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To cite this version:

Johan Six, Christian Feller, Karolien Denef, Stephen Ogle, Joao Carlos de Moraes Sa, et al.. Soil organic matter, biota and aggregation in temperate and tropical soils - Effects of no-tillage. Agronomie, EDP Sciences, 2002, 22 (7-8), pp.755-775. <10.1051/agro:2002043>. <hal-00885974>

HAL Id: hal-00885974
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Soil organic matter, biota and aggregation in temperate and tropical soils – Effects of no-tillage

Johan SIXa,c*, Christian FELLerb, Karolien DENEFc, Stephen M. OGLEc, Joao Carlos de MORAESSAb, Alain ALBRECHTd

a Department of Agronomy and Range Science, University of California, Davis, CA 95616, USA
b CENA-USP/IRD, Caixa Postal 96, 13400-970 Piracicaba, SP, Brazil
c Natural Resource Ecology Laboratory Colorado State University, Fort Collins CO 80523, USA
d ICRAF/IRD, PO Box 30677, Nairobi, Kenya

(Received 30 October 2001; accepted 28 May 2002)

Abstract – The long-term stabilization of soil organic matter (SOM) in tropical and temperate regions is mediated by soil biota (e.g. fungi, bacteria, roots and earthworms), soil structure (e.g. aggregation) and their interactions. On average, soil C turnover was twice as fast in tropical compared with temperate regions, but no major differences were observed in SOM quality between the two regions. Probably due to the soil mineralogy dominated by 1:1 clay minerals and oxides in tropical regions, we found a higher aggregate stability, but a lower correlation between C contents and aggregate stability in tropical soils. In addition, a smaller amount of C associated with clay and silt particles was observed in tropical versus temperate soils. In both tropical and temperate soils, a general increase in C levels (∼325 ± 113 kg C·ha⁻¹·yr⁻¹) was observed under no-tillage compared with conventional tillage. On average, in temperate soils under no-tillage, compared with conventional tillage, CH₄ uptake (∼0.42 ± 0.10 kg C-CH₄·ha⁻¹·yr⁻¹) increased and N₂O emissions increased (∼1.95 ± 0.45 kg N-N₂O·ha⁻¹·yr⁻¹). These increased N₂O emissions lead to a negative global warming potential when expressed on a CO₂ equivalent basis.

soil carbon / aggregation / N₂O emissions / tillage / temperate and tropical soil

Résumé – Matière organique du sol, activité biologique et agrégation dans les régions tempérées et intertropicales. Effet du non-labour. La stabilisation à long terme de la matière organique du sol (MOS) dans les régions tempérées et intertropicales est sous la dépendance de l’activité biologique (champignons, bactéries, macrofaune et racines), de la structure du sol (agrégation) et de leurs interactions. En moyenne, si le turnover du carbone du sol (C) est environ deux fois plus rapide en régions intertropicales qu’en régions tempérées, peu de différences apparaissent toutefois quant à la qualité de la MOS sous ces climats différents. La stabilité de l’agrégation est plus élevée pour les sols des régions intertropicales, ceci étant probablement dû à leur minéralogie dominée par des argiles de type 1:1 associées à des oxihydroxides métalliques. Toutefois, pour les sols tropicaux, la corrélation entre teneur en C et stabilité de l’agrégation est plus faible et de moindres quantités de C sont associées avec les éléments fins (argile+limon). Aussi bien sous climats tempéré que tropical et subtropical, une augmentation générale des stocks de C du sol (∼325 ± 113 kg C·ha⁻¹·an⁻¹) est observée avec les pratiques de non labour. Pour les sols des régions tempérées, si une fixation de CH₄ (= 0.42 ± 0.10 kg C-CH₄·ha⁻¹·an⁻¹) est mesurée sous non-labour, parallèlement une émission de N₂O est observée (= 1.95 ± 0.45 kg N-N₂O·ha⁻¹·an⁻¹), conduisant finalement à un bilan négatif en terme de réchauffement global exprimé en équivalents de flux de C-CO₂.

carbone du sol / agrégation / émissions N₂O / non-labour / régions tempérées et intertropicales

1. INTRODUCTION

The conservation of sufficient soil organic matter (SOM) levels is crucial for the biological, chemical and physical soil functioning in both temperate and tropical ecosystems. Appropriate levels of SOM ensure soil fertility and minimize agricultural impact on the environment through sequestration of carbon (C), reducing erosion and preserving soil biodiversity. Many different soil types are found within the vast tropical and temperate regions. Consequently, the distinction between tropical and temperate soils is rather artificial and makes the comparison between the two soil categories difficult. However, there are soil characteristics (e.g. soil...
moisture, soil temperature and mineralogy) that are often different between temperate and tropical soils across all soil types within these two big soil categories. Consequently, the comparison can be made and forms an avenue for advancing our understanding of soil processes in drastically different soils. For this review, we assigned soils to these two categories in accordance with location and climate. In the rest of the text we use the simplified denomination of “temperate soils” versus “tropical soils” to refer to soils of the corresponding climatic areas. We included subtropical soils within the tropical category because most subtropical soils have more characteristics similar to tropical soils (e.g. mineralogy) compared with the temperate soils. Within our data sets, mineralogical dominance mostly coincided with our division based on location and climate, i.e., 1:1 clays and oxides dominated most tropical soils whereas 2:1 minerals dominated temperate soils. However, some smectitic Vertisols and allophanic Andosols were included within the tropical soils.

The long-term stabilization of C and nitrogen (N) in temperate and tropical soils is mediated by soil biota (e.g. fungi, bacteria, roots and earthworms), soil structure (e.g. aggregation) and their interactions, and is influenced by agricultural management. Because it has been shown, in both temperate and tropical soils, that aggregation decreases C and N mineralization, the focus of this review is on aggregate dynamics and its interaction with SOM and soil biota in order to synthesize the current knowledge on long-term stabilization of C and N. As a case study for the effect of agricultural management, we chose the no-tillage/cover crop system. No-tillage (NT) practices have been adopted at high rates in the US and Brazil, giving us the opportunity to compare a widely used agricultural practice under tropical and temperate conditions.

The objective of the first section of this review was to do a general comparison of SOM stabilization mechanisms in tropical and temperate soils. In a second section we focus on the effects of NT practices on carbon and nitrogen dynamics in tropical and temperate soils.

2. GENERAL COMPARISON BETWEEN TROPICAL AND TEMPERATE SOILS

2.1. Soil organic matter turnover, stabilization and quality

Primary plant production and soil microbial activity are the two main biological processes governing inputs and outputs of SOM. The balance between them determines SOM turnover and is controlled by biotic and abiotic factors. Climate, parent material, biota, topography and time are the major controlling factors on production and decomposition (by microorganisms) of SOM [153]. Climate, parent material and biota (e.g. vegetation) are the factors that differ the most between tropical and temperate regions.

It is generally assumed that organic compounds [18] and SOM [248] have a faster turnover in tropical than temperate soils due to the enhanced decomposition under the higher moisture and temperature regimes of the tropics. For example, Trumbore [248] found a mean residence time (MRT) of C in the surface layer (0–22/23 cm), estimated with radiocarbon, of 470 versus 990 years for a tropical and temperate soil, respectively. Another way to estimate C turnover and MRT relies on the difference in 13C natural abundance between plants (and the SOM-C derived from them) with different photosynthetic pathways (Calvin cycle [C3 plants] vs. Hatch- Slack cycle [C4 plants]) [63]. A change in vegetation type results in a change to the 13C natural abundance signature of the soil C, which enables one to calculate the proportion of C derived from the original vegetation. The turnover of C derived from the original vegetation is then calculated by using a first-order decay model [20, 63]. Table I contains a summary of published estimates of C turnover as determined by the 13C natural abundance technique. This summary indicates a 1.8 times longer average MRT of C in the soil surface of temperate compared with tropical soils (63 ± 7 years versus 35 ± 6 years). This confirms the general assumption that there is a faster C turnover in tropical than temperate soils. However, the range in estimated turnovers was similar for tropical and temperate soils (13–108 years versus 14–141 years), indicating the great variability in estimates and the substantial overlap in C turnover between tropical and temperate ecosystems.

