Legume-based cropping systems have reduced carbon and nitrogen losses

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In agricultural systems, optimization of carbon and nitrogen cycling through soil organic matter can improve soil fertility and yields while reducing negative environmental impact. A basic tenet that has guided the management of soil organic matter for decades has been that equilibrium levels of carbon and nitrogen are controlled by their net input and that qualitative differences in these inputs are relatively unimportant[1–3]. This contrasts with natural ecosystems in which there are significant effects of species composition and litter quality on carbon and nitrogen cycling[4,5]. Here we report the net balances of carbon and nitrogen from a 15-year study in which three distinct maize/soybean agroecosystems are compared. Quantitative differences in net primary productivity and nitrogen balance across agroecosystems do not account for the observed changes in soil carbon and nitrogen. We suggest that the use of low carbon-to-nitrogen organic residues to maintain soil fertility, combined with greater temporal diversity in cropping sequences, significantly increases the retention of soil carbon and nitrogen, which has important implications for regional and global carbon and nitrogen budgets, sustained production, and environmental quality.

We studied carbon and nitrogen balances in two legume-based and one conventional, fertilizer-driven agroecosystem. The conventional system consisted of a maize/soybean rotation; a mineral nitrogen fertilizer was applied before maize was planted and pesticides were used as needed. The other two cropping systems depended on legumes for nitrogen fixation and were managed on the basis of 'organic' (US) or 'ecological' (Europe) strategies, avoiding the use of synthetic fertilizers and pesticides[6]. One system simulated a beef operation in which crop biomass (legumes and grasses) was fed to beef cattle and the manure was subsequently returned to the field as the primary nitrogen source for maize (MNR system). The other system received nitrogen directly from legumes through incorporation of leguminous biomass before maize planting (LEG system). Maize and soybeans were not present as frequently in these systems as in the conventional system, because small grains and several other legumes were also included in the rotation. Ten-year averages for 1986–95 maize yields were 7,140, 7,100 and 7,170 kg ha^{-1} in the MNR, LEG and conventional systems, respectively, and were not significantly different (analysis of variance ANOVA, $P > 0.5$). For the past ten years of the experiment, economic profitability from the three systems has been comparable[7].

As a result of these distinct management strategies, there were significant quantitative and qualitative differences in organic residue inputs and in soil carbon sequestration. The conventional system had greater mean cumulative above-ground net primary productivity (ANPP, Table 1) and returned more crop residues to the soil than did both of the legume-based systems. The MNR system had the greatest harvest intensity; only 36% ANPP was returned to the soil as crop residues. Total carbon returned to the soil in the MNR and conventional systems, however, was not significantly different, because of steer manure additions in the MNR system (Table 1). The quantity of carbon inputs was not the major factor affecting soil carbon storage in these cropping systems. Even though the MNR and conventional systems received equal amounts of carbon, only the MNR system showed a significant increase in carbon stored in soil (Table 1). The LEG system, with lower average carbon inputs from above-ground sources, also showed an increase in soil carbon.

In contrast to the conventional system, which received only senescent-crop residues (Table 1), the two legume-based systems received relatively diverse residues that differed in terms of biochemical composition (the residues were from senescent crops, leguminous biomass and/or steer manure). Studies of litter-quality effects using agricultural residues have produced inconsistent results[1–3,8,9]. It is likely that the increased carbon storage in the MNR system is partially due to the return of steer manure to the field. Compared with senescent-crop residues, a larger proportion of manure-derived carbon is retained in soil, probably because manure is already partly decomposed and contains a larger proportion of chemically recalcitrant organic compounds[8,9]. On the other hand these studies did not find significant effects of types of plant species on long-term carbon equilibrium[1,8,9].

