Conservation tillage induced changes in organic carbon, total nitrogen and available phosphorus in a semi-arid alkaline subtropical soil

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Abstract

A multi-year experiment was conducted to compare the effects of conservation tillage (no-till and ridge-till) with conventional plow tillage on organic C, N, and resin-extractable P in an alkaline semi-arid subtropical soil (Hidalgo sandy clay loam, a fine-loamy, mixed, hyperthermic Typic Calciustoll) at Weslaco, TX (26°9’N 97°57’W). Tillage comparisons were established on irrigated plots in 1992 as a randomized block design with four replications. Soil samples were collected for analyses 1 month before cotton planting of the eighth year of annual cotton (planted in March) followed by corn (planted in August).

No-till resulted in significantly \( p < 0.01 \) greater soil organic C in the top 4 cm of soil, where the organic C concentration was 58\% greater than in the top 4 cm of the plow-till treatment. In the 4–8 cm depth, organic C was 15\% greater than the plow-till control. The differences were relatively modest, but consistent with organic C gains observed in hot climates where conservation tillage has been adopted. Higher concentrations of total soil N occurred in the same treatments, however a significant \( p < 0.01 \) reduction in N was detected below 12 cm in the ridge-till treatment. The relatively low amount of readily oxidizable C (ROC) in all tillage treatments suggests that much of the soil organic C gained is humic in nature which would be expected to improve C sequestration in this soil.

Against the background of improved soil organic C and N, bicarbonate extractable P was greater in the top 8 cm of soil. Some of the improvement, however, appeared to come from a redistribution or “mining” of P at lower soil depths. The results indicate that stratification and redistribution of nutrients were consistent with known effects of tillage modification and that slow improvements in soil fertility are being realized. Published by Elsevier Science B.V.

Keywords: Plow tillage; Ridge tillage; No-tillage; Organic carbon; Organic nitrogen; Phosphorus; Stratification

1. Introduction

Soil organic C is a dynamic pool determined by the opposing processes of C inputs and losses. Promoting accretion of soil organic C depends mainly on modifying the input–output relationships, i.e. by increasing inputs or decreasing losses, or by a combination of both. Conservation tillage is promoted, in part, for its beneficial effects on carbon retention that occur with time. Since about 37\% of agricultural land in USA is currently managed with conservation tillage (Lal et al., 1998), and because it is estimated to increase to 75\%
by 2020 (Lal, 1997), it becomes increasingly important to understand the potentials and limitations of this management practice for agriculture under varied environmental conditions and cropping systems.

Reducing tillage affects several aspects of the soil. With time, conservation tillage improves soil quality indices (Dick, 1983; Lal et al., 1998), including soil organic C storage (Dick, 1983; Lamb et al., 1985; Dao, 1991; Unger, 1991; Edwards et al., 1992; Eghball et al., 1994; Bruce et al., 1995; Potter et al., 1998). Several factors probably contribute to the rate of soil improvement when tillage is reduced. Clay content (Rhoton, 2000), cropping history and soil fertility (Martens, 2001), and crop diversity (Bruce et al., 1994; Unger, 1991; Edwards et al., 1992; Eghball et al., 1994) have also been demonstrated where conventional tillage was employed (Lamb et al., 1985; Studdert et al., 1997).

During the first 4 years of tillage, Rhoton (2000) determined a 10% loss of initial soil organic matter content with plow tillage. A loss (0.3 kg ha\(^{-1}\)) of surface soil (0–2.5 cm) organic matter also occurred between 4 and 8 years under no-till corn (Rhoton, 2000). Losses of soil organic matter caused by tillage have been estimated to be between 16 and 77% (Mann, 1986).

Grisi et al. (1998) concluded that organic matter in tropical soils is more humified than that in temperate soils. This is an important aspect of C sequestration since humified C is reported to be the largest and least variable fraction of soil organic C (Rosell et al., 2000), and constitutes the longest lived soil C fraction.

Carbon sequestration was found to occur at low rates across an 1100 km transect of Texas (Potter et al., 1998), and to be inversely related to mean annual temperature. The slight positive effect of tillage reduction and the fact that fertilization had little effect on organic C sequestration in that study suggest that the physical environment, characterized by hot and relatively dry conditions constitutes a great challenge to increasing soil organic matter content.