The higher turnover rate for tropical soils is primarily due to faster turnover rates of the slow C pool in tropical soils [102]. Feller and Beare [102] compared the incorporation rates of C derived from new vegetation in particle size classes (sand, silt and clay) in temperate and tropical surface soils. They found that, for all fractions, the time period before half of the C associated with the fractions was derived from the new vegetation was longer for temperate than for tropical soils. However, the differences in half-lives were much larger for the slow C compartment (i.e., the silt plus clay fraction; 29–38 years) than for the more active C compartment (i.e., the sand fraction; 13 years).

Three main mechanisms of C stabilization have been proposed: (1) biochemical stabilization, (2) stabilization by association with silt and clay particles, and (3) physical protection within aggregate structures [71]. Biochemical

<table>
<thead>
<tr>
<th>Region</th>
<th>Sites and sources</th>
<th>Low</th>
<th>High</th>
<th>Average ± stderr</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical</td>
<td>10/13</td>
<td>13</td>
<td>108</td>
<td>36 ± 5</td>
</tr>
<tr>
<td>Temperate</td>
<td>19/12</td>
<td>14</td>
<td>141</td>
<td>63 ± 7</td>
</tr>
</tbody>
</table>

Table I. Carbon mean residence time (MRT) in tropical and temperate soils estimated with 13C technique.
stabiliization of SOM is due to the recalcitrance of compounds such as lignin and polyphenols [52]. Table II is a synthesis of SOM quality parameters and parameters indicating the degree of SOM decomposition across sand-, silt- and clay-sized particle size classes. All four ratios presented in Table II indicate a greater degree of decomposition when they are greater. For example, the mass ratio of acids to aldehydes of vanillyl (ac/al) and syringyl (ac/al) structural units determined by alkaline CuO oxidation have been used to determine the degree of microbial alteration of the recalcitrant component, lignin [138]. We found no differences in the ratios for the clay-sized particle size class, indicating that long-term stabilized SOM by clay does not differ in quality between tropical and temperate soils. However, a trend to higher (ac/al), and (ac/al), ratios was observed for tropical compared with temperate soils in the sand- and silt-sized particle size classes (Tab. II). These higher ratios suggest a proportionally greater stabilization of highly decomposed and more recalcitrant materials in tropical soils than in temperate soils. Other measures of the decomposition stage of SOM, such as the alkyl/O-alkyl ratio determined by $^{13}$C nuclear magnetic resonance and the ratio of glucose + mannose/xylose + arabinose (GM/AX), did not reveal a clear difference between tropical and temperate soils (Tab. II). The alkyl/O-alkyl ratio also tended to be higher in tropical soils than in temperate soils in the sand- and silt-sized particle fractions but the opposite trend was observed in the clay-sized particle fraction. The tendency of higher alkyl/O-alkyl ratios in the sand- and silt-sized particle fractions corroborates the CuO-oxidation data in that SOM in tropical soils is more decomposed than in temperate soils. In conclusion, the SOM quality parameters did not reveal drastic differences and were even contradictory. However, they indicated a tendency for more decomposed and chemically recalcitrant forms of short-term stabilized SOM associated with sand and silt particles in tropical than temperate soils. Consequently, further research and more sensitive analyses are needed to draw firm conclusions concerning SOM quality.

The stabilization of C and N by association with silt and clay particles has been investigated in many studies. Numerous studies reported a relationship between clay or silt plus clay content and the preservation of organic C and N [102, 135, 189, 238]. It has also been reported that not only the clay content but also the clay type influences the preservation of organic C and N [165, 238, 246]. In accordance with Hassink [135], we investigated the C protective capacity of silt and clay particles in temperate and tropical soils (Fig. 1); we regressed the amount of C associated with silt and clay (g silt and clay associated C kg$^{-1}$ soil) versus the silt and clay content (%) for tropical and temperate soils. Both regression lines had a positive slope and were highly significant, indicating a positive influence of clay and silt particles on C stabilization. However, the coefficient of determination was lower in temperate than in tropical soils ($r^2 = 0.39$ versus 0.66). Our results also indicate a lower stabilization of C per unit of silt and clay particles and, hence, a lower C protective capacity of the silt and clay particles in tropical versus temperate soils (Fig. 1). This lower stabilization of C in tropical soils is probably mostly related to the different clay types dominant in the

### Table II. Comparison of degree of soil organic matter decomposition between tropical and temperate soils in the sand, silt and clay fraction (average ± stderr).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Climate</th>
<th>Sand</th>
<th>Silt</th>
<th>Clay</th>
</tr>
</thead>
<tbody>
<tr>
<td>(ac/al)$_v$</td>
<td>tropical</td>
<td>0.33 ± 0.08</td>
<td>0.60 ± 0.16</td>
<td>0.79 ± 0.15</td>
</tr>
<tr>
<td></td>
<td>temperate</td>
<td>0.21 ± 0.02</td>
<td>0.30 ± 0.03</td>
<td>0.59 ± 0.05</td>
</tr>
<tr>
<td>(ac/al)$_s$</td>
<td>tropical</td>
<td>0.84 ± 0.22</td>
<td>1.13 ± 0.22</td>
<td>1.42 ± 0.31</td>
</tr>
<tr>
<td></td>
<td>temperate</td>
<td>0.42 ± 0.02</td>
<td>0.64 ± 0.03</td>
<td>0.90 ± 0.05</td>
</tr>
<tr>
<td>Alkyl/O-alkyl $^{a}$</td>
<td>tropical</td>
<td>0.58 ± 0.08</td>
<td>0.76 ± 0.08</td>
<td>0.70 ± 0.14</td>
</tr>
<tr>
<td></td>
<td>temperate</td>
<td>0.49</td>
<td>0.64</td>
<td>0.86</td>
</tr>
<tr>
<td>GM/AX $^{a}$</td>
<td>tropical</td>
<td>0.55 ± 0.05</td>
<td>1.26 ± 0.15</td>
<td>1.68 ± 0.13</td>
</tr>
<tr>
<td></td>
<td>temperate</td>
<td>0.94 ± 0.15</td>
<td>1.53 ± 0.15</td>
<td>1.96 ± 0.19</td>
</tr>
</tbody>
</table>

$^{a}$ The proportions of alkyl-C and O-alkyl-C were determined by $^{13}$C NMR.

$^{b}$ GM/AX is the ratio of glucose + mannose/xylose + arabinose.

$^{c}$ Data from [19, 31, Bayer et al., unpublished, 61, 101, 103, 120, 129, Larre-Larrouy et al., unpublished, Nacro et al., unpublished, 184, 237, 240] for tropical soils and from [6, 7, 68, 118, 128, 175, 180, 249] for the temperate soils.

---

**Figure 1.** Carbon stabilization by association with silt and clay particles in temperate versus tropical and subtropical soils. Data from [29, 44, 48, 80, 102, 127, 195, 249] for tropical soils and from [4, 23, 44, 69, 70, 99, 128, 135, 170, 187, 224, 266] for temperate soils.
two categories of soil. Different types of clay (i.e., 1:1 versus 2:1 clays) have substantial differences in specific surface areas and cation exchange capacities (CEC) [121] and should, consequently, have different capacities to bind and stabilize organic materials. Our data support this because the tropical soils, dominated by 1:1 clays and consequently lower CEC’s stabilized less C than the temperate soils, dominated by 2:1 clays and consequently higher CEC’s. However, the effect of climate cannot be ignored in this comparison. The higher temperature and precipitation in tropical regions probably also induce a faster decomposition rate and therefore contribute to the lower stabilization of C per unit of clay and silt.

