

Review

# What Agriculture Can Learn from Native Ecosystems in Building Soil Organic Matter: A Review

Timothy E. Crews <sup>1,\*</sup> and Brian E. Rumsey <sup>2</sup>

<sup>1</sup> The Land Institute, 2440 E. Water Well Rd., Salina, KS 67401, USA

<sup>2</sup> Environmental History, University of Kansas, 3650 Wescoe Hall, Lawrence, KS 66045, USA;  
brian.rumsey@gmail.com

\* Correspondence: crews@landinstitute.org; Tel.: +1-785-823-5376

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**Abstract:** Over the last century, researchers and practitioners with diverse backgrounds have articulated the importance of improving soil organic matter (SOM) contents in agricultural soils. More recently, climate change scientists interested in CO<sub>2</sub> sinks, and agroecologists interested in ecological intensification have converged on the goal of building SOM stocks in croplands. The challenge is that agriculture itself is responsible for dramatic losses of SOM. When grassland or forest ecosystems are first converted to agriculture, multiple mechanisms result in SOM declines of between 20% and 70%. Two of the most important mechanisms are the reduction in organic matter inputs from roots following the replacement of perennial vegetation with annual crop species, and increases in microbial respiration when tillage breaks open soil aggregates exposing previously protected organic matter. Many agricultural practices such as conservation tillage and integration of cover crops have been shown to achieve some degree of SOM improvement, but in general adoption of these practices falls short of accumulating the SOM stocks maintained by grasslands, forests or other native ecosystems that agriculture replaced. Two of the overarching reasons why native terrestrial ecosystems have achieved greater soil organic matter levels than human agroecosystems are because they direct a greater percentage of productivity belowground in perennial roots, and they do not require frequent soil disturbance. A growing body of research including that presented in this review suggests that developing perennial grain agroecosystems may hold the greatest promise for agriculture to approach the SOM levels that accumulate in native ecosystems. We present calculations that estimate potential soil organic carbon accumulation rates in fields converted from annual to perennial grains of between 0.13 and 1.70 t ha<sup>-1</sup> year<sup>-1</sup>.

**Keywords:** annual; carbon; ecological intensification; microbial respiration; native ecosystem; perennial; soil organic matter; tillage

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## 1. Introduction

Soils play a central role in the global carbon cycle, storing two to three times as much carbon in organic forms as there is carbon in the atmosphere [1,2]. Changes in land use and land cover rank second behind the combustion of fossil fuels as the most important anthropogenic sources responsible for increasing atmospheric CO<sub>2</sub> concentrations [3]. Agriculture in particular has been responsible for somewhere in the range of 50–78 Pg of C loss to the atmosphere [4,5] This transfer of C represents about 3.8% of global median estimates for total soil organic carbon (SOC) in terrestrial ecosystems [1], and it represents about 5.5 years of global CO<sub>2</sub> emissions from fossil fuels at 2014 rates [6].

There is considerable interest by climate change scientists in reversing the transfer of carbon from soils to atmosphere [7]. There is also a great deal of interest from agricultural scientists in this reversal since the carbon losses from soils originated primarily from the depletion of soil organic matter (SOM)

stocks [8]. In this paper we will discuss SOM, which is 58% carbon, but also includes oxygen, hydrogen, nitrogen, phosphorus, sulfur and other elements in simple and complex molecules [9]. In some cases, however, we will refer to SOC, especially when discussing sequestration of atmospheric carbon in agricultural soils.

Numerous approaches have been suggested for how to re-accumulate in SOM the carbon that has been lost over time from soils to the atmosphere [7,10,11]. To assess the potential SOM-building potential of different approaches, it is important to understand the mechanisms driving the depletion of SOM following the conversion of native ecosystems to agriculture. McLauchlan [8] lists three mechanisms of agricultural reduction in SOM:

1. The quantity of C inputs to soil are reduced in annual cropping systems compared to perennial native vegetation.
2. The physical disturbance of tillage increases SOM decomposition rates. It does this in part by destroying aggregates and physical structure, exposing previously physically protected SOM to decomposition.
3. Tillage and lack of plant cover on agricultural fields enable soil erosion to occur which can remove large quantities of SOM.

