/2009003.

Galvez, L., D. D. Douds, L. E. Drinkwater, and P. Wagoner. 2001. Effect of tillage and farming system upon VAM fungus populations and mycorrhizas and nutrient uptake of maize. *Plant and Soil* 228 (2):299–308. doi:10.1023/A:1004810116854.

García, C., C. E. Alvarez, A. Carracedo, and E. Iglesias. 1989. Soil fertility and mineral nutrition of a biodynamic avocado plantation in Tenerife. *Biological Agriculture and Horticulture* 6 (1):1–10. doi:10.1080/01448765.1989.9754497.

Giovannetti, M., and B. Mose. 1980. An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. *New Phytologist* 84 (3):489–500. doi;10.1111/j.1469–8137.1980.tb04556.x.

Gliessman, S. R. 2014. *Agroecology: The ecology of sustainable food systems*. Florida: CRC Press.

Groenewald, S. F., and M. Van Den Berg. 2012. Smallholder livelihood adaptation in the context of neoliberal policy reforms: A case of maize farmers in Southern Veracruz, Mexico. *The Journal of Development Studies* 48 (3):429–44. doi:10.1080/00220388.2011.615923.

Hargreaves, J. C., M. S. Adl., and P. R. Warman. 2008. A review of the use of composted municipal solid waste in agriculture. *Agriculture, Ecosystems & Environment* 123 (1–3):1–14. doi:10.1016/j.agee.2007.07.004.

Harinikumar, K. M., D. J. Bagyaraj, and B. C. Mallesha. 1990. Effect of intercropping and organic soil amendments on native VA mycorrhizal fungi in an oxisol. *Arid Soil Research and Rehabilitation* 4 (3):193–97. doi:10.1080/15324989009381248.

Hatt, S., F. Boeraeve, S. Artru, M. Dufrêne, and F. Francis. 2018. Spatial diversification of agroecosystems to enhance biological control and other regulating services: An agroecological perspective. *Science of the Total Environment* 621:600–11. doi:10.1016/j.scitotenv.2017.11.296.

Helgason, B. L., F. L. Walley, and J. J. Germida. 2010. No-till soil management increases microbial biomass and alters community profiles in soil aggregates. *Applied Soil Ecology* 46 (3):390–97. doi:10.1016/j.apsoil.2010.10.002.

Herridge, D. F., M. B. Peoples, and R. M. Boddey. 2008. Global inputs of biological nitrogen fixation in agricultural systems. *Plant and Soil* 311 (1–2):1–18. doi:10.1007/s11104-008-9668-3.

Hewitt, E. J. 1966. *Sand and water culture: Methods used in the study of plant nutrition, second ed. commonwealth agricultural Bureaux*. Farnham Royal.

Hinsinger, P., E. Betencourt, L. Bernard, A. Brauman, C. Plassard, J. Shen, X. Tang, and F. Zhang. 2011. P for two, sharing a scarce resource: Soil phosphorus acquisition in the rhizosphere of intercropped species. *Plant Physiology* 156 (3):1078–86. doi:10.1104/pp.111.175331.

Hodge, A., and A. H. Fitter. 2010. Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. *PNAS* 107 (31):13754–59. doi:10.1073/pnas.1005874107.

Ion, V., A. G. Băsa, G. Temocico, G. Dicu, L. I. Epure, and D. State. 2014. Maize plant biomass at different hybrids. *Plant Populations, Row Spacing and Soil Conditions. Romanian Biotechnological Letters* 19 (4):9543–52.

Isakson, S. R. 2009. No hay ganancia en la milpa: The agrarian question, food sovereignty, and the on-farm conservation of agrobiodiversity in the Guatemalan highlands. *The Journal of Peasant Studies* 36 (4):725–59. doi:10.1080/03066150903353876.

Iskrenova-Tchoukova, E., A. G. Kalinichev, and R. J. Kirkpatrick. 2010. Metal cation complexation with natural organic matter in aqueous solutions: Molecular dynamics simulations and potentials of mean force. *Langmuir* 26 (20):15909–19. doi:10.1021/la102535n.