2.2. Aggregation, biota and soil carbon and nitrogen dynamics

2.2.1. Model of interactions between aggregation and biota activity

Aggregates are known to physically protect C and N [40, 96, 150, 209, 210, 230, 232, 245]. Aggregates physically protect SOM by (1) forming a physical barrier between microorganisms plus microbial enzymes and their substrates, (2) controlling food web interactions, and (3) influencing microbial turnover [97]. A closer look at the processes involved in aggregate formation and stabilization in temperate versus tropical soils illustrates the close relationship between soil biota and SOM dynamics. In both temperate and tropical soils, there are several biological processes responsible for the formation of initial unstable “biological” macroaggregates (Fig. 2):

(A) Fresh plant- and root-derived residues form the nucleation sites for the growth of fungi and bacteria [150, 210]. *Fungal hyphae* initiate macroaggregate formation by enmeshing fine particles into macroaggregates [245]. *Microbial (bacterial and fungal) exudates*, produced as a result of decomposition of fresh residue, form binding agents that further stabilize macroaggregates (t1,A).

(B) Biological macroaggregates also form around actively growing roots in both temperate and tropical soils. Similar to fungal hyphae, roots can provide the mechanical framework for initial formation of macroaggregates by enmeshing particles and production of cementing agents (root exudates), which stimulates microbial activity (t0,B to t1,B) [151].

![Figure 2](image.png)

**Figure 2.** Aggregate formation and degradation mechanisms in temperate and tropical soils. Fungal and bacterial activity, active root growth and earthworm activity are the biological aggregate formation agents in both temperate and tropical soils, whereas the mineral-mineral interactions in tropical soils are the physicochemical aggregate formation agents. Based on [Albrecht, unpubl., 10, 116, 119, 150, 207, 230–232, 257]. UA = unstable aggregates; WSA = water-stable aggregates.
(C) A third common mechanism of biological macroaggregate formation in temperate and tropical soils is through the activity of soil fauna, i.e., earthworms [43, 181], ants and termites [47]. As an example, earthworms produce casts that are rich in organic matter (t_{1,D}). However, casts are not stable when they are freshly formed and wet [181]. When earthworms ingest soil and particulate organic matter, large amounts of watery mucus are added to it and the soil undergoes a thorough kneading. This moulding of the soil will break bonds between soil particles, thereby reducing stability [125, 251]. However, this close contact between organic matter, mucus and soil particles in casts can lead to highly stable casts upon drying [181].

The importance of organic matter as a primary binding agent for soil aggregates holds true for moderately weathered soils dominated by 2:1 clay minerals. However, highly weathered soils of the tropics are generally well known for their large content of mineral particles with variable charge (oxides and 1:1 clay minerals) (t_{1,D}). Based on micro-electrophoretic measurements, [200] reported points of zero net charge (PZNC) for 1:1 clay minerals, such as kaolinites, ranging from < 3.5 to nearly 4.6. Ionic adsorption data indicated that positive charges were persisting in kaolinites up to pH values as high as 8–10 [223]. The co-existence of negative and positive charges at prevailing field pH [99] can explain the capacity of these soils for mineral-mineral bindings resulting in “physicochemical” macroaggregates (t_{1,D}). Moreover, in the presence of oxides, this mineral binding tendency is even enhanced because of higher PZNC values of both Fe(III)- and Al-oxides and their hydroxides [15, 98, 200] compared with kaolinites. These young “physicochemical” macroaggregates are only held together by mineral electrostatic interactions, which are strong but have a limited range of action. Therefore, on a macroaggregate scale, they are probably not strong enough to resist slaking (t_{1,D}).

All these forces (biological and physicochemical) can play a role in initial macroaggregate formation. However, at t_{1}, the young, freshly formed macroaggregates (unstable macroaggregates; UA), are only stable when treated in the most gentle fashion (i.e., when the aggregates are taken from the field and brought to field capacity or from an incubation where the water content is at field capacity, subsequently immersed in water and retained when gently sieved). The formation of water-stable aggregates (WSA) that can resist slaking (i.e., air drying and quick submersion in water before sieving) occurs through several processes (t_{1} to t_{2}):

(1) Under wet conditions, ageing may increase the stability of biological macroaggregates by thixotropic processes and binding through microbial activity. Microbial activity is stimulated inside the biological macroaggregates (and especially inside worm casts) because of their high organic matter content. As a result, substantial amounts of polysaccharides and other organics are deposited and serve to further stabilize the macroaggregates.

(2) Dry-wet cycles can cause closer arrangements of primary particles, resulting in stronger bonding and increased aggregate stability [156].

(3) In the presence of active root growth, biological and physicochemical macroaggregates can become even more stabilized due to biological and physical processes induced by the roots penetrating the aggregates. As mentioned before, roots can produce cementing agents (root exudates), which can strongly adsorb to inorganic materials, thereby helping to stabilize aggregates [244]. In addition, root exudation stimulates microbial activity with subsequent production of microbial binding agents. Furthermore, roots physically influence aggregation by (i) exerting lateral pressures inducing compaction, and by (ii) continually removing water during plant transpiration. This results in localized drying of the soil and cohesion of soil particles around the roots.

The crucial role played by roots in the formation of water-stable aggregates has been recognized for some time [244], but only recently published results [116, 208, 257] have reported that roots are more important than shoots in the formation of aggregates and stabilization of aggregate-associated SOM (Tab. III). They found that more root-derived (2.7–22.6%) than shoot-derived (1.1–3.7%) C was stabilized as particulate organic matter (POM) and occluded within aggregates (Tab. III). However, the ratio of root- over shoot-derived C decreased with time: from 6.1 after 5 months to 2.9 after 12 months and to 1.8 and 1.2 after 18 months of addition of labeled plant material. Consequently, it has to be determined how much root- versus shoot-derived C is stabilized in the long term.

During macroaggregate stabilization (t_{1} to t_{2}), the intra-aggregate POM (i.e., the fresh plant material that was incorporated in the macroaggregates during “biological” aggregate formation) is further decomposed by microorganisms and fragments into finer POM [230]. This fine POM becomes increasingly encapsulated with minerals and microbial products, forming new microaggregates (53–250 μm) within the macroaggregates [10, 116, 150, 207, 230]. With active root growth stabilizing macroaggregates, intense biological activity (induced by root exudation) may also cause further encrustation of microbial products and mineral particles, forming microaggregates around root-derived POM [116]. It has been found that this microaggregate formation within macroaggregates is crucial for the long-term sequestration of C [231, 232] because microaggregates have a greater stability.

<table>
<thead>
<tr>
<th>System [reference]</th>
<th>Time (months)a</th>
<th>Root-derived (%)b</th>
<th>Shoot-derived (%)</th>
<th>Root/shoot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vetch (CT [208])</td>
<td>5</td>
<td>22.6</td>
<td>3.7</td>
<td>6.1</td>
</tr>
<tr>
<td>Wheat (NT [116])</td>
<td>12</td>
<td>3.2</td>
<td>1.1</td>
<td>2.9</td>
</tr>
<tr>
<td>Corn (CT [257])</td>
<td>18</td>
<td>3.3</td>
<td>1.8</td>
<td>1.8</td>
</tr>
<tr>
<td>Corn (NT [257])</td>
<td>18</td>
<td>2.7</td>
<td>2.2</td>
<td>1.2</td>
</tr>
</tbody>
</table>

a Time = time since single addition of labeled root and/or shoot material.
b Percentage of initially added material remaining in the occluded particulate organic matter.
capacity to protect C against decomposition compared with macroaggregates [24, 40, 234].

The final step of the aggregate turnover cycle ($t_1 \rightarrow t_3$) is when the macroaggregates break down and release microaggregates and microbially processed SOM particles. The macroaggregates break up because over time with further decomposition the labile constituents of the coarse sized SOM are consumed, microbial production of binding agents diminishes and the degree of association between SOM and the soil matrix decreases. However, microaggregates are still stable enough and not as sensitive to disruptive forces as the macroaggregates, and therefore survive.