Based on McLauchlan's three mechanisms of SOM reduction by agriculture, it follows that the native ecosystems preceding agriculture generally maintained relatively high quantities of C inputs into soils, experienced low levels of soil disturbance and maintained year-round vegetative cover which protected against erosion.

In this review, we will consider proposed changes in agricultural management that have received the greatest attention for their potential to decrease atmospheric CO<sub>2</sub> by increasing SOM stocks. The review is not intended to be an exhaustive evaluation of each different approach. Rather, we will explore further the mechanisms by which agriculture causes reductions in SOM compared to native ecosystems, and we will consider the extent to which different strategies for re-building SOM reverse these mechanisms.

### 1.1. Background

Given our current understanding of how organic matter is lost from soils following disturbances such as tillage, it is safe to suggest that grain agriculture has been responsible for the degradation of soil through loss of organic matter since its inception [8,12–14]. As we will discuss below, the acts of disturbing soil through digging or tillage, coupled with the replacement of perennial vegetation with annual crops, have consistently resulted in SOM depletion [8,14–16]. Nevertheless, almost all traditional, indigenous farmers were, knowingly or not, careful managers of SOM, as fertility-generating cover crop rotations, pasture or shrub fallows, and applications of farmyard manure were essential to maintaining fertility [17,18].

The advent and widespread adoption of synthetic fertilizers in the 20th century allowed farmers to reduce their intensive management of soil organic matter. No longer was it necessary to laboriously haul manure from farmstead to fields, or tie up land that could be producing commercial crops with fertility-building cover crops or pasture rotations. It did not take long before critiques of industrial agriculture were published, such as Sir Albert Howard's *An Agricultural Testament* in 1940 [19] identifying neglect of SOM as a serious mistake. Neglecting SOM translated into reduced nutrient supply, water holding capacity, disease resistance, soil structure, and greater soil erosion [9,19]. Since Howard's time, the goal to improve the organic matter content in croplands has been central to almost every reformist or alternative approach to the industrial model [20–23].

In recent decades, the research community's most common impetus for improving SOM has not been the improvement of agroecosystem functioning but rather the transfer of carbon from CO<sub>2</sub> in the atmosphere to stable forms of organic matter in the soil. Since highly industrialized countries are far from reducing dependency on fossil fuel energy sources, researchers have been

looking for CO<sub>2</sub> sinks to help mitigate anthropogenic greenhouse gas increases [7]. Numerous land management opportunities to sequester carbon have been assessed [8] and global sequestration values of 0.6–1.2 Pg year<sup>-1</sup> or a cumulative cropland sink capacity of 30–60 Pg in the next 50 to 90 years bracket what many researchers think is possible [9,10].

Critics of targeting soil carbon to mitigate climate change point out that the total global sequestration potential represents a small percentage of anthropogenic emissions projected by IPCC models [24]. A recent comprehensive study drawing on field experiments in North America, Europe and Asia suggests that climate warming could drive the loss of 55 Pg of carbon from upper soil horizons by 2050, predominantly in arctic and subarctic regions [25]. Thus very aggressive efforts to sequester C in SOM on farms may be counterbalanced by losses of SOM in tundra for decades to come. But regardless of the role that farm management might play in the global carbon balance, improvements in cropland SOM status would profoundly influence food security, especially in less affluent countries [26].

### 1.2. SOM and Ecological Intensification

The challenge of feeding over nine billion people while minimizing negative impacts to soils, water bodies and biodiversity has led many researchers to embrace the idea of ecological intensification [27,28]. In the twentieth century, agricultural productivity per area of land and per worker increased substantially in industrialized and many developing countries due to input intensification in the forms of synthetic fertilizers, pesticides and irrigation [29]. While hugely successful at increasing yields, input intensification is widely seen as being too costly—economically, socially and environmentally—to maintain or further increase food production in the twenty first century [29,30].

Ecological intensification—supplanting the need for purchased inputs with ecological processes that come about through more sophisticated agroecological design—has been proposed as an alternative to input intensification [31,32]. As with terms such as sustainable, organic, and biological that preceded it, ecological intensification has been used to describe a wide range of practices. The original definition put forth by Cassman [27] focused predominantly on achieving high levels of resource use efficiency and closing yield gaps through the deployment of technologies such as variable rate fertilizer application or sprinkler irrigation. Since Cassman's original paper, researchers have tapped the discipline of community ecology to identify processes that occur broadly in native ecosystems that have the potential to improve agroecosystem functions. For example, community ecologists' understanding of the relationships between plant diversity and insect or pathogen populations has been successfully applied to the control of agricultural pests [33,34].