We studied the potential role of plant-species differences on soil carbon storage, using variations in the natural abundance of δ^{13}C associated with photosynthetic pathways to estimate the relative contribution of C_4 and C_3 plants to soil organic matter (SOM). Maize, the only C_4 crop present, accounted for 74%, 48% and 22% of the returned residues in the conventional, LEG and MNR systems, respectively. In the conventional system, maize-derived carbon still replaces the original soil carbon deposited by the C_3 temperate forests that preceded agriculture in this region. In this case, net soil carbon levels did not change because the loss of C_3-derived carbon was nearly equivalent to the gain of C_4-derived carbon (Fig. 1). In contrast, the net gains in soil carbon seen in the LEG and MNR systems were due to significant increases in C_3-derived carbon. Levels of soil carbon derived from C_4 plants did not change in the MNR and LEG systems. In the LEG system levels of C_3-derived carbon were disproportionately high, accounting for 88% of the net increase in soil carbon although only half of the

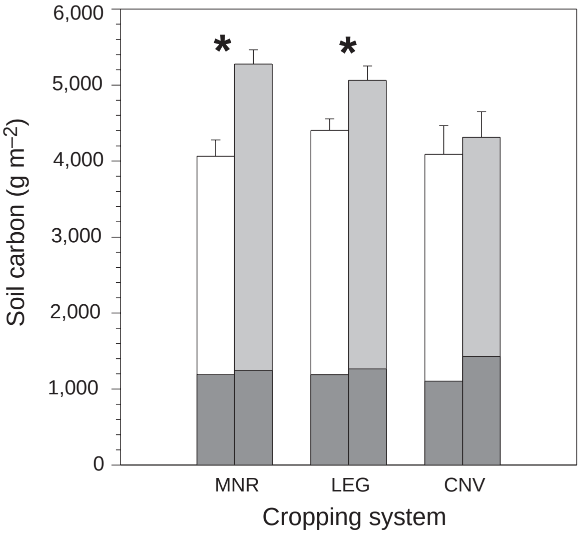

Figure 1 Soil carbon levels in 1981 (left-hand bars) and 1995 (right-hand bars); means ± s.e.m. are shown. MNR, manure as N source; LEG, N directly from legumes; CNV, conventional system (see text). The amount of C_4-derived carbon is indicated by the dark grey portion of each bar; the remainder of each bar represents C_3-derived carbon. Asterisks indicate significant differences in 1995 mean soil carbon levels compared with 1981 levels, ANOVA, $P < 0.05$. In addition to residues from maize, the MNR system also receives unknown amounts of C_4-derived carbon inputs from the steer manure, making a quantitative comparison of the proportion of C_4 inputs and C_4-derived soil carbon impossible in this system.

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Table 1 Plant productivity and changes in soil carbon 1981–95

Cropping system	Net primary productivity*	Plant residues returned†			Manure input†	Total organic residue input†	Change in soil carbon 1981 to 1995‡
		Senescent	Living	Total			
MNR	69a	21	3.7	25a	19	44b	12
LEG	68a	31	7.5	39b	0	39a	6.6
Conventional	75b	43	0	43c	0	43b	2.2§

* Cumulative carbon fixed by annual above-ground net primary productivity; † Carbon in residues returned to the soil; and ‡ net changes (increases) in soil carbon; all over 15 years. Senescent residues are from crops and weeds. Residues incorporated from living plants were mainly of leguminous origin in the LEG system but were predominantly from grasses in the MNR system. Numbers within a column followed by a different letter are significantly different at the 0.05 probability level (protected Scheffe's). § There was no significant change in soil carbon in the conventional system (ANOVA, $P > 0.05$). Values are kg carbon $\times 10^{-3}$ per ha.

residues returned were from C_3 plants. Replacement of C_4-derived soil carbon in pools with turnover times of less than 20 years, which accounts for about 5% of the total soil carbon[10], cannot explain this discrepancy. These changes in the natural abundance of $\delta^{13}C$ in SOM in the LEG system indicate that differences in plant-species composition have contributed to differential retention of soil carbon. Plant species can affect carbon equilibrium through differences in below-ground net primary productivity (NPP)[11], the timing and level of root turnover/exudates[12], litter quality[4], tendencies to foster the formation of soil aggregates[13], and changes in microbial community structure and function[14,15].

Qualitative differences in nitrogen inputs also had a major influence on nitrogen retention in these agroecosystems. Nitrogen losses due to leaching in 1991–95 were comparable in the LEG and MNR systems, averaging 13 kg nitrogen $ha^{-1} yr^{-1}$, but were about 50% higher in the conventional system, averaging 20 kg $ha^{-1} yr^{-1}$, (ANOVA, $P = 0.06$; Fig. 2). Seasonal effects in all cropping systems were similar, with the greatest losses occurring during the late-fall to early-spring months when mineralization tends to exceed crop demand. Leaching losses were greatest from late fall of 1991 to spring of 1993 compared with the later half of the rotation cycle, particularly in the conventional system.