Johansen, A., and E. S. Jensen. 1996. Transfer of N and P from intact or decomposing roots of pea to barley interconnected by an arbuscular mycorrhizal fungus. *Soil Biology and Biochemistry* 28 (1):73–81. doi:10.1016/0038-0717(95)00117-4.

Kabir, Z., I. P. O'Halloran, J. W. Fyles, and C. Hamel. 1998. Dynamics of the mycorrhizal symbiosis of corn (*Zea mays* L.): Effects of host physiology, tillage practice and fertilization on spatial distribution of extra-radical mycorrhizal hyphae in the field. Agriculture. *Ecosystems and Environment* 68 (1–2):151–63. doi:10.1016/S0167-8809(97)00155-2.

Koerselman, W., and A. M. Meuleman. 1996. The vegetation N: P ratio: A new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* 33 (6):1441–50. doi:10.2307/2404783.

Lambert, J. D. H., and J. T. Arnason. 1986. Nutrient dynamics in milpa agriculture and the role of weeds in initial stages of secondary succession in Belize. *C.A. Plant and Soil* 93 (3):303–22. doi:10.1007/BF02374282.

Leyva-Madrigal, K., P. Báez-Astorga, S. Negrete-Yankelevich, A., G. Nuñez-de La Mora, Amescua-Villela, I. E. Maldonado-Mendoza, and G. Amescua-Villela. 2020. Maize genetic diversity in traditionally cultivated polycultures in an isolated rural community in Mexico: Implications for management and sustainability. *Plant Ecology & Diversity* 13 (1):15–28. doi:10.1080/17550874.2019.1708985.

Li, L., S. Yang, X. Li, F. Zhang, and P. Christie. 1999. Interspecific complementary and competitive interactions between intercropped maize and faba bean. *Plant and Soil* 212 (2):105–14. doi:10.1023/A:1004656205144.

Lin, B. B. 2011. Resilience in agriculture through crop diversification: Adaptative management for environmental change. *BioScience* 61 (3):183–93. doi:10.1525/bio.2011.61.3.4.

Lopez-Ridaura, S., L. Barba-Escoto, C. A. Reyna-Ramirez, C. Sum, N. Palacios-Rojas, and B. Gerard. 2021. Maize intercropping in the milpa system. Diversity, extent and importance for nutritional security in the Western Highlands of Guatemala. *Scientific Reports* 11 (1):3696. doi:10.1038/s41598-021-82784-2.

Maherali, H., and J. N. Klironomos. 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* 316 (5832):1746–48. doi:10.1126/science.1143082.

Masood, S., and A. Bano. 2016. Mechanism of potassium solubilization in the agricultural soils by the help of soil microorganisms. In *Potassium solubilizing microorganisms sustainable agriculture*, ed. V. S. Meena, B. R. Maurya, J. P. Verma, and R. S. Meena, 137–47. India: Springer.

Matsuoka, Y., Y. Vigouroux, M. M. Goodman, J. Sanchez, E. Buckler, and J. Doebley. 2002. A single domestication for maize shown by multilocus microsatellite genotyping. *PNAS* 99 (9):6080–84. doi:10.1073/pnas.052125199.

McGonigle, T. P., M. H. Miller, D. G. Evans, G. L. Fairchild, and J. A. Swan. 1990. A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. *New Phytologist* 115 (3):495–501. doi:10.1111/j.1469-8137.1990.tb00476.x.

Molina-Anzures, M. F., J. L. Chávez-Servia, A. Gil-Muñoz, P. A. López, E. Hernández-Romero, and E. Ortíz-Torres. 2016. Productive efficiencies in corn, bean and squash (*Cucurbita pepo* L.) associations, intercropped with rows of fruit trees. *Phyton, International Journal of Experimental Botany*. (accessed 31 May 2020). https://www.revistaphyton.fund-romuloraggio.org.ar/vol85/Molina_Anzures.pdf/ .