SOM has also received a great deal of attention by those working on ecological intensification of agriculture because of its multi-faceted influence on crop production [23,33]. SOM is widely known to positively affect soil fertility and nutrient supplying capacity, soil structure, water holding capacity, disease suppression and the functioning of the soil microbiome [35]. Yet in spite of the pivotal role of SOM in ecological intensification, most work to date recommends changes in farm management that fall short of achieving SOM levels of the native ecosystems that preceded agriculture (Table 1). Why the shortfall? We suggest there are areas of ecology that help explain the answer, but have not been applied to agriculture [36]. In the same way the sub-discipline of community ecology sheds light on the management of pest dynamics in agroecosystems, the sub-discipline of ecosystem ecology provides insight into SOM dynamics. For example, the process of how newly developing soils (primary succession) or recently disturbed soils (secondary succession) accumulate SOM has been studied a great deal, and is directly relevant to improving agriculture.

**Table 1.** Mean stocks of soil organic matter of major ecosystem types.

Ecosystem Type	kg SOM m <sup>-2</sup>
Tropical forest	17.9
Temperate forest	20.3
Boreal forest	25.7
Woodland and shrubland	11.9
Tropical savanna	6.4
Temperate grassland	33.1
Tundra and alpine	37.2
Desert scrub	9.7

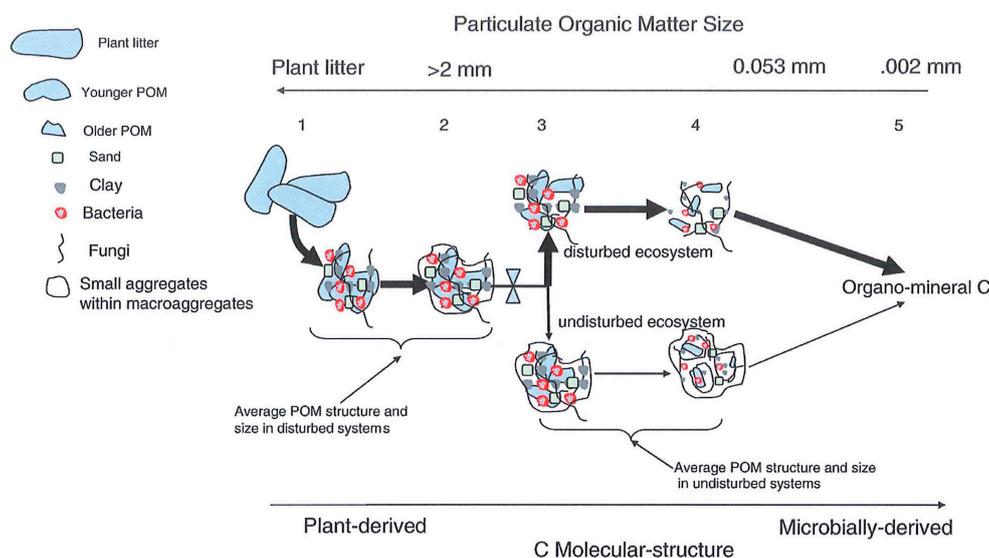
Values derived from Schlesinger [37].

Simply viewed, SOM contents of a soil represents differential rates of organic matter inputs and losses [38]. Inputs ultimately come from photosynthesis, and in most ecosystems originate from plants' roots and shoots growing and senescing on site. Plants are also responsible for supplying organic matter to soils through symbioses with mycorrhizal fungi [39]. When plants and associated mycorrhizae die and senesce, the residues are consumed by microbes, which in turn feed a larger food web of microbes and micro-animals. With time, the belowground food web results in the accumulation of "necromass" or organic matter comprised to a large extent of microbial tissues that stably bind to soil particles and resist further decomposition (Figure 1) [40,41]. As plant matter, fungi, bacteria, nematodes and other members of the soil food web are consumed, carbon-based compounds are mineralized and released mostly in the form of CO<sub>2</sub> to the atmosphere. Surface SOM can also be lost via selective erosion when slopes are steep or soils are exposed by tillage or herbicides, even on gently sloping ground [4,8].