Cumulative nitrogen additions were similar in the conventional and MNR systems, as were nitrogen exports from non-leguminous crops (Fig. 3a, b). Over the course of 15 years, nitrogen inputs from soil amendments have exceeded exports by crops by a total of 520 kg ha^{-1} in the conventional and 540 kg ha^{-1} in the MNR systems (Fig. 3c). Despite these similarities in net balance, there were significant differences in soil nitrogen storage. Most of the surplus nitrogen received by the MNR system over the 15 years can be accounted for by the significant increase in soil nitrogen from 1981 to 1995 (Fig. 3d), whereas in the conventional system soil nitrogen levels have decreased since 1981 (Fig. 3d).

Nitrogen inputs into the LEG system are more difficult to quantify because nitrogen fixed by the green manure was the major nitrogen input. However, we have estimated the maximum nitrogen input from the green manure over 15 years to be 840 kg nitrogen ha^{-1}. If the proportion of nitrogen fixed ranged from 75% to 100%, nitrogen inputs from the green manure would have been 630–840 kg ha^{-1} (Fig. 3a). Non-leguminous exports were not significantly different from those in the conventional system, but were somewhat lower than those in the MNR system (protected Scheffe's, $P < 0.05$; Fig. 3b). Soil nitrogen levels in this system have not changed significantly (Fig. 3d).

The nitrogen unaccounted for in our balance calculations was +240, ±100 and +1,020 kg ha^{-1} in the MNR, LEG and conventional systems, respectively, and probably reflects differences in gaseous losses and nitrogen fixation by soybeans not included in our calculations. Although we have no measurements of gaseous losses, we can estimate the potential impacts of soybeans on nitrogen balance on the basis of data from the experiment. Nitrogen balances suggest that nitrogen fixation was probably lower in conventional-system soybeans and greater in LEG-system soybeans. Calculations for possible nitrogen-fixation scenarios in the LEG and conventional systems show that even large differences in soybean nitrogen-fixation rates between systems did not alter the basic trends in nitrogen balance. For example, if nitrogen fixed by soybeans were 75% of total soybean nitrogen in the LEG system, the net nitrogen input from senescent roots and shoots would have been only 60–140 kg ha^{-1} over 15 years. Likewise, nitrogen extrac-

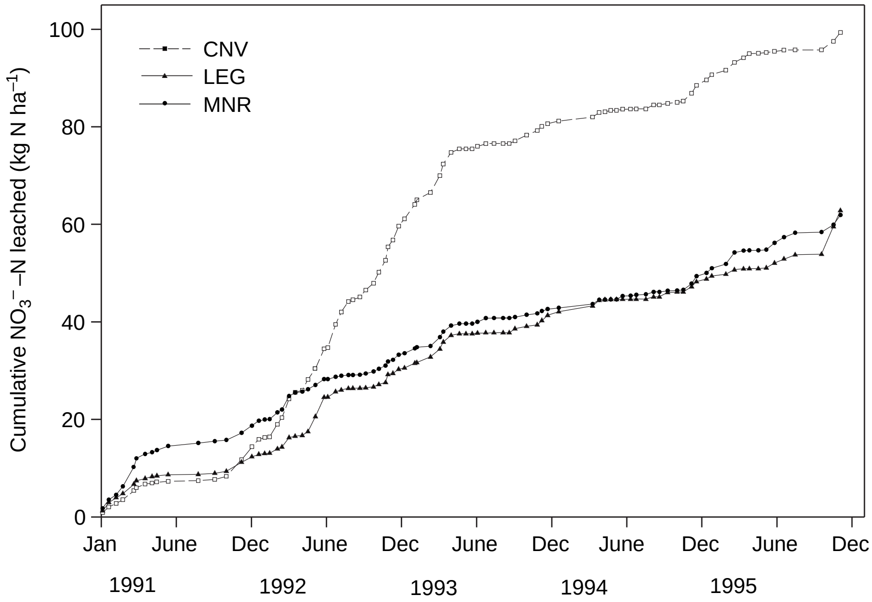

Figure 2 Cumulative nitrate leaching during 1991 to 1995. Means of data from lysimeters installed in three entry points of four replicates are shown. Cumulative nitrogen leached over five years was significantly different across cropping systems (ANOVA, $P = 0.06$).