### 2.2.2. Carbon turnover and C and N mineralization for different aggregate classes

The higher protection of C exerted by microaggregates than macroaggregates is illustrated by the faster average C turnover times associated with macroaggregates versus microaggregates (Tab. IV). Data from Table IV indicate that C associated with macroaggregates had an average MRT of 42 ± 18 years, whereas C associated with microaggregates had an average MRT of 209 ± 95 years. The slower turnover of micro- than macroaggregate-associated C was observed both for tropical and temperate soils. Not only is C protected, N is also protected against mineralization within aggregates. Many studies have used incubations of crushed and intact aggregates to determine the C and N protection level (see references for Tab. V). In Table V, studies that crushed soil to a size considerable smaller than 250 $\mu$m were considered as assessments of macroaggregate protection whereas studies that crushed soil to a size considerably smaller than 250 $\mu$m were classified as assessments of microaggregate protection. It is evident from the crushed/intact mineralization data that in both tropical and temperate soils, both macro- and microaggregates protect C and N against mineralization because mineralization was higher when the macro- and/or microaggregate structure was disrupted (i.e., crushed). However, the ratios of crushed/intact mineralization were substantially higher when microaggregates were disrupted versus when only macroaggregates were disrupted, indicating that microaggregates protect labile C and N to a larger extent than macroaggregates in both tropical and temperate soils. Balesdent et al. [24] also concluded that microaggregates protect C more than macroaggregates. This conclusion is in agreement with the higher MRT of microaggregate-associated C than macroaggregate-associated C. It is also interesting to note that the crushed/intact N mineralization tended to be higher than the C mineralization. This higher N mineralization led to a lower C/N ratio of the mineralized SOM in crushed versus intact macroaggregates (temperate macroaggregates: 11.5 ± 1.7 versus 14.0 ± 2.1; tropical macroaggregates: 8.9 ± 0.0 versus 9.5 ± 0.4). The calculated C/N of the SOM released by crushing of macroaggregates was 4.1 ± 1.1 and 7.2 ± 0.3 in temperate and tropical soils, respectively. This indicates that SOM released from macroaggregates upon crushing is in a more decomposed stage and primarily of microbial origin.

### Table IV. Mean residence time (MRT) of macro- and microaggregate-associated C (adopted from [229]).

<table>
<thead>
<tr>
<th>Ecosystem [reference]</th>
<th>Aggregate Size class $^a$ ($\mu$m)</th>
<th>MRT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical pasture [234]</td>
<td>M $&gt;$ 200</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td>m $&lt; 200$</td>
<td>75</td>
</tr>
<tr>
<td>Temperate pasture grasses [152]</td>
<td>M 212–9500</td>
<td>140</td>
</tr>
<tr>
<td></td>
<td>m 53–212</td>
<td>412</td>
</tr>
<tr>
<td></td>
<td>m 100–250</td>
<td>7</td>
</tr>
<tr>
<td>Corn [192]</td>
<td>M $&gt;$ 250</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>m 50–250</td>
<td>61</td>
</tr>
<tr>
<td></td>
<td>m 50–250</td>
<td>691</td>
</tr>
<tr>
<td></td>
<td>m 53–250</td>
<td>137</td>
</tr>
<tr>
<td></td>
<td>m 53–250</td>
<td>79</td>
</tr>
<tr>
<td>Average ± stderr $^b$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>42 ± 18</td>
</tr>
<tr>
<td></td>
<td>m</td>
<td>209 ± 95</td>
</tr>
</tbody>
</table>

$^a$ M = macroaggregate; m = microaggregate.

$^b$ stderr = standard error.

The stabilization of organic C and N within aggregates is partly related to the decreased oxygen concentration in the center of the micro- and macroaggregates. Several studies investigating oxygen profiles across aggregates have reported steep declines in oxygen concentrations over small distances from the aggregate surface [142, 225, 227]. This more anaerobic condition in the center of macroaggregates results in a decreased C and N mineralization, but increases denitrification rates and consequently gaseous N losses [142, 225]. Increasing N$_2$O fluxes with increasing water-stable aggregate size class have been observed [37, 243], and gradients of oxygen and N$_2$O concentrations are asymmetrical across macroaggregates [142, 225], suggesting hot spots of anaerobiosis and denitrification within macroaggregates. The occlusion of POM within the aggregates favors denitrification because POM is a substrate for microbial activity, and consequently a source of carbon and nitrate within an oxygen-limited environment [202]. The anaerobic sites within the macroaggregates presumably occur in both tropical and temperate soils.

### 2.2.3. Carbon content and aggregate stability

Since tropical soils have the potential to form biological as well as physiochemical macroaggregates, we hypothesized that WSA formation should be more independent from organic matter inputs in tropical soils than in temperate soils. With low organic matter inputs, physiochemical aggregates can become stabilized through the physical action of living roots that penetrate the unstable aggregates and subsequently increase their stability by the same physical forces as
described above. In addition, the previously described biological forces associated with living roots will further enhance the formation of WSA. We tested the hypothesized lower dependency of WSA on SOM by comparing the relationship between C content and aggregate stability in tropical versus temperate soils (Fig. 3).

In a first test, we collected published data on aggregate stability determined with the method of [157]. Except, we only took data from studies that used surface soil sieved through a 2–4.75 mm sieve and air-dried prior to wet sieving with a 200 or 250 µm sieve in order to have only slaking-resistant macroaggregates. The analysis corroborated our hypothesis because we found for a certain C content a higher aggregate stability in tropical than in temperate soils, but a lower significant correlation ($r^2 = 0.10$ versus $0.44$) between C content and aggregate stability in tropical than in temperate soils (Fig. 3a). For this data set, we did not find any correlation between clay content and aggregate stability, which excludes a clay effect on the difference in aggregate stability between tropical and temperate soils. In a second test, we investigated the relationship between organic matter (OM) content and the aggregate stability after benzene treatment (Agb) as proposed by [191]. The benzene pretreatment is adopted from the Henin-protocol [140] and tests specifically the effect of hydrophobicity on aggregation. Therefore, it emphasizes the effect of SOM on WSA in medium to high OM-containing soils. Monnier [191] found a close relationship between Agb and $100 \times \text{OM} \% / \text{clay} \%$, the OM% being the OM associated with the heavy fraction (if OM% < 7 then heavy fraction > 2.0 g·cm$^{-3}$; if OM% > 7 then heavy fraction 1.75 g·cm$^{-3}$). We adopted the data from Monnier [191] for the temperate soils and combined it with data from Boyer and Combeau [46], Combeau [75] and Martin [183] for tropical soils. However, the OM% for the tropical soils represents total soil OM and not only OM associated with the heavy fraction. Consequently the OM% is overestimated for the tropical