Another mechanism by which soil organic matter is retained in conservation-tillage systems may be due to reduced oxygen availability below the surface of no-till systems, which affects decomposition rates (Wershaw, 1993) and the distribution of aerobic and anaerobic microbes and microbial processes (Doran, 1980). Slower subsurface decomposition rates would lower oxidative losses of organic C. Residues left on the surface often undergo wider fluctuations in moisture content, ranging from wet to dry (Franzluebbers et al., 1994), and these extremes are a clear contrast to the environmental conditions of buried residues (Douglas et al., 1980; Schomberg et al., 1994). Buried residues decomposed at 3.4 times the rate of residues left on the soil surface (Beare et al., 1993). This suggests that reduced oxygen availability may not decrease decomposition rate as much as greater soil–residue contact and improved moisture conditions accelerate it. Reduced residue–soil contact and extreme variation in moisture and temperature at the soil surface undoubtedly play significant roles in reducing surface residue decomposition rates. However, surface (0–30 cm) soil itself in a no-till system was shown to contain more moisture and to be cooler than a comparable plow-tillage soil (Doran et al., 1998).

In addition to increases in soil organic matter concentration (Doran and Smith, 1987; Havlin et al., 1990; Lal et al., 1998; Drinkwater et al., 1998; McCarty et al., 1998; Franzluebbers et al., 1998; Potter et al., 1998; Wander et al., 1998; Rhoton, 2000; Martens, 2001), changes attributable to a reduction in tillage intensity have also been demonstrated for soil microbes and microbial activity (Linn and Doran, 1984; Doran, 1987; Franzluebbers et al., 1994b, 1995; Martens, 2001), and for soil physical properties, including soil structure (Bowman et al., 1990; Franzluebbers et al., 1994b). The biological component of soil can be a good integrator of factors that affect soil quality (Potter et al., 1998). Microbial biomass is the smallest portion of organic C in soil (Martens, 2001). Microbial biomass is more sensitive to changes in soil conditions than is the content of total C (Sparling, 1992), and it has been proposed that the ratio of microbial C to total C in the soil (C\(_{mic}\)/C\(_{org}\)) may be a sensitive index of changes in soil organic matter dynamics (Powlson et al., 1987; Wardle, 1992). Tillage greatly affects the size of soil microbial biomass (Martens, 2001). Soil cultivation reduced soil microbial biomass in the Midwestern United States from 57% of native levels for no-till to 36% with plow-till (Follett and Schimel, 1989). Similarly, microbial biomass was found to range from 1.2 to 1.4% of the organic C with plow tillage and from 3.5 to 5.1% for no-tillage (Angers et al., 1993). Tillage also affects the distribution of the soil microbial biomass, being displaced toward the soil surface with no-tillage, and toward lower depths with plow tillage.
after 4 years (Carter and Rennie, 1982). Specific microbial population distributions may also be affected by tillage (Doran, 1980). Holland and Coleman (1987) reported an increase in the fungal to bacterial ratio with no-tillage, which may have implications for C and N cycling in the soil.

Tillage has been shown to disproportionately affect the more labile forms of organic carbon in soil (Cambardella and Elliott, 1992), including the fraction that accounts for most of the simpler polymers involved in macroaggregate formation. Soil organic C loss with tillage and continuous cropping may be minimized by proper residue management and crop selection (Studdert et al., 1997) and by increasing cropping intensity (Doran et al., 1998).

Stratification of soil properties is a natural consequence of soil development that can become accentuated in soils subjected to reduced tillage. Unger (1991) and Bruce et al. (1995) reported that soil nutrients become stratified when no-till management is employed. There is a marked stratification of soil organic matter with soil depth under no-tillage (Blevins et al., 1984). Havlin et al. (1990) determined that reducing tillage and maintaining surface residues in a long-term study increased soil organic C and N in the surface 2.5 cm of soil. When corn stover was returned to the soil, Clapp et al. (2000) reported a 14% increase in soil organic C in the top 15 cm, but soil organic C content decreased in the 15–30 cm depth. Similar apparent re-distributions of soil C, where increases in surface organic C generated by conservation tillage were offset by decreases in subsurface organic C content, have been documented (Ellert and Bettany, 1995). Soil-specific responses to tillage-induced C storage were reported by Wander et al. (1998) in which carbon accretion was not apparent in all soils in that trial. Plowing was shown to move dispersed organic C from the 0–20 cm soil depth down to the 60–80 cm depth in corn plots (Römkens et al., 1999).