A wide range of organic compounds fall into the category of SOM. For many years, SOM decomposition models emphasized the relative susceptibility of different types of molecules to microbial attack (e.g., cellulose, humus) as a primary governing factor regulating SOM steady state dynamics [40,42,43]. Recently this view has been challenged with evidence that environmental conditions (including the physio-chemical "protection" of organic compounds from microbes and other organisms in soil aggregates) are at least if not more important than SOM recalcitrance at regulating rates of decomposition [40,43,44]. That deserts, grasslands, tundra and rainforests accumulate different amounts of SOM reflects the differential responses of producers (plants) and consumers (microbes, microfauna, arthropods) to environmental conditions. Temperature and precipitation have strong but slightly different influences on the activities of both producers and consumers while soil textural class has greater influence on microbial activity [40]. The SOM levels in tundra and desert ecosystems illustrate how producers and consumers respond differently to climate. Net primary productivity of deserts and tundra is similarly low, about 250 and 180 g C m<sup>-2</sup> y<sup>-1</sup>, respectively [45], while mature tundra ecosystems accrue almost four times the average SOM as deserts (21.6 vs. 5.6 kg C m<sup>-2</sup>, respectively) [37]. Microbial activity is more responsive to the increases in temperature than plant productivity, resulting in a smaller pool of SOM in deserts [35]. At a finer grain scale, plant physiognomy, tissue quality and microbial community composition also interact to influence SOM pool sizes and turnover rates [41,46].

Whether an ecosystem at steady state maintains on average 192 t SOM ha<sup>-1</sup> such as a temperate grassland, or on average 37 t ha<sup>-1</sup> as in tropical savannas [37], the conversion of native ecosystems to annual crop agriculture has the universal effect of reducing SOM levels by 20–70% [15,16]. This decline in SOM is attributable to changes in both producer and consumer activities. When native vegetation is replaced with annual crops, net primary productivity frequently declines [47]. But even when total net primary productivity (NPP) does not decline, the replacement of perennial life-forms with annual crops results in a decrease in allocation of productivity belowground (BNPP) from ~67% to between 13% and 30% [48,49]. There is growing consensus that root turnover and exudates comprise the most

important source of plant inputs for SOM formation [43]. Therefore the change in allocation patterns of producers is one explanation for why SOM declines in annual crop agriculture [8,14,50].



**Figure 1.** Schematic overview of soil aggregate formation and breakdown processes and their effects on particulate organic matter structure and size. The width of the arrows shows the rate of particulate C transfer between pools, as well as the potential for CO<sub>2</sub> loss during the transition. 1. Plant litter (e.g., sloughed roots) entering the soil becomes colonized by bacterial communities and fungi and begins to become coated with clay particles; 2. Macroaggregates (>250 μm) form with particulate organic matter (POM) in their core; 3. In ecosystems that are repeatedly disturbed (e.g., tillage, mining, annual cropping) macroaggregates are rapidly destroyed and the intensely disturbed aggregates persist and POM oxidation proceeds substantially slower; 4. Free (inter-aggregate) POM continues to be rapidly broken down to smaller sizes in disturbed systems; in less disturbed systems such as perennial crops or no-till, POM is incorporated into very small aggregates within the macroaggregate, further contributing to its physical protection; 5. Eventually, some POM C will become mineral-associated. In disturbed ecosystems POM breakdown, loss, and transfer to mineral fractions occurs very rapidly and in these systems POM structure has a younger, more plant-like molecular signature which is dominated by the structure of plant inputs. In ecosystems with minimal disturbance, particulate C with a molecular signature of older, partially decomposed C accumulates in macroaggregates and in the smaller aggregates therein (figure and caption from Grandy and Neff [8]).

The second explanation for SOM decline is that microbial access to SOM increases with tillage, as soil aggregates are broken open, exposing previously protected organic matter (Figure 1) [11,14,43,51,52]. As a result, carbon losses through microbial respiration increase and nutrients such as nitrogen and phosphorus are mineralized. Thus in the conversion of native to agricultural ecosystems, inputs of organic matter into the soil system are reduced, and losses of soil carbon via microbial respiration are increased. In combination, these processes often result in decades of a negative net carbon balance and substantial associated declines in SOM stocks [16,36].