Montesinos-Navarro, A., A. Valiente-Banuet, and M. Verdú. 2019. Plant facilitation through mycorrhizal symbiosis is stronger between distantly related plant species. *New Phytologist* 224 (2):928–35. doi:10.1111/nph.16051.

Morales, H., I. Perfecto, and B. Ferguson. 2001. Traditional fertilization and its effect on corn insect populations in the Guatemalan highlands. *Agriculture, Ecosystems and Environment* 84 (2):145–55. doi:10.1016/S0167-8809(00)00200-0.

Moreno-Calles, A. I., A. Casas, E. García-Frapolli, and I. Torres-García. 2012. Traditional agroforestry systems of multi-crop “milpa” and “chichipera” cactus forest in the arid tehuacán valley, Mexico. *Their Management and Role in People’s Subsistence. Agroforestry Systems* 84:207–26. doi:10.1007/s10457-011-9460-x.

Moreno-Espíndola, I. P., M. J. Ferrara-Guerrero, M. L. Luna-Guido, D. A. Ramírez-Villanueva, A. S. de León-lorenzana, S. Gómez-Acata, E. González-Terreros, B. Ramírez-Barajas, Y. E. Navarro-Noya, L. M. Sánchez-Rodríguez, et al. 2018. The bacterial community structure and microbial activity in a traditional organic milpa farming system under different soil moisture conditions. *Frontiers in Microbiology* 9:2737. doi:10.3389/fmicb.2018.02737.

Negrete-Yankelevich, S., I. E. Maldonado-Mendoza, J. O. Lázaro-Castellanos, W. Sangabriel-Conde, and J. C. Martínez-Álvarez. 2013a. Arbuscular mycorrhizal root colonization and soil P availability are positively related to agrodiversity in Mexican maize polycultures. *Biology and Fertility of Soils* 49 (2):201–12. doi:10.1007/s00374-012-0710-5.

Negrete-Yankelevich, S., L. Porter-Bolland, J. L. Blanco-Rosas, and I. Barois. 2013b. Historical roots of the spatial, temporal and diversity scales of agriculture in Sierra de Santa Marta, Los Tuxtlas. *Environmental Management* 52 (1):45–60. doi:10.1007/s00267-013-0095-8.

Njeru, E. M., L. Avio, C. Sbrana, A. Turrini, G. Bocci, P. Bàrberi, and M. Giovannetti. 2014. First evidence for a major cover crop effect on arbuscular mycorrhizal fungi and organic maize growth. *Agronomy for Sustainable Development* 34 (4):841–48. doi:10.1007/s13593-013-0197-y.

O’Connor, G. E., J. Evans, S. Black, N. Fettell, B. Orchard, and R. Theo. 2010. Influence of agronomic management of legume crops on soil accumulation with nitrate. *Nutrient Cycling in Agroecosystems* 86 (2):269–86. doi:10.1007/s10705-009-9291-6.

Oehl, F., E. Frossard, A. Fliessbach, D. Dubois, and A. Oberson. 2004. Basal organic phosphorus mineralization in soils under different farming systems. *Soil Biology and Biochemistry* 36 (4):667–75. doi:10.1016/j.soilbio.2003.12.010.

Oyarzun, P. J., R. M. Borja, S. Sherwood, and V. Parra. 2013. Making sense of agrobiodiversity, diet, and intensification of smallholder family farming in the highland Andes of Ecuador. *Ecology of Food and Nutrition* 52 (6):515–41. doi:10.1080/03670244.2013.769099.

Phillips, J. M., and D. S. Hayman. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Transactions of the British Mycological Society* 55 (1):158–61. doi:10.1016/S0007-1536(70)80110-3.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. Core Team. 2017. nlme: LinearandNonlinearMixedEffectsModels_.Rpackageversion3.1-131.https://CRAN.R-project.org/package=nlme >

Piperno, D. R., and K. V. Flannery. 2001. The earliest archaeological maize (Zea mays L.) from highland Mexico: New accelerator mass spectrometry dates and their implications. *PNAS* 98 (4):2101–03. doi:10.1073/pnas.98.4.2101.