Soil P occupies a central position in the organic matter decomposition paradigm. Unlike C and N, P does not readily undergo oxidation–reduction reactions in the common processes of organic matter decomposition. Phosphorous readily precipitates with metal ions and often becomes deficient in many soils. Fe-, Al-, and Ca-phosphates often control the solubility of P in soils (Tate and Salcedo, 1988), and these compounds are sparingly soluble. This leads to low P uptake efficiencies by crops and even P added to alleviate the deficiency can readily precipitate in soils (Tisdale et al., 1993). This problem becomes particularly pronounced in soils of high pH and those of high carbonate content as often occur in South Texas. Plants and microbes can immobilize P, which generates organically bound P in soils. Organically bound P constitutes a more labile P pool that is mineralized as organic matter decomposes. Where organic matter is present in soil, there are essentially two P cycles, an inorganic cycle, driven by pedological processes such as leaching and acid formation, and a biological cycle, driven by plants and microbes (Tate and Salcedo, 1988). Where crop residues are returned to the soil, an increase in P availability may occur by decreasing the adsorption of P to mineral surfaces (Ohno and Erich, 1997) which complements biologically mediated release of P to improve crop P status. Conservation-tillage methods are designed to retain crop residues and thus should impact the P status of soils. Response to soil management changes may be related to the nature of the P pools in the soil (Wright and Coleman, 1999). Soil P accumulation rates may be different than that seen for C or N. Soil P did not accumulate to the same degree as C or N in one system studied (Weil et al., 1988), leading to higher C:P ratios. Given the unique aspects of P cycling in soils managed with conservation tillage, it is important to understand the dynamics of soil P to ensure adequate P nutrition of crops produced in conservation-tillage systems. Few studies have included soil P evaluations along with C and N (Schomberg and Steiner, 1999).

The objective of this investigation was to evaluate the long-term effects of two conservation-tillage methods on soil organic C and N, and on P mineralization potential in an alkaline, semi-arid soil under subtropical conditions.

2. Materials and methods

2.1. Soil characteristics and plot history

Tillage comparisons were established in 1992 as a randomized block design with four replications on irrigated plots at the USDA Research Farm in Weslaco, Texas (26°9′N 97°57′W) on Hidalgo sandy clay loam (fine-loamy, mixed, hyperthermic Typic

Calciustoll). Prior to establishment of the tillage experiment, the area was under plow-tillage agriculture for at least 70 years. Plots were cropped to cotton (Gossypium hirsutum L.) in March and corn (Zea mays L.) in August of each year using only nitrogen fertilizer (90 and 168 kg N ha\(^{-1}\) for cotton and corn, respectively). P fertilization is often not used in this region because soil tests report high levels of P in the soils. Lack of P fertilization in the current experiments allowed evaluation of tillage effects on P solubilization from native sources.

For ridged plots, ridges were reformed and bedded immediately before (March) and after (July) cotton culture. A Buffalo\(^1\) cultivator was used to clear furrows for irrigation of those treatments midway into both cotton and corn cycles, approximately May and September, respectively. No-tillage plots were not tilled in any way, and were flood irrigated. Conventional-tillage plots were prepared by moldboard plowing to 40 cm, disking and re-bedding immediately after corn harvest (January).

2.2. Soil sampling and chemical characterization

Plots were sampled in February when the mean soil temperature was 24 °C. Fifty soil core samples (2.5 cm x 25 cm deep) were taken randomly within the plant row of each replicate plot. These were combined, mixed and sieved (4 mm) field moist. Subsamples of composited soil were analyzed for chemical and biochemical properties. Chemical analysis was done on 0.5 M sodium bicarbonate extracts (1:20 soil:extractant, Kuo, 1996) by inductively coupled plasma spectroscopy. CEC was calculated by the summation of bases. Soil carbonates were determined by a manometric technique (Loeppert and Suarez, 1996), and soil particle size analysis by the hydrometer method (Gee and Bauder, 1986).