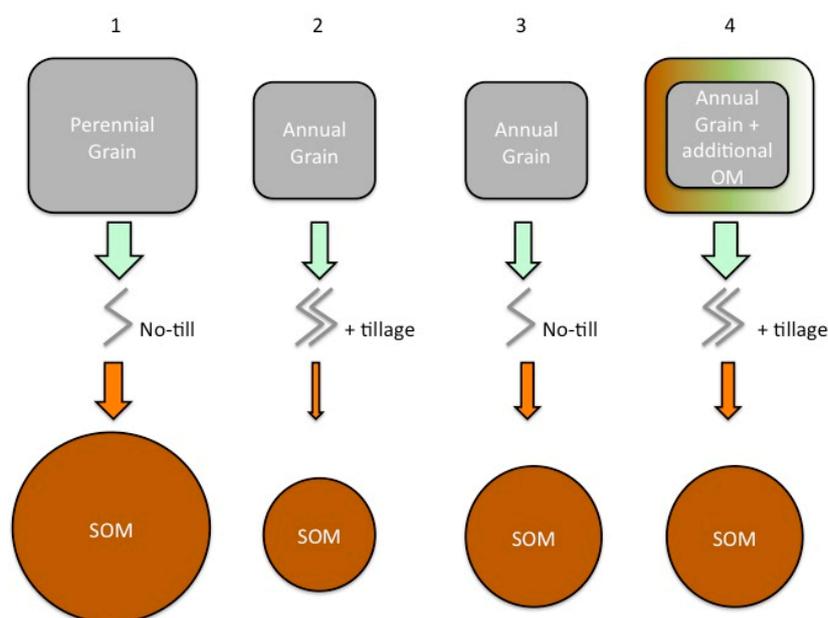
## 2. Approaches to Rebuilding SOM in Croplands

Due to tillage, croplands are estimated to have lost somewhere in the range of 50–78 Pg of carbon globally [4,53]. This figure is important because the amount of C that has been lost also represents the likely maximum level of sustainable accumulation that can theoretically be achieved with changes in management. However, Lal [54] raises the point that many lands have degraded substantially over the time they have been farmed, especially through soil erosion. He speculates that these degraded soils may only be able to re-capture 50–66% of the SOM they contained before agricultural conversion.

Others suggest that more than 90% of original SOM could be re-captured [55]. As discussed above, numerous approaches to re-carbonize soils are receiving research attention, and almost all rely on an underlying mechanism that addresses the producer-consumer (plant-microbe) steady state.

### 2.1. Reducing SOM Losses from Microbial Respiration

Tillage reduction, and especially tillage elimination (no-till), are among the most commonly implemented practices that may increase carbon sequestration, though recent research and commentary has called their effectiveness into question [56,57]. Tillage reduction and elimination are primarily practiced for other reasons than carbon sequestration, including reductions in labor requirements and erosion. The mechanism by which they may promote carbon sequestration—reduced disturbance of physio-chemically protected SOM—is straightforward (Figure 2). However, comparative studies between till and no-till systems have been confounded by the fact that carbon distribution in soil profiles begins to change dramatically as soon as tillage is initiated or discontinued. For example, some studies have found that no-till management can increase carbon levels near the soil surface, but will lower levels of SOC at greater soil depths [50,58]. In a review of research on no-till and C sequestration in Canada, VandenBygaert and colleagues [59] examined the results of almost 100 studies of sequestration rates. When these data were sorted by sampling depth, as done by Baker and colleagues [50], the trials that sampled to 30 cm or less reported an average C accumulation rate of  $0.38 \text{ t C ha}^{-1} \text{ year}^{-1}$ . However, for the trials that sampled to depths greater than 30 cm, the average was a loss of  $0.23 \text{ t C ha}^{-1} \text{ year}^{-1}$ . In a 28-year study in Indiana, Gal and colleagues [60] found that no-till soil C accumulation was over twice as high when measured to 30 cm than when measured to 1 m soil depth.