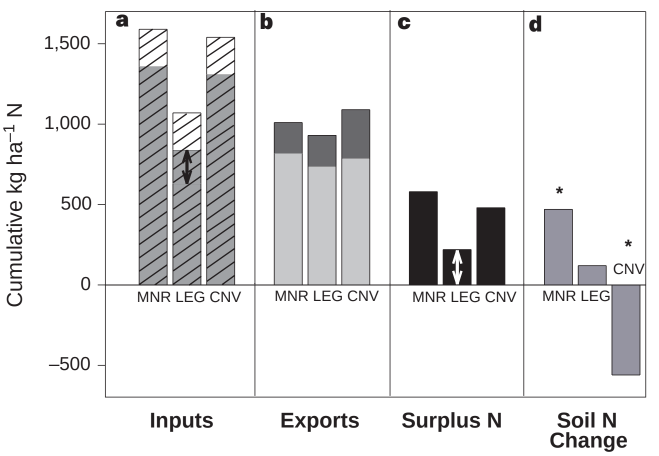

Figure 3 Comparison of cumulative nitrogen inputs and exports and changes in soil nitrogen storage after 15 years. **a**, Nitrogen inputs under the control of the manager (grey with stripes represents nitrogen input from steer manure, leguminous biomass or mineral fertilizers) and estimated environmental nitrogen inputs (white with stripes represents atmospheric nitrogen deposition and nitrogen fixation by free-living bacteria). **b**, Exports of nitrogen from non-leguminous crops (light grey) combined with nitrate leaching losses (dark grey). **c**, Nitrogen surplus based on inputs minus exports. **d**, The change in soil nitrogen is the difference between nitrogen contents in the plough layer for 1995 compared to 1981; asterisks indicate statistical significance, ANOVA, $P < 0.05$. Arrows in LEG-system bars indicate the possible range of nitrogen-fixation inputs.

tion by soybeans in the conventional system can account for only part of the missing 1,020 kg of nitrogen (surplus + change in soil nitrogen); that is, a nitrogen-fixation rate of 40% of soybean total nitrogen would result in the extraction of 280–350 kg ha^{-1} over 15 years, a fairly typical outcome for highly determinant soybeans in maize rotations[16].

These results for nitrogen parallel our findings for carbon, indicating that quantitative differences in nitrogen balance were not the major factor affecting soil nitrogen retention. Instead, qualitative differences in the form of nitrogen inputs and subsequent effects on internal nitrogen cycling had a significant impact on long-term soil nitrogen retention. Detailed microplot studies using ^{15}N as a tracer showed that there are differences in the partitioning of nitrogen from organic versus mineral sources, with more legume-derived nitrogen than fertilizer-derived nitrogen immobilized in microbial biomass and SOM[17,18]. If immobilization is lower in the conventional system compared with in the other two systems, this may explain the greater leaching of NO_3^- that we observed in this system. Differences in plant-species composition may contribute to reducing NO_3^- leaching by scavenging soil nitrogen during periods in which summer cash crops, such as maize and soybeans, are not active[19].