2.3. Organic C and total N

Finely ground (<250 μm) soil was treated with H\(_2\)SO\(_3\) (Nelson and Sommers, 1996) to decompose carbonates prior to dry combustion for organic C and total N determination using a Carlo-Erba CE 2500 (CE Elantech, Lakewood, NJ 08701).

2.4. Readily oxidizable soil C (ROC)

Readily mineralized C is the active fraction of soil organic matter (Magdoff, 1996) and may be estimated by determining that part of the organic C that is easily oxidizable by chemical means. Nelson and Sommers (1996) suggest that most of the active fraction is oxidized by dichromate methods. Soil samples were subjected to chemical oxidation with a 0.167 M K\(_2\)Cr\(_2\)O\(_7\) in the presence of concentrated sulfuric acid, followed by titration with 0.5 M FeSO\(_4\) as described by Nelson and Sommers (1996), but no external heat was used, nor was a correction factor applied to the results. The measure was used as an estimate of the active fraction of soil organic C.

2.5. Resin-extractable P

Solubilized orthophosphate was determined by shaking 2 g soil with 20 ml water containing an anion exchange resin membrane strip (5 cm x 2.25 cm; AR 204, Dynambio, Madison, WI) for 16 h. Membrane resin strips were removed, gently washed with water and placed into a 50 ml centrifuge tube with 20 ml of 1 M NaCl and shaken for another 2 h. The equilibrated liquid was analyzed for orthophosphate by the malachite green method (Ohno and Zibilske, 1991).

All data were analyzed with the General Linear Model of Systat (Version 8.0, SPSS Corp., Chicago, IL) with standard errors calculated using appropriate error terms, alpha level 0.05. Mean separation was done by the Fisher’s LSD method.

3. Results and discussion

3.1. Soil chemical and physical properties

The results of the current experiments are point-in-time estimates of the changes elicited by adoption of conservation tillage on these plots in 1992. Soil samples from previous years were not available for analysis. However, the long history of conventional production on the plots (>70 years) implies that the

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\(^1\) Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the US Department of Agriculture.
plots reached an equilibrium in term of carbon inputs–outputs long ago and may be considered adequate beginning conditions for the current experimental objectives. The following soil properties were determined: 54.3% sand; 20.5% silt; 22.9% clay; pH 7.9; bicarbonate extractable (mg kg\(^{-1}\)) P, 6.4; K, 25.4; Ca, 44.4; Mg, 12.4; Na, 80.2; soluble salts (1:1), 0.021 S m\(^{-1}\); CEC, 18.7 cmol kg\(^{-1}\); and carbonates, 21.1%.

3.2. Soil organic carbon

Concentration of soil organic C after 9 years of tillage experiments is shown in Fig. 1. No-till resulted in significantly \((p < 0.01)\) greater soil organic C in the top 4 cm of soil, which was 57.8% greater than that in the top 4 cm of the plow-till. In the second 4 cm depth, organic C concentration was 15.1% greater than the plow-till. In the 8–30 cm depths, the organic C concentration was not different \((p = 0.25)\) among tillage systems. The pattern for organic C distribution in the ridge-till treatment was similar to that seen in the no-till, with 44.2% greater organic C in the top 4 cm, and 12.9% higher in the 4–8 cm depth. The apparent subsurface organic C depletion in conservation tillage noted by these results is consistent with the findings of Dick and Durkalski (1987). After 11 years of another experiment, no-tillage soil organic C increased 65, 17, and 7% over plow-tillage soil in the 0–5, 5–10, 10–20 cm depths in Texas (Dao, 1998).

3.3. Readily oxidizable soil carbon (ROC)

Tillage modification resulted in differences in ROC (Fig. 2). The differences were most apparent in the top 0–4 cm of the soil of both conservation-tillage treatments. At lower depths, however, differences were less apparent. Greater variability in ROC content below the 4 cm depth of the conservation-tillage treatments is in contrast to the relative homogeneity of the organic C measurements (Fig. 1). Some of the variability undoubtedly arises from the much smaller size of the ROC fraction compared to that of the organic C. Plow-till produced, as expected, non-significant differences \((p > 0.05)\) in ROC through depth. The mixing of the soil by tillage precludes the stratification observed in the conservation-tillage treatments.