**Figure 2.** Schematic overview of how crop inputs and microbial mineralization interact to influence SOM stocks. Gray squares represent crop allocation of organic matter inputs belowground. The larger square of perennial grains (1) reflects greater belowground allocation to roots compared to annual grains (2–4). The larger outer square on the far right (4) reflects greater organic matter inputs when annual crop biomass (inner square) is enhanced with addition organic matter inputs from crop residues, cover crops, double cropping or imports of manures or composts from off-site. The grey zig-zag lines represent net microbial mineralization of organic matter inputs. The double zig-zags represent enhanced net microbial mineralization associated with the destruction of soil aggregates caused by tillage. The brown circles represent relative size of SOM pools maintained once the producers (crops) and consumers [soil microbes and other organisms] approach a steady state.

Syswerda and colleagues [61] found that no-till agriculture led to an average SOC accumulation rate of  $0.33 \text{ t C ha}^{-1} \text{ year}^{-1}$  to 1 m soil depth, but noted that higher variability in SOC at greater depths can make meaningful measurements difficult. Kravchenko and Robertson [62] used the study by Syswerda and colleagues [61], to support the argument that the natural variability of carbon stocks in soils is so great that most studies that have failed to see whole profile treatment differences between tilled and no-till management have lacked adequate replication to make defensible statistical comparisons. Baker and colleagues [50] reviewed evidence that reduced tillage reduces root growth, and therefore carbon deposition, at greater depths. They contend that root growth is inhibited by lower temperatures, greater resistance to penetration, higher bulk density, and a lower proportion of aggregates less than 5 mm. Some evidence suggests that any benefits from elimination of tillage may not accrue for several years. Six and colleagues [63] found that while cessation of tillage led to immediate increases in SOC levels in humid climates, it did not begin to increase for more than ten years, on average, in dry climates. While researchers continue to debate the extent of C sequestration attributable to no-till conversion, it makes good theoretical sense that no-till should increase SOM levels over tilled systems at least in silt or clay textured soils given the reduction in soil disturbance and increased protection from microbial attack [14] (Figure 1). That said, the maximum C sequestration achievable in no-till is expected to fall below that of native perennial ecosystems given the lower belowground allocation of annual crops (Figure 2).

## 2.2. Increasing SOM by Increasing Crop Inputs

In contrast to no-till, which has the potential to increase SOM by reducing net microbial mineralization relative to tilled systems, several management approaches have the potential to improve SOM stocks by increasing plant inputs (Figure 2). Historically, crop residues have been removed from fields for animal fodder or eliminated by burning. More recently there has been interest in using residues as biofuels. Leaving and incorporating crop residues in fields may help build SOM, but to what extent is unclear. Reviewing 25 experiments from Europe, North America and Australia, Powlson and colleagues [64] found that annual cereal straw incorporations into soil led to some increases in SOC levels, but that the increases were frequently insignificant. In contrast, Blanco-Canqui found significant declines in SOC with the removal of corn stover, regardless of tillage or cropping system [65].

Another approach to increase organic matter inputs is for farmers to replace periods of bare fallow with secondary or cover crops. In a review of green-manure cover crops covering 139 plots at 37 sites, Poeplau and Don [66] found an average sequestration rate of  $0.32 \text{ t C ha}^{-1} \text{ year}^{-1}$ . West and Post [67] reported that in wheat-fallow rotations, adding a second planting of wheat, reducing fallow but not increasing diversity, led to an average accumulation of  $0.06 \text{ t C ha}^{-1} \text{ year}^{-1}$ . Planting a different crop (sunflower or legume) in place of the fallow led to a relative increase of  $0.51 \text{ t C ha}^{-1} \text{ year}^{-1}$  [67].

Soil carbon that is more deeply buried has been shown to be less vulnerable to decomposition [68]. Modern crop breeding has paid little attention to root depth, favoring instead increased yield and ease of harvest [69,70]. While the root depths of most cultivated crop plants are 1 m or less, there are several that could potentially be bred for roots to 2 m depth [69,70]. Crop breeding work to increase allocation to roots in annual species is just underway so there are few C accumulation data to report. However, Kell posits that crop plants bred for deeper roots could sequester  $50 \text{ t C ha}^{-1}$  over an unspecified amount of time [69]. This is an optimistic calculation, using the total amount of carbon lost via agricultural practices as a lower limit for potential sequestration. Besides C accumulation, deeper roots would also likely provide access to more water and nutrients. However, if aboveground net primary productivity stays constant, total crop productivity may decline if a larger fraction of plant productivity is allocated to root production.