### Table V. Carbon and nitrogen mineralization of intact and crushed macro- and microaggregates.

<table>
<thead>
<tr>
<th>Land use [reference]</th>
<th>Organic C (%)</th>
<th>Organic N (%)</th>
<th>Crushed/intact C mineralization</th>
<th>Crushed/intact N mineralization</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Macroaggregates</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><strong>Average ± stderr</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Temperate soils</strong></td>
<td></td>
<td></td>
<td><strong>1.14 ± 0.05</strong></td>
<td><strong>1.35 ± 0.06</strong></td>
</tr>
<tr>
<td>Native [96]</td>
<td>2.35</td>
<td>0.22</td>
<td>1.04</td>
<td>1.38</td>
</tr>
<tr>
<td>Cultivated [96]</td>
<td>1.82</td>
<td>0.19</td>
<td>1.19</td>
<td>1.41</td>
</tr>
<tr>
<td>Native [131]</td>
<td>3.86</td>
<td>0.34</td>
<td>1.14</td>
<td>1.43</td>
</tr>
<tr>
<td>Cultivated [131]</td>
<td>2.04</td>
<td>0.20</td>
<td>1.05</td>
<td>1.18</td>
</tr>
<tr>
<td>Cultivated [122]</td>
<td>2.19</td>
<td>Nd</td>
<td>1.29</td>
<td>Nd</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Subtropical soils</strong></td>
<td></td>
<td></td>
<td><strong>1.21 ± 0.03</strong></td>
<td><strong>1.31 ± 0.10</strong></td>
</tr>
<tr>
<td>No-tillage [36]</td>
<td>2.46</td>
<td>0.21</td>
<td>1.30</td>
<td>1.40</td>
</tr>
<tr>
<td>Conv. tillage [36]</td>
<td>1.35</td>
<td>0.12</td>
<td>1.17</td>
<td>1.21</td>
</tr>
<tr>
<td>No-tillage [45]</td>
<td>2.27</td>
<td>Nd</td>
<td>1.20</td>
<td>Nd</td>
</tr>
<tr>
<td>Conv. tillage [45]</td>
<td>1.01</td>
<td>Nd</td>
<td>1.17</td>
<td>Nd</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Microaggregates</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><strong>Average ± stderr</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><strong>5.20 ± 1.16</strong></td>
<td><strong>2.31 ± 0.69</strong></td>
</tr>
<tr>
<td><strong>Temperate soils</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cultivated [122]</td>
<td>2.19</td>
<td>Nd</td>
<td>2.06</td>
<td>Nd</td>
</tr>
<tr>
<td>Cultivated [239]</td>
<td>0.80</td>
<td>Nd</td>
<td>4.30</td>
<td>Nd</td>
</tr>
<tr>
<td></td>
<td>1.30</td>
<td>Nd</td>
<td>6.90</td>
<td>Nd</td>
</tr>
<tr>
<td></td>
<td>2.00</td>
<td>Nd</td>
<td>10.80</td>
<td>Nd</td>
</tr>
<tr>
<td></td>
<td>2.40</td>
<td>Nd</td>
<td>6.40</td>
<td>Nd</td>
</tr>
<tr>
<td>Native [205]</td>
<td>2.95</td>
<td>0.29</td>
<td>2.49</td>
<td>1.61</td>
</tr>
<tr>
<td>Cultivated [205]</td>
<td>1.07</td>
<td>0.12</td>
<td>3.48</td>
<td>3.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Subtropical soils</strong></td>
<td></td>
<td></td>
<td><strong>1.56 ± 0.20</strong></td>
<td>Nd</td>
</tr>
<tr>
<td>No-tillage [45]</td>
<td>2.27</td>
<td>Nd</td>
<td>1.76</td>
<td>Nd</td>
</tr>
<tr>
<td>Conv. tillage [45]</td>
<td>1.01</td>
<td>Nd</td>
<td>1.37</td>
<td>Nd</td>
</tr>
</tbody>
</table>

*a* stderr = standard error.

*b* Nd = not determined.
soils. In agreement with the Kemper and Rosenau [157] data, tropical soils had a higher Agb for a given OM/clay ratio but a lower significant coefficient of determination ($r^2 = 0.26$ versus 0.95) between Agb and OM/clay than temperate soils (Fig. 3b). If we had had the OM% of the heavy fraction instead of the total soil OM for the tropical soils, then the tropical soils would have had an even higher stability for a given OM/clay ratio than the temperate soils.

In a third test, we used the Henin instability index (Is):

$$\text{Is} = \frac{(A+\text{LF})_{\text{max}}\%}{1/3\text{Ag}\% - 0.9\text{SG}\%}$$

where $(A+\text{LF})_{\text{max}}\%$ is the maximum percentage of dispersed clay + silt fraction (0–20 µm) obtained after three pretreatments: (1) air-dried (2) immersed in alcohol, and (3) immersed in benzene; Ag% is the sum of the percentages of >200 µm aggregates of the three pretreatments retained after shaking in water (30 manual turnings and sieving); SG% is the percent of coarse mineral sand (>200 µm). We opted for this index because it integrates the processes of clay dispersion and aggregate slaking [140]. The beauty of this index is that a close relationship between Is and the infiltration rate ($K$) has been found (Fig. 4), associating this index with a functional attribute of soils. We compared the Is versus C content of medium (16.7–44.3% clay + silt) textured temperate [76] and tropical soils [75]. In agreement with the previous two tests, the temperate soils had a higher instability (i.e., lower stability) and coefficient of determination ($r^2 = 0.31$ versus 0.07) than the tropical soils (Fig. 3c). The regression for tropical soils was also not significant. The average instability indexes for the data set used of the temperate and tropical soils are 1.11 ± 0.04 and 0.55 ± 0.05, respectively. These instability indexes correspond to infiltration rates of 4.2 ± 0.15 and 7.6 ± 0.7 cm·h$^{-1}$ for temperate versus tropical soils.

Figure 3. Relationship between aggregate stability and soil carbon content. (a) Relationship between soil carbon content and aggregate stability measured according to Kemper and Rosenau [157]. Data from [27, 28, 49, 64, 112, 162, 163, 240] for (sub)tropical soils and from [86, 92, 164, 169, 186, 213, 262] for temperate soils. (b) Relationship between soil organic matter, clay and aggregate stability measured after a benzene pretreatment as proposed by Monnier [191]. Data from [46, 75, 183] for tropical soils and from [191] for temperate soils. (c) Relationship between soil carbon content and the instability index measured according to Henin et al. [140]. Data from [75] for tropical soils and from [76] for temperate soils.

Figure 4. Relationship between the Henin instability index (Is) and infiltration rate ($K$). Adapted from [185].
Figure 4. Faster infiltration rates for low activity clay (LAC) tropical soils compared with temperate soils have been attributed to the strong pseudosand aggregation of kaolinite, oxyhydroxides and organic matter in LAC soils [90]. The higher aggregate stability of LAC tropical soils than temperate soils is mostly related to the difference in mineralogy between the soil categories and not to climate differences. This is illustrated in Figure 5, where we compared soils within the same tropical region (Martinique) that are dominated by 1:1 clays and oxides (LAC) versus soils dominated by 2:1 clays (Vertisols). Within these tropical soils, the LAC soils had a greater amount of water-stable aggregates and the amount of water-stable aggregates was less related to total soil organic C content than in the 2:1 clay-dominated soil.

However, it is important to note that the studied Vertisols are easily dispersible, partly because of their high percentage of exchangeable Mg + Na on the ionic complex [1]. Also, Denef et al. [81] found a greater response in aggregation to organic matter addition in an Alfisol with a mixed mineralogy (vermiculite, kaolinite and oxides) compared to an Oxisol dominated by kaolinite and oxides and a Mollisol dominated by 2:1 clays. This greatest response in aggregation in a mixed mineralogy soil is probably a result of all possible binding mechanisms occurring, i.e., electrostatic bindings between 2:1 clays and oxides/2:1 and 1:1 clays/1:1 clays and oxides, in addition to OM functioning as a binding agent between 2:1 clays/2:1 and 1:1 clays.