The lack of residue incorporation in no-tillage accounts for the significantly \((p < 0.05)\) greater ROC in the top 4 cm of soil. In ridge-till, surface crop residues are buried periodically as irrigation furrows are renewed by moving residues and soil from the furrows to the top of ridges. Burying residues has been shown to increase decomposition rates (Beare et al., 1993), but a trend toward stratification may be responsible for the alternating higher and lower ROC concentrations with depth as residues are successively buried with each ridge-renewing tillage operation. More ROC accumulated in the upper soil...
depth of the conservation-tillage treatments. While no-till promotes conservation of mineralizable C from crop residues (Franzluebbers et al., 1994a), cultivation and high soil temperatures promote organic C loss (Dao, 1998), and soil organic matter in tropical soils has been reported to be more humic in character than that from temperate regions (Grisi et al., 1998). A direct relationship between mean annual temperature and soil organic C loss has also been documented for three sites in Texas (Potter et al., 1998). ROC comprises a small part of organic C in this soil which is probably due to the high temperatures of the region that promote rapid organic matter decomposition.

3.4. Soil organic nitrogen

Tillage-induced changes in soil organic N are often directly related to changes in soil organic C. Both no-till and ridge-till promoted significantly \((p < 0.05)\) greater concentrations of soil organic N at the soil surface (Fig. 3), but it was uniformly distributed with depth under plow tillage. Soil organic N contains compounds that are more resistant to decomposition and which consequently can affect N dynamics in the soil. In another study employing no-tillage, soil N losses were reduced, but short-term N availability was also reduced (Reeves et al., 1997). Potential immobilization of N is greater near readily mineralizable C (Doran et al., 1998; McCarty et al., 1998), which accumulates near the soil surface in reduced tillage systems. Losses of soil N with increased tillage follow a pattern similar to that seen for soil organic C. Immobilization of fertilizer N may account for the generally lower efficiency of N use by crops managed with no-till (Carter and Rennie, 1984). However, long-term loss reductions and greater retention of fertilizer N due to immobilization may improve crop N use efficiency by subsequent re-mineralization of the N in better synchrony with crop needs.

In the ridge-till treatment, total N was reduced in the lower three depths (12–30 cm). Orthogonal contrasts were used to compare the surface three depths to the bottom three depths. A significant decrease was detected \((p = 0.03)\) for ridge-till that was found in neither the no-till nor plow-till. Reasons for this effect are unknown. Denitrification was not measured, but probably was not a large factor due to the lack of large amounts of readily decomposable organic C in those depths (Fig. 2).

3.5. Carbon:nitrogen ratio

Nitrogen mineralization–immobilization transformations in soil are largely dependent on C:N ratios of added crop residues and on the bioavailability of external N. Carbon and N quality in residues are of
fundamental importance in predicting N mineralization (Frankenberger and Abdelmagid, 1985). Soil C:N ratios (Fig. 4) reveal a contrasting situation between no-till and ridge-till systems. For the no-till system, little difference was detected in the C:N ratio through most of the depths examined. This indicates that the crop residues have undergone a large degree of humification, having attained a C:N ratio of approximately 10. Even the 0–4 cm depth, which might be expected to have a higher C:N ratio because of its proximity to residues on the soil surface, did not differ from lower depths. Comparing ridge-till and no-till, C:N ratios differed significantly at all depths and the magnitude of difference increased with depth (Fig. 4). From 8 to 30 cm, C:N ratios increased with depth. This effect is probably related to the anomaly of decreased N content of the lower three depths of that treatment (Fig. 3).

Some change in the nature of decomposition may have occurred in the plow-till treatment. The C:N ratios (Fig. 4) of the soil depths were higher (approximately 13)
than those of no-till (approximately 10). If C:N ratios of the lower soil depths are discounted, ridge-till yielded C:N ratios around 11, about midway between the no-till and plow-till treatments. These observations may reflect a difference in the location of the residue humification process between the three tillage treatments. In no-till, the process may be nearer the interface of the soil surface and residue cover. In the plow-till treatment, residues are distributed through the soil profile, and are decomposed in a more homogeneous environment, with high soil-residue contact. Ridge-till might be considered intermediate between the plow-till and no-till treatments in its modification of the decomposition environment for crop residues, with less homogenous residue distribution. Mechanisms that drive these differences could be related to oxygen availability (Wershaw, 1993) and to differences in the biological environments (Doran et al., 1998) among the tillage treatments.