Porter, W. M. 1979. The 'most probable number' method for enumerating infective propagules of vesicular arbuscular mycorrhizal fungi in soil. *Australian Journal of Soil Research* 17 (3):515–19. doi:10.1071/SR9790515.

Reicosky, D. C. 2015. Conservation tillage is not conservation agriculture. *Journal of Soil and Water Conservation* 70 (5):103A–108A. doi:10.2489/jswc.70.5.103A.

Reyna-Ramírez, C. A., L. M. Rodríguez-Sánchez, G. Vela-Correa, J. Etchevers-Barra, and M. Fuentes-Ponce. 2018. Redesign of the traditional Mesoamerican agroecosystem based on participative ecological intensification: Evaluation of the soil and efficiency of the system. *Agricultural Systems* 165:177–86. doi:10.1016/j.agsy.2018.06.013.

Richards, S. A. 2015. Likelihood and model selection. In *Ecological statistics contemporary theory and application*, ed. G. A. Fox, S. Negrete-Yankelevich, and J. V. Sosa, 58–80. Oxford: Oxford University Press.

Rillig, M. C., C. A. Aguilar-Trigueros, T. Camenzind, T. R. Cavagnaro, F. Degrune, P. Hohmann, D. R. Lammel, I. Mansour, J. Roy, M. G. van der Heijden, et al. 2019. Why farmers should manage the arbuscular mycorrhizal symbiosis. *New Phytologist* 222 (3):1171–75. doi:10.1111/nph.15602.

Rogovska, N., D. A. Laird, S. J. Rathke, and D. L. Karlen. 2014. Biochar impact on Midwestern Mollisols and maize nutrient availability. *Geoderma* 230-231:340–47. doi:10.1016/j.geoderma.2014.04.009.

Rosen, C. J., and D. L. Allan. 2007. Exploring the benefits of organic nutrients sources for crop production and soil quality. *HortTechnology* 17 (4):422–30. doi:10.21273/HORTTECH.17.4.422.

Rowley, M. C., S. Grand, and É. P. Verrecchia. 2018. Calcium-mediated stabilisation of soil organic carbon. *Biogeochemistry* 137:27–49. doi:10.1007/s10533-017-0410-1.

Ryan, M. H., and J. H. Graham. 2018. Little evidence that farmers should consider abundance or diversity of arbuscular mycorrhizal fungi when managing crops. *New Phytologist* 220 (4):1092–107. doi:10.1111/nph.15308.

Sangabriel-Conde, W., I. E. Maldonado-Mendoza, M. E. Mancera-López, J. D. Cordero-Ramírez, D. Trejo-Aguilar, and S. Negrete-Yankelevich. 2015. Glomeromycota associated with Mexican native maize landraces in Los Tuxtlas, Mexico. *Applied Soil Ecology* 87:63–71. doi:10.1016/j.apsoil.2014.10.017.

Sangabriel-Conde, W., S. Negrete-Yankelevich, S. I. E. Maldonado-Mendoza, and D. Trejo-Aguilar. 2014. Native maize landraces from Los Tuxtlas, Mexico show varying mycorrhizal dependency for P uptake. *Biology and Fertility of Soils* 50 (2):405–14. doi:10.1007/s00374-013-0847-x.

Singh, P. K., M. Singh, and B. N. Tripathi. 2013. Glomalin: An arbuscular mycorrhizal fungal soil protein. *Protoplasma* 250 (3):663–69. doi:10.1007/s00709-012-0453-z.

Stavi, I., G. Bel, and E. Zaady. 2016. Soil functions and ecosystem services in conventional, conservation, and integrated agricultural systems. *A Review. Agronomy for Sustainable Development* 36 (2):32. doi:10.1007/s13593-016-0368-8.

Stratton, A. E., L. Kuhl, and J. Blesh. 2020. Ecological and nutritional functions of agroecosystems as indicators of smallholder resilience. *Frontiers in Sustainable Food Systems* 4:543914. doi:10.3389/fsufs.2020.543914.