Our results show that even in these intensively managed agro-ecosystems, plant-species composition and litter quality influence SOM turnover markedly. Increases in SOM in the MNR and LEG systems were highly significant in terms of ecosystem function and soil quality. Greater retention of both carbon and nitrogen suggests that use of low carbon-to-nitrogen residues to maintain soil fertility combined with increased temporal diversity restores the biological linkage between carbon and nitrogen cycling in these systems and could lead to improved global carbon and nitrogen balances. Application of these practices in the major maize/soybean growing region in the USA would increase soil carbon sequestration by $0.13–0.30 \times 10^{14}$ g yr^{-1}. This is equal to 1–2% of the estimated annual carbon released into the atmosphere from fossil fuel combustion in the USA[20] (1.4×10^{15} g carbon yr^{-1}, 1994) and is a significant contribution considering that the USA has agreed to reduce average CO_2 emissions to 7% below 1990 levels by 2008–2012 as part of the Kyoto Protocol. In addition, CO_2 emissions from the two legume-based systems are lower than emissions from the conventional system because of a 50% reduction in energy use[21]. The potential effects on the nitrogen cycle are much greater in magnitude because the fixed nitrogen used in agricultural activities is responsible for a 60% increase in global levels of biologically active nitrogen[22]. Reduced nitrogen losses combined with increased soil nitrogen storage will lead to reductions in the amount of nitrogen that must be applied to maintain yields. ☐

Methods

The experiment covered 6 ha and consisted of a randomized, complete block design. Details of experimental design and farming practices are described elsewhere[23]. Carbon contents of organic residues are calculated from plant biomass data collected from 1981–1995 assuming a carbon content of 42% on a dry weight basis.

Soil analyses. Composite soil samples collected in 1981 and 1995 were analysed for total carbon and nitrogen with the Leco CN-2000 analyser (Leco Corporation). Natural abundance of ^{13}C was determined by combustion of triplicate samples with a Europa Scientific carbon–nitrogen analyser connected to a Europa Scientific Tracermass mass spectrometer. To estimate the original ^{13}C natural abundance before the introduction of C_4 plants, we collected a composite soil sample along two transects from a forested, never-farmed site located ~0.5 km from the experiment. The proportion of carbon derived from corn residues, C_4%, was calculated for 1981 and 1995 as $C_4\% = (\delta_m - \delta_f)/(\delta_{mr} - \delta_f) \times 100$, where $\delta_m = \delta^{13}$C content of soil after maize cultivation; $\delta_r = -25.58‰$ the Δ^{13}C content of soil under the nearby native mixed hardwood forest; and $\delta_{mr} = -13.1‰$ the δ^{13}C content of maize residues[24].

Nitrogen budget. Nitrogen inputs from leguminous green manures were calculated by using above-ground biomass nitrogen content data and adjusting for below-ground contributions using root biomass data and nitrogen content from the experiment in 1997. Values for total nitrogen fixation in these plants were taken from published studies to estimate the minimum proportion of nitrogen fixed[16,25]. Soybeans, which were present in all three cropping systems, were not included in nitrogen-budget calculations because of the potential for variability in nitrogen fixation by soybeans[16]. However, we used our data on soybean yields, residue returns and nitrogen contents to estimate potential impacts on nitrogen balance. Usually, no more than 50% of total soybean nitrogen is derived from nitrogen fixation and generally two-thirds of the total nitrogen is exported from the beans[3,16]. Nitrogen fixation by free-living bacteria, which represents a minor contribution to nitrogen inputs in agricultural systems using tillage, was assumed to be 5 kg nitrogen ha^{-1} yr^{-1} (ref. 26). In earlier work we did not find significant differences in the potential for nitrogen fixation by free-living organisms in these cropping systems[27]. We estimated nitrogen inputs from atmospheric deposition to be 15 kg nitrogen ha^{-1} yr^{-1} on the basis of data for northeastern USA[28]. Estimates of nitrate leaching for the 15-year period were based on five years of data collected in this experiment during 1991–95 from intact-core below-ground lysimeters installed in 4 replicates × 3 entry points, for a total of 36 lysimeters (each 0.45 m^2 in area)[29].

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Motion integration in a thalamic visual nucleus

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Thalamic nuclei have long been regarded as passive relay stations for sensory information en route to higher level processing in the cerebral cortex. Recently, physiological and theoretical studies have reassessed the role of the thalamus and it has been proposed that thalamic nuclei may actively participate with cortical areas in processing specific information[1–4]. In support of this idea, we now show that a subset of neurons in an extrageniculate visual nucleus, the lateral-posterior pulvinar complex, can signal the true direction of motion of a plaid pattern, indicating that thalamic cells can integrate different motion signals into a coherent moving percept[5–8]. This is the first time that these computations have been found to occur outside the higher-order cortical areas[5,6,9,10]. Our findings implicate extrageniculate cortico–thalamo–cortical loops in the dynamic processing of image motion, and, more generally, as basic computational modules involved in analysing specific features of complex visual scenes.