3. NO-TILLAGE IN TROPICAL VERSUS TEMPERATE CLIMATE

3.1. History of no-tillage in Brazil and the USA

No-tillage (NT) practices have been widely adopted in North and South America. In the US, the adoption of NT spread from several locations (Fig. 6a). In the late 50s and early 60s several agricultural experiments were virtually simultaneously set up in the US Corn Belt (Blacksburg, VA; Columbus, OH; Dixon Springs, IL and Lexington, KY) [141] and the Great Plains (Sidney MT; North Platte, NE and Bushland, TX). A farmer, Harry Young, from Herndon, KY is considered the “father of no-tillage” because he was the first farmer to adopt NT in 1961 [82, 141]. One big push for the development of NT systems was the significant progress in herbicide technology with the introduction of atrazine in the late 50s and paraquat in the early 60s [141]. The farmers’ reasons for switching from conventional tillage (CT) to NT differed somewhat between the Great Plains and the Corn Belt. In the Great Plains, the high moisture retention under NT was a major incentive for adoption of NT practices in this semi-arid region [14, 41, 236, 261]. The high moisture retention allowed farmers to reduce the frequency of fallow, leading to cropping intensification. In the Corn Belt soil erosion control was a major incentive for NT practices. In both regions, the economical advantages of NT have played a role in the adoption of the practice [141]. The Conservation Technology Information Center in the USA reports 21.1 million ha or 17.6% of cropland under NT. However, this includes short-term NT, such as soybean/corn rotations in which soybean is under NT but tillage is used before and during corn growth. Taking this into account, the most current estimate is...
9.9 million ha or 8.8% of cropland is under continuous (> 5 yr) NT management in the USA (Eve, pers. Comm.). In Brazil, the practice of NT spread from the first NT experiment established in 1972 in the state of Paraná (Fig. 6b). The continuous summer soybean/winter wheat rotation widely practiced in Paraná had caused serious erosion problems. The current estimate of annually harvested production under NT covers 13.5 million ha, (Rio Grande do Sul, Santa Catarina and Parana; Federacao Brasileira de Planto Direto Napalha), which accounts for approximately 32% of the cultivated grain area in Brazil, and about 70% is in the southern subtropical states of Brazil. The current expansion frontier is in the central tropical region of the Cerrado (Fig. 6b). The reasons for adoption of NT are: (1) erosion control, (2) smaller number of field operations which reduces fuel input, tractor-time and labor requirements, resulting in lower total cropping costs than with CT practices, and (3) less cropping risks due to the early planting option. In the future, it is projected that NT will expand to 20 to 25 million ha in Brazil between 2007 and 2010. The most important reasons for the future expansion will be agricultural sustainability and environmental benefits.

3.2. Effect of no-tillage on carbon and nitrogen dynamics

3.2.1. Carbon sequestration under no-tillage

It is generally accepted that no-tillage/cover crop systems have beneficial effects on soil fertility by, for example, decreasing erosion, increasing aggregation and potentially increasing SOM contents. It is also known that microbial biomass and earthworm abundance is higher under NT than under CT [87, 88, 201]. In addition to the higher microbial biomass, NT favors the fungal over bacterial populations [34, 91, 115], leading to higher fungal-derived glucosamine to bacterial-derived muramic acid ratios [115, 130]. The preferential stabilization of fungal over bacterial biomass can lead to more efficient C and N cycling [33, 115].

We found that with years under NT, both tropical and temperate soils had an increasing SOC stock compared with CT (Figs. 7 and 8). Based on a first approximation by regression analyses, we found twice as much annual sequestration of C in the 0–10 cm layer of tropical soils versus temperate soils (0.43 versus 0.16 Mg C·ha⁻¹·yr⁻¹; Fig. 7). However, the intercept for the tropical soils is −0.108 Mg C·ha⁻¹ versus 0.145 Mg C·ha⁻¹ for the temperate soils and the regression line for the tropical soils is highly influenced by the 20- and 22-year-old experiments reported by Sa et al. [219]. In addition, only the 0–10 cm surface layer is considered in this analysis whereas plowing depth is often 15–25 cm. A more rigorous comparison between CT and NT systems should include at least the whole plow depth. Carbon inputs are distributed over the whole plow layer or even preferentially to lower depths within the plow layer in CT systems. Therefore, we reanalyzed the data using linear mixed effect modeling (S-PLUS 2000 Professional Release 3; Insightful Corporation, Seattle WA) with time, depth and climate as fixed effects and site as a random effect. The random effect for site is to take into account differences between sites and the dependency between multiple samples across depth within one site (see [198] for further details). We also tried to account for temporal trends at the same site, but there were not enough sites with repeated measurements to account for this effect in the model. The results from this analysis suggest a similar C sequestration rate in the 0–30 cm layer of NT systems in tropical and temperate regions (i.e., 325 ± 113 kg C·ha⁻¹·yr⁻¹) (Fig. 8a). In the tropics, the intercept was a little smaller, but it was not significantly different from the temperate region. The 325 kg C·ha⁻¹·yr⁻¹ sequestration rate falls well within the range of estimates by West and Marland [260] and Eve et al. [100] for temperate regions. West and Marland [260] reported a mean C sequestration rate of 337 kg C·ha⁻¹·yr⁻¹ for 76 long-term experiments and Eve et al. [100] found a mean C sequestration rate of 200–520 kg C·ha⁻¹·yr⁻¹ across regions of the conterminous USA. It is important to note that in both climates an initial decline in soil C was observed under NT compared with CT. This has also been observed in other short-term studies [111, 139, 186]. However, after 6–8 years of NT practices, an accumulation of C was observed for the 0–30 cm layer (Fig. 8a). The initial decrease in C content under NT is probably related to the slower decomposition and lower C input with less incorporation of surface residue carbon. In order to further investigate the effect of NT on C distribution with depth, we used the linear mixed effect model to assess C sequestration to a depth of 50 cm after 20 years of NT (Fig. 8b). There were not enough data available to assess C sequestration at a deeper depth than 50 cm. No differences were found in C sequestration across depth between tropical and temperate soils. In both soil categories, the highest C

![Figure 7](https://example.com/image7.png)
Sequestration due to NT practices was in the surface layers (~7 Mg·ha⁻¹ over 20 years in the 0–10 cm layer). Greater stratification of organic carbon is common in agricultural soils following conversion to no-till (e.g., [11, 105, 186, 221, 256]). The stratification of C is less in CT compared with NT because plowing distributes C inputs more evenly throughout the plow layer. However, a net C sequestration was observed to a depth of 50 cm after 20 years under NT (~3 Mg·ha⁻¹ for the 0–50 cm layer). Consequently, the gains in C at the surface under NT seem to exceed any offsetting C increases at depth in CT.

### 3.2.2. Mechanisms of C sequestration under no-tillage

Since the differences in C input between NT and CT are generally small [203] the differences in C sequestration between the two systems is mostly related to differences in C decomposition rates. Estimates of the MRT of total soil organic C based on the ¹³C natural abundance technique reflect a reduced decomposition rate of C derived from the original vegetation in NT versus CT soils in the temperate region (Tab. VI). All published values for temperate soils corroborated this reduced C turnover under NT compared with CT, except for the non-fertilized treatment in Rosemount, Minnesota (Tab. VI). On average, the MRT was 1.5 times larger under NT than CT for temperate soils. No comparative data between NT and CT could be found for tropical soils.

The direct and indirect effects of tillage on aggregation can partially explain the increased decomposition rate under CT. Conventional tillage is generally detrimental to soil structure by continually exposing new soil to wet-dry and freeze-thaw cycles at the surface [35, 217], thereby increasing the disruption of aggregates. Converting from CT to NT generally increases aggregation (Fig. 9). Increased aggregation under NT is probably not just a direct function of the lack of physical disturbance due to plowing. As mentioned before, fauna and microbial biomass, particularly fungal biomass, is higher under NT [88, 115, 242], which probably results in the formation of more binding agents (e.g., extra-cellular polysaccharides) and the development of hyphal networks enmeshing particles and favoring aggregate stability. The increased aggregation with NT compared with CT during the first 15 years was more pronounced in the tropical soils than in the temperate soils (Fig. 9). This more pronounced aggregation increase does, however, not seem to lead to an

---

**Figure 8.** Carbon sequestration under no-tillage (NT) compared to conventional tillage (CT) with time (a) and by depth (b) in (sub)tropical and temperate soils; carbon sequestration assessed by a linear mixed effect model. Data from [3, 26, 30–32, 35, 38, 59, 65, 77, 79, 109, 111, 113, 114, 139, 164, 172, 173, 177, 194, Paustian and Elliott, unpublished, 214, 219, 220, 241] for (sub)tropical soils and from [2, 11, 22, 42, 50, 54–56, 58, 67, 72, 78, 84, 85, 89, 93, 95, 96, 104, 105, 133, 134, 136, 146, 154, 155, 157, 168, 176, 186, 190, 197, Paustian and Elliott, unpublished, 204, 206, 211, 214, 233, 256, 259, 263, 265] for temperate soils.