### 2.3. Increasing SOM by Increasing Off-Farm Inputs of Organic Matter

SOM can be increased via additions of off-site inputs such as manure and composted plant matter [11]. Composted plant matter and manure have long been added to croplands to maintain fertility e.g., [71], and while they usually increase SOM where they are applied in the short term, long term improvements without repeated applications are less likely. Increasing SOM through the application of amendments in one ecosystem typically results in a reduction of SOM where the organic matter was originally produced [72]. This is perfectly fine if the goal is to subsidize the fertility of a farm, but not helpful if the goal is net sequestration of atmospheric CO<sub>2</sub>. Exceptions may exist where applications of composted materials prevent the disposal of organic wastes in landfills or slurry ponds, thus avoiding the production of more potent greenhouse gases methane and nitrous oxide [73]. The addition of composted materials to croplands will increase SOM on those lands directly, and often indirectly by increasing crop productivity and associated belowground inputs of organic matter. However, once additions of compost are discontinued, the soils will be expected to experience greater losses of carbon through microbial respiration than gains in carbon through crop production, eventually reaching a steady state similar to what existed before compost was first applied.

Biochar offers a potential exception to the carbon-equilibrium “rule” in which SOM accumulation is limited by a site-specific relationship between plant production inputs and microbial respiration losses. Biochar is a compound produced by the partial combustion of organic matter under low oxygen conditions; a process called pyrolysis. It is highly recalcitrant, leading to a good deal of recent attention to its potential for sequestering carbon in soils. Recalcitrant C is especially attractive for sequestration because if applied to soils at levels above their C equilibrium points, it is expected to persist longer by simple virtue of its resistance to decomposition. Biochar does not occur naturally in large quantities, and to produce quantities that could offer significant levels of soil carbon sequestration, large amounts of biomass must be converted into biochar and then applied to soils. Woolf and colleagues [74] estimate that biochar can potentially offset up to 1.8 Pg C equivalent per year, globally, with half of that number (0.9 Pg) in the form of carbon sequestered in soil, while using biomass at sustainable levels. Other fractions of the 1.8 Pg are replacement of fossil fuels by pyrolysis energy (30%) and avoided emissions of CH<sub>4</sub> and N<sub>2</sub>O (20%).

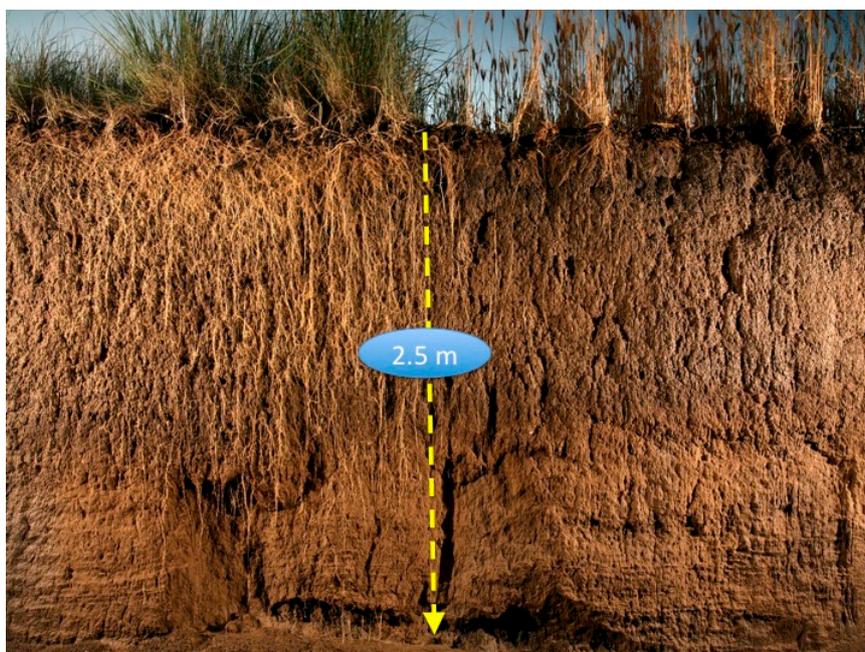
Aside from soil carbon sequestration, the main selling point of biochar is its potential to improve soil tilth and nutrient retention. These benefits are of greatest value in highly weathered soils that occur mainly in the tropics and sub-tropics. Indeed, biochar is thought to have first been used by indigenous Amazonian peoples who cultivated highly weathered Ultisols and Oxisols [75,76]. Biochar’s nutrient content is variable but typically low [76], and since it does not decompose readily, it does not offer the same level of fertility enhancement as composts or manures. While the extent of cropland that could be theoretically treated with biochar is almost unlimited [11], the energy required to harvest and transport biomass coupled with the practicality of producing and distributing the amendment could significantly limit the land area that receives biochar applications.