The integration of motion signals is usually considered to be a two-stage process[5,11]. The first stage involves the analysis of object features as one-dimensional components, which are integrated at a second stage. It has been argued that the first stage is inherently limited in its coding of local motion signals (the aperture problem[5]), and that the second stage, combining the outputs from the first, is necessary to generate a global percept of an object in motion. This second stage has been attributed to cortical networks, as have all forms of higher-order processing. However, models have been proposed in which thalamic nuclei participate in these processes, interacting closely with the neocortex[1–4,12–14]. A common implication of these models is that cells on both sides of the cortico–thalamic loop have similar higher-order response properties, although there has been no clear demonstration of subcortical neurons responding to higher-order visual stimuli. In well-developed visual systems, the pulvinar region is a likely candidate for a subcortical counterpart to the cortex where a loop involved in the analysis of moving objects could be established. The pulvinar complex represents a higher-order nucleus because it receives its major input from layer V cortical neurons, rather than directly from retinal ganglion cells; it is also in reciprocal communication with virtually all visual and associative cortical areas[15,16]. This region is often associated with visual attention[17,18] and visually guided movement[19], but theories of its function remain speculative[15]. In cats, the physiological response properties in the lateral-posterior pulvinar (LP-pulvinar) complex indicate that these cells code attributes of image motion such as direction, velocity, and the relative motion between an object and its background[20]. On the basis of these response properties and connectivity patterns, we considered that the LP-pulvinar complex could participate in analysing the global motion of complex scenes. We therefore studied the sensitivity of cells in the cat's LP-pulvinar complex to moving plaid patterns. This stimulus comprises two superimposed drifting gratings differing only in orientation. A human observer perceives a single rigid pattern moving unambiguously with a direction and velocity uniquely consistent with the constraints imposed by the motion of the individual components[5,7,8]. At the neuronal level, a cell that is selective for the global motion of the plaid pattern responds with a profile similar to that of a single grating moving in the integrated direction ('pattern'-motion selectivity), rather than

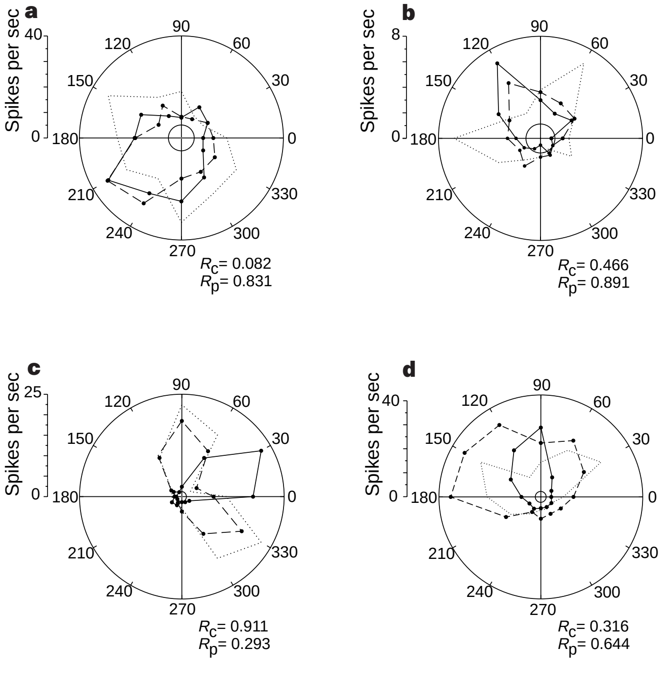

Figure 1 Polar graphs illustrating the responses of LP-pulvinar neurons to gratings (solid line) and plaid patterns (dashed line) drifting in 12 directions of motion. We considered the response to gratings alone as the predicted profile for a truly pattern-motion selective unit. The dotted line represents the predicted response to plaids for a component-motion selective unit. **a**, **b**, Pattern-motion selective neurons. **c**, The response of a component-motion selective cell. **d**, The discharges of an unclassified direction-selective cell. The small central circles represent spontaneous activity levels.