---

**Table VI.** Carbon mean residence time (MRT) in no-tillage and conventional tillage systems estimated with ¹³C technique (adopted from [229]).

<table>
<thead>
<tr>
<th>Site [reference]</th>
<th>Cropping, pasture or forest system</th>
<th>Depth (cm)</th>
<th>t¹ (yr)</th>
<th>MRT (yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sidney, Nebraska [230]</td>
<td>Wheat-fallow (NT)</td>
<td>0–20</td>
<td>26</td>
<td>73</td>
</tr>
<tr>
<td></td>
<td>Wheat-fallow (CT)</td>
<td></td>
<td></td>
<td>44</td>
</tr>
<tr>
<td>Delhi, Ontario [218]</td>
<td>Corn (NT)</td>
<td>0–20</td>
<td>5</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>Corn (CT)</td>
<td></td>
<td></td>
<td>14</td>
</tr>
<tr>
<td>Boigneville, France [22]</td>
<td>Corn (NT)</td>
<td>0–30</td>
<td>17</td>
<td>127</td>
</tr>
<tr>
<td></td>
<td>Corn (CT)</td>
<td></td>
<td></td>
<td>55</td>
</tr>
<tr>
<td>Rosemount, Minnesota [72]</td>
<td>Corn (NT, 200 kg N·ha⁻¹·yr⁻¹)</td>
<td>0–30</td>
<td>11</td>
<td>118</td>
</tr>
<tr>
<td></td>
<td>Corn (CT, 200 kg N·ha⁻¹·yr⁻¹)</td>
<td></td>
<td></td>
<td>73</td>
</tr>
<tr>
<td></td>
<td>Corn (NT, 0 kg N·ha⁻¹·yr⁻¹)</td>
<td></td>
<td></td>
<td>54</td>
</tr>
<tr>
<td></td>
<td>Corn (CT, 0 kg N·ha⁻¹·yr⁻¹)</td>
<td></td>
<td></td>
<td>72</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td><strong>NT</strong></td>
<td>80 ± 19</td>
<td><strong>CT</strong></td>
<td>52 ± 11</td>
</tr>
</tbody>
</table>

¹ Time period of experiment.
² stderr = standard error.
increased C sequestration in tropical soils (Fig. 8). This is probably a result of the mineral-mineral bindings that occur in tropical soils. Aggregates formed by this mechanism (i.e., physicochemical aggregates) will form faster but also protect less C upon conversion to NT than aggregates in temperate soils (i.e., biological aggregates). In the latter, the binding action of SOM leads to the incorporation of SOM within aggregates, where it is then protected against decomposition. Consequently, first SOM has to build up before a greater aggregation level is attained and there is a lag-phase associated with this build-up of SOM under NT (Fig. 8a). However, these biological aggregates protect more C because they incorporated more C during their formation.

Six et al. [230, 231] indicated that in addition to the amount of aggregation, the rate of turnover of soil aggregates influences C stabilization. They developed a conceptual model of aggregate and SOM turnover in NT and CT systems in the temperate region (Fig. 10), based on the concepts presented in Figure 2 and additional data collected, specific to NT and CT systems. According to the model, fresh plant material provides the POM that acts as a nucleation site for the growth of fungi and other soil microbes [5, 150, 209]. Microbial growth and the resulting production of extracellular polysaccharides bind residue and soil particles into macroaggregates. Following the incorporation of fresh plant material, microorganisms utilize the more easily decomposable carbohydrates, yielding intra-aggregate POM (iPOM). This iPOM is further decomposed and fragmented into smaller particles, but decomposition occurs at a slower rate within macroaggregates as compared with non-aggregate-associated POM. Some of this finely fragmented iPOM becomes encrusted with mineral particles and microbial byproducts, leading to the formation of microaggregates within macroaggregates and consequently an increased physical protection of the iPOM. As the binding agents generated by decomposition of young POM are lost, highly recalcitrant residual POM and stabilized microaggregates are released. These materials may subsequently be reincorporated into new aggregates (Fig. 10). This occurs in both the CT and NT systems but at different rates and the new macroaggregates do not have the same composition. Six et al. [232] found that

![Figure 9](image-url) Relative soil aggregation under no-tillage (NT) versus conventional tillage (CT), expressed as the ratio of the mean weight diameter of water-stable aggregates. Data from [35, 57, 59, 60, 106, 111, 132, 137, 164, 188, 216, 228] for (sub)tropical soils and from [8, 53, 108, 115, 161, 233, 250, 264] for temperate soils.

![Figure 10](image-url) This conceptual model of the ‘life cycle’ of a macroaggregate shows the diminished formation of new microaggregates within macroaggregates and the reduced protection of carbon within these microaggregates by tillage (adapted from [232]).

### Table VII. Percent microaggregates in macroaggregates and concentrations of inter-microaggregate particulate organic matter (POM) and intra-microaggregate POM in no-tillage (NT) and conventional tillage (CT) surface layer (0–5 cm) layer in Sidney, NE (adopted from [232]).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Microaggregates in macroaggregates&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Inter-microaggregate POM</th>
<th>Intra-microaggregate POM</th>
<th>g C·kg&lt;sup&gt;−1&lt;/sup&gt; sandfree macroaggregates</th>
</tr>
</thead>
<tbody>
<tr>
<td>NT</td>
<td>47.1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.3</td>
<td>11.1</td>
<td></td>
</tr>
<tr>
<td>CT</td>
<td>27.0</td>
<td>2.8</td>
<td>3.8</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>The data presents the% of macroaggregate soil found in microaggregates (sand-corrected).
microaggregates within macroaggregates accounted for only 27% of the macroaggregate weight in CT, compared with 47% of the macroaggregate weight in NT (Tab. VII). Hence, the formation of new microaggregates within macroaggregates was reduced by a factor of about 2 (27% vs. 47%) in CT compared with NT. In addition, the concentration of intra-microaggregate POM-C was three-fold greater in NT while the concentration of inter-microaggregate POM-C (i.e., POM-C held within macroaggregates but not within microaggregates) was two-fold greater in CT compared with NT (Tab. VII). The lower amount of microaggregates within macroaggregates and lower stabilization of intra-microaggregate POM in CT compared with NT is congruent with the faster turnover of macroaggregates in CT compared with NT (Tab. IV). Thus, macroaggregate turnover, microaggregate formation and stabilization of C appear to be linked: a faster turnover of macroaggregates reduces the microaggregate formation within macroaggregates and stabilization of fine iPOM. The greater accumulation of microaggregates rich in fine iPOM contributes to the greater total SOM-C under NT.

3.2.3. Greenhouse gas balance for no-tillage

It was previously suggested that congruent with the stabilization of C and N an increase in N$_2$O fluxes could occur. Therefore, we collected and synthesized published N$_2$O-flux data from CT and NT systems in order to have an example where management changes C and N stabilization and might lead to differences in N$_2$O fluxes. We found data for several temperate sites, but only a single subtropical site (Fig. 11). Consequently, tropical soils could not be considered for this comparison. For temperate soils, N$_2$O-fluxes were often found to be greater under NT than under CT management.

The average N$_2$O-flux difference between NT and CT management presented in Figure 11 is 2.91 ± 0.78 kg N-N$_2$O-ha$^{-1}$-yr$^{-1}$ (Tab. VIII). This is a relatively small flux versus the yearly N input as crop residue and fertilizer, but it is a substantial flux from a global change standpoint. The global warming potential of N$_2$O is 310 CO$_2$ equivalents per N$_2$O molecule, resulting in large global change impacts of small N$_2$O fluxes. This is illustrated in the greenhouse balance presented in Table VIII. Previously, we indicated that NT results in a greater total SOM-C under NT. Six et al. [234] found that the increase in total fine iPOM (i.e., inter- plus intra-microaggregate iPOM) alone accounted, on average, for 21% of the total C difference between NT and CT at four temperate agricultural experiment sites.