3.6. Resin-extractable P

Anion exchange resin-extractable P was used to estimate P that would become plant available over a period of time (16 h). As measured, it is a rate of solubilization, rather than an estimate of plant available P. The high soil pH (7.9) and the low extractability of P suggested that the soil might contain mostly stable and meta-stable P forms. The high carbonate content of the soil suggested that the soil may also “fix” inorganic P. In such a soil, organic P becomes an important source of plant available P (Linquist et al., 1997). Resin P was significantly \( p < 0.001 \) greater in the 0–4 and 4–8 cm depths of both conservation-tillage treatments as well as in the plow-till treatment (Fig. 5). While resin-P in the plow-till was much lower in the top two depths than in the conservation-tillage treatments, it was higher in the lowest three depths than in corresponding depths of both conservation-tillage treatments. This suggests a re-distribution of native P with time toward the surface in the conservation-tillage treatments. Weil et al. (1988) found increased resin-P in the upper 5 cm of no-tilled soil. However, they attributed the increase to chelation of inorganic P by the accumulated soil organic matter. This explanation would not seem to accommodate the apparent decline in P in lower depths of both conservation-tillage treatments, compared to plow-till, in the present experiment. Higher P in the plow-tillage treatment may be due to vertical distribution of P from residues. Rhoton (2000) also found a higher amount of P in the 2.5 cm depth under no-tillage. The apparent “mining” of P from lower soil depths and retention in upper depths in conservation-tillage systems is probably due to immobilization of P, which promotes the organic P cycle, and to the chelation effect of organic compounds on soluble P, as noted by Weil et al. (1988). Sources of P have been attributed to microbial

![Fig. 5. Resin-extractable (16 h) phosphorus by depth after 9 years of no-till, ridge-till or plow-till treatment. Read across at each depth, the same letter adjacent to data points indicates no significant difference between the means by Fisher’s LSD (0.05).](image-url)
biomass (Tate and Salcedo, 1988) and to the passage of P through microbial biomass during decomposition (Brookes et al., 1984). Phosphorus stratification in the present experiment suggests a changing status of P fertility due to tillage effects. Results indicate an increased capacity of soils managed with conservation tillage to supply P from organic sources. Microbes (and plants) drive this supply via the enzymatic hydrolysis of P-containing organic compounds. The contribution of organic P sources to soil fertility is directly related to the amount of organic matter in the soil. This soil, under conservation tillage for 9 years, is slowly accreting organic C and N, but it is probably not yet capable of supplying all the P needed for crop needs. Pedological transformations that release P in alkaline carbonate-rich soils are extremely slow. These data indicate that promotion of the organic P cycle may yield significant improvements in crop nutrition. It has been proposed that sustaining P cycling through active microbial populations is essential for maintaining soil fertility (Harrison, 1985), and organic matter itself may be considered an important source for P recycling in the short and long-term (Wright and Coleman, 1999). With time, soil and crop residue management practices that promote organic matter accumulation would be expected to improve P nutrition of crops.

4. Conclusions

Application of conservation tillage to an alkaline soil in a semi-arid subtropical climate for 8 years markedly improved organic C and N concentrations. Gains of up to 0.5% in organic C are relatively modest, but are consistent with organic C gains observed in hot climates where conservation tillage has been adopted. However, measurable gains in organic C and similar gains in organic N suggest a balanced improvement in soil fertility is underway. Accumulation of C and N within the top 8 cm of soil resulted in greater stratification under conservation tillage. The relatively low amount of ROC suggests that much of the soil organic C gained is humic in nature which would be expected to improve organic C sequestration in this soil.

Against the background of improved soil organic C and N, P solubilization was greater in the top 8 cm of soil under conservation tillage. Some of the difference, however, appeared to come from a redistribution or “mining” of P at lower soil depths. The results indicate that stratification and redistribution of nutrients were consistent with known effects of tillage reduction and that slow improvements in soil fertility are being realized.

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References