### 3. Perennials Address the Root of the Problem

Crews and colleagues [36] suggest that the agriculture with the greatest potential to re-capture the SOM of the native ecosystem that preceded it is the one that most closely resembles the native ecosystem in structure and function. They further suggest that the two features that most dramatically distinguish the structure of native ecosystems from agricultural ecosystems is that the former is dominated by perennial, often highly diverse communities, while the latter is dominated by annual, often low diversity communities. Higher belowground allocation of carbon resources, and reduced soil disturbance promote the accumulation of SOM in perennial-based ecosystems up to an equilibrium determined by climate, soil texture and plant tissue chemistry [77]. Studies of soil development following grassland restoration and the establishment of perennial bioenergy crops have measured soil C accumulation rates of 0.33–0.96 and 1.09–1.88 t C ha<sup>-1</sup> year<sup>-1</sup>, respectively (Table 1). Paustian and colleagues [11] estimate that on the order of 100 million ha of degraded lands could theoretically be

planted to perennial grassland or bioenergy species due to marginal productivity or poor suitability as cropland. If perennial grain crops were developed to replace annual grain species, the area that could be planted to perennials today would expand to over one billion hectares [78].

The development of new perennial crop species, while a multi-decadal proposition, is gaining momentum as a promising approach to change the fundamental nature of ecosystem processes in agriculture (e.g., Figure 3) [36,79–81]. Improvements in carbon balance, nutrient retention, soil water uptake efficiency, soil microbiome functions, and weed suppression are predicted as agriculture based on high soil disturbance is replaced by ecosystems that require minimal disturbance [36,82]. The reasons why early agriculturalists originally domesticated annual grain crops reflect the tools, energetic constraints and understanding of biological processes that humans had in the Neolithic era, 5000–10,000 years BP [83]. In the last century, the sciences of evolutionary biology, genetics and plant breeding have expanded tremendously, and many researchers believe it is now possible to breed perennial cereal, legume, fiber and oilseed crops that would yield sufficiently to eventually occupy large areas currently planted to annual species [80,84,85]. When considering steps towards greater agricultural sustainability, the prospect of increasing ecological function through perennial crops is very significant, but so are discussions of land tenure, scale of production, energy return on investment and diversity of crops at both farm and regional scales [86–88].



**Figure 3.** A Mollisol soil profile from central Kansas USA exposing roots to a depth of 2.5 m from perennial wheatgrass on the left (*Thinopyrum intermedium*) and annual wheat (*Triticum aestivum*) on the right. The wheatgrass is being bred to produce the grain Kernza™ (photo: J. Richardson and J. Glover).

Research undertaken to quantify rates of SOM accumulation under perennial grain proto-crops that are being currently bred is lacking. However, numerous studies, including many meta-analyses, have evaluated SOM changes when lands managed for annual crop production were converted to perennial grasslands [89–99]. Rates of C accumulation in diverse grassland plantings range from 0.33–1.01 t ha<sup>-1</sup> year<sup>-1</sup> in meta-analyses and reviews, whereas high-yielding, low diversity perennial grasses for bioenergy have been found to increase SOC in the range of 1.09–1.88 t ha<sup>-1</sup> year<sup>-1</sup> (Table 1). The range of 0.3–0.5 t C ha<sup>-1</sup> year<sup>-1</sup> accumulated following adoption of no-till or other SOM-enhancing management approaches described above, overlaps with the low end of the carbon accumulation range of perennial grasslands.

The wide range of carbon accumulation