Taiz, L., and E. Zeiger. 2010. *Plant physiology*. fifth ed. Sinauer Associates Inc, Sunderland Massachusetts.

Tamburini, G., R. Bommarco, T. C. Wanger, C. Kremen, M. G. A. van der Heijden, M. Liebman, and S. Hallin. 2020. Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science Advances* 6 (45). doi: 10.1126/sciadv.aba1715.

Thomazini, A., E. S. Mendonça, J. L. Souza, I. M. Cardoso, and M. L. Garbin. 2015. Impact of organic no-till vegetables systems on soil organic matter in the Atlantic Forest biome. *Scientia Horticulturae* 182:145–55. doi:10.1016/j.scienta.2014.12.002.

Tian, H., R. A. Drijber, X. Li, D. N. Miller, and B. J. Wienhold. 2013. Arbuscular mycorrhizal fungi differ in their ability to regulate the expression of phosphate transporters in maize (*Zea mays* L.). *Mycorrhiza* 23 (6):507–14. doi:10.1007/s00572-013-0491-1.

Tian, H., R. A. Drijber, X. S. Niu, J. L. Zhang, and X. L. Li. 2011. Spatio-temporal dynamics of an indigenous arbuscular mycorrhizal fungal community in an intensively managed maize agroecosystem in North China. *Applied Soil Ecology* 47 (3):141–52. doi:10.1016/j.apsoil.2011.01.002.

Tooker, J. F., S. D. Frank, and I. Steffan-Dewenter. 2012. Genotypically diverse cultivar mixtures for insect pest management and increased crop yields. *Journal of Applied Ecology* 49 (5):974–85. doi:10.1111/j.1365-2664.2012.02173.x.

Ureta, C., E. Martínez-Meyer, H. R. Perales, and E. R. Álvarez-Buylla. 2012. Projecting the effects of climate change on the distribution of maize races and their wild relatives in Mexico. *Global Change Biology* 18 (3):1073–82. doi:10.1111/j.1365-2486.2011.02607.x.

van Kessel, C., P. W. Singleton, and H. J. Hoben. 1985. Enhanced N-transfer from a soybean to maize by vesicular arbuscular mycorrhizal (VAM) fungi. *Plant Physiology* 79 (2):562–63. doi:10.1104/pp.79.2.562.

Wang, M., Q. Zheng, Q. Shen, and S. Guo. 2013. The critical role of potassium in plant stress response. *International Journal of Molecular Sciences* 14 (4):7370–90. doi:10.3390/ijms14047370.

Weng, L., F. A. Vega, and W. H. Van Riemsdijk. 2011. Competitive and synergistic effects in pH dependent phosphate adsorption in soils: LCD modeling. *Environmental Science Technology* 45 (19):8420–28. doi:10.1021/es201844d.

Wezel, A., M. Casagrande, F. Celette, J. F. Vian, A. Ferrer, and J. Peigné. 2014. Agroecological practices for sustainable agriculture. *A Review. Agronomy for Sustainable Development* 34 (1):1–20. doi:10.1007/s13593-013-0180-7.

WRB. World reference base for soil resources. http://www.fao.org/3/y1899e/y1899e02.htm#TopOfPage/ (accessed 26 February 2019).

Yang, X., X. Chen, and X. Yang. 2019. Effect of organic matter on phosphorus adsorption and desorption in a black soil from Northeast China. *Soil & Tillage Research* 187:85–91. doi:10.1016/j.still.2018.11.016.

Zhang, F., and L. Li. 2003. Using competitive and facilitative interactions in intercropping systems enhances crop productivity and nutrient-use efficiency. *Plant and Soil* 248 (1/2):305–12. doi:10.1023/A:1022352229863.

Zizumbo-Villarreal, D., A. Flores-Silva, and P. Colunga-García. 2012. The archaic diet in Mesoamerica: Incentive for milpa development and species domestication. *Economic Botany* 66 (4):328–43. doi:10.1007/s12231-012-9212-5.