![Figure 11. Difference in annual N$_2$O fluxes between no-tillage (NT) and conventional tillage (CT) agroecosystems in temperate and (sub)tropical regions. Data from [126] for the (sub)tropical soils and from [13, 16, 17, 25, 48, 117, 158, 159, 171, 174, 178, 179, 199, 215] for the temperate soils.](image)

Table VIII. Greenhouse gas balance for no-tillage.

<table>
<thead>
<tr>
<th>Greenhouse gas flux</th>
<th>GWP$^a$</th>
<th>CO$_2$-equivalents</th>
</tr>
</thead>
<tbody>
<tr>
<td>325 ± 113 kg C-ha$^{-1}$-yr$^{-1}$</td>
<td>1</td>
<td>1192 ± 414</td>
</tr>
<tr>
<td>−2.91 ± 0.78 kg N$_2$O-N-ha$^{-1}$-yr$^{-1}$</td>
<td>310</td>
<td>−1418 ± 382</td>
</tr>
<tr>
<td>0.42 ± 0.10 kg CH$_4$-C-ha$^{-1}$-yr$^{-1}$</td>
<td>21</td>
<td>11.8 ± 2.8</td>
</tr>
<tr>
<td><strong>Balance</strong></td>
<td></td>
<td><strong>−214</strong></td>
</tr>
</tbody>
</table>

$^a$ GWP = Global warming potential [149].

Table IX. Methane uptake (kg CH$_4$·ha$^{-1}$·yr$^{-1}$) in no-tillage (NT) versus conventional tillage (CT) systems.

<table>
<thead>
<tr>
<th>Site [reference]</th>
<th>NT</th>
<th>CT</th>
<th>NT-CT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scotland [25]</td>
<td>2.56</td>
<td>1.92</td>
<td>0.64</td>
</tr>
<tr>
<td>Michigan, USA [215]</td>
<td>0.89</td>
<td>0.71</td>
<td>0.18</td>
</tr>
<tr>
<td>Nebraska, USA [159]</td>
<td>2.74</td>
<td>2.15</td>
<td>0.59</td>
</tr>
<tr>
<td>Alaska [73]</td>
<td>1.17</td>
<td>0.84</td>
<td>0.33</td>
</tr>
<tr>
<td>Germany [147]</td>
<td>0.95</td>
<td>0.13</td>
<td>0.82</td>
</tr>
<tr>
<td><strong>Average ± stderr</strong></td>
<td><strong>0.42 ± 0.10</strong></td>
<td><strong>0.82 ± 0.33</strong></td>
<td><strong>−214</strong></td>
</tr>
</tbody>
</table>

$^a$ stderr = standard error.

bacteria in NT compared with CT [148]. The higher CH$_4$-uptake and increased C sequestration, however, do not counterbalance the greater N$_2$O-fluxes under NT; this results in an overall negative greenhouse gas balance of 214 kg CO$_2$-equivalents-ha$^{-1}$-yr$^{-1}$. However, it is evident from the error terms...
associated with each of the greenhouse gas fluxes that the error for the balance should also be large. We could not estimate the error associated with the balance because we could not account for interactions between the different greenhouse gas fluxes. Another word of caution is related to the fact that C sequestration with NT only lasts for 20–30 years as C stocks reach a new equilibrium [149], whereas the change in N2O-fluxes with long-term NT is not known. The N2O-fluxes presented in Figure 11 could suggest that the difference in N2O-fluxes between NT and CT decreases with years under NT, but it needs to be pointed out that the older sites in our summary are not fertilized. Consequently, the trend with time in Figure 11 is probably contingent on differences in fertilization between the sites and not a temporal effect.

We presented here a first approximation of a greenhouse gas balance for NT systems compared with CT systems based on average values across a wide range of agroecosystems. Consequently, local differences between agroecosystems might lead to a different balance. In addition, we only included in our data synthesis studies that held other management practices equivalent to NT and CT treatments. Consequently, our comparison did not consider the effects of any other changes in management. For example, NT practices can allow farmers in the Great Plains to intensify (i.e., more crops in rotation) their cropping system, which leads to more C-sequestration. In Brazil, farmers often combine their NT practices with the introduction of cover crops, which also have the potential to augment C sequestration, but also increase the risk of more N2O emissions if cover crops are legumes. Even without considering other management impacts, this first approximation of a greenhouse gas balance for NT and CT still reveals some important issues. First, there is a need to consider the small difference in N2O-fluxes between NT and CT in studies concerning global change. Second, comparative data between NT and CT for N2O-fluxes and CH4-uptake are lacking for tropical soils. Third, from a global change standpoint, agricultural management practices that may reduce N2O-fluxes (e.g., application time and method of N fertilizer, precision farming techniques, alternative crop rotations, type of cover crop, addition of nitrification inhibitors) should be investigated and implemented if found to be feasible.

4. SUMMARY AND CONCLUSIONS

In conclusion, carbon turnover is generally faster in tropical soils than temperate soils. This faster turnover seems to be related to (1) a lower protective capacity of silt and clay particles in tropical than in temperate soils, and (2) a less tight feedback between aggregation and C content. The faster C turnover in tropical soils tends to lead to a proportionally greater stabilization of more recalcitrant C compounds, but this conclusion needs further corroboration. Even though the feedback between SOM and aggregation is less tight in tropical than temperate soils, three "biological" aggregate formation agents were identified for both soil categories, including microbial activity, actively growing roots and fauna (e.g. earthworms). In tropical soils, additional aggregate formation agents are the oxides, leading to the formation of "physicochemical" aggregates. The three biological aggregate formation agents in temperate soils, along with the physicochemical interaction in tropical soils have to work in consortium over time to form water-stable macroaggregates. Since all four aggregate forming processes can occur in soils with mixed mineralogy, we hypothesize that these soils have the highest aggregate formation potential. During formation of water-stable macroaggregates, microaggregates are formed within macroaggregates, which leads to the long-term stabilization of C and N. However, the formation of macroaggregates is suggested to also increase denitrification and N2O emissions. No-tillage practices have been widely adopted in the US and Brazil because of reduced erosion, increased moisture retention, improved soil fertility and generally better soil quality. No-tillage has also been identified as an option to mitigate greenhouse gas emissions [149]. Indeed, we found a general increase in soil C levels (= 325 ± 113 kg C·ha−1·yr−1) under NT compared with CT for both tropical and temperate systems. Increased soil C levels under NT compared with CT are a result of a 1.5 times slower C turnover, partially induced by an increased macroaggregation and a decreased macroaggregate turnover, leading to a stabilization of C within microaggregates. In addition to the soil C sequestration, CH4 uptake (= 0.42 ± 0.10 kg C·CH4·ha−1·yr−1) increased in temperate NT systems. However, N2O emissions were = 2.91 ± 0.78 kg N·N2O·ha−1·yr−1 higher under NT compared with CT in temperate regions. Calculating a greenhouse gas balance by expressing all greenhouse gas fluxes in CO2-equivalents revealed a negative balance of 214 kg C-equivalents·ha−1·yr−1 for temperate soils. Consequently, from an agronomic standpoint NT is beneficial, but from a global change standpoint more research is needed to investigate the interactive effects of tillage, fertilizer application methodology and crop rotation as they affect C-sequestration, CH4-uptake and N2O-fluxes, especially in tropical soils, where data on this matter is lacking.

Acknowledgements: The help with collecting French and Portuguese publications by B. Barthes, P. Machado, L. Zotarelli and T. Amado is greatly appreciated. K. Howerton, S. Schakel and R. Conant are acknowledged for their help with developing the databases for this manuscript. We also would like to especially thank S. Recous and B. Nicolardot for being given the opportunity to present and write up this work for the 11th N Workshop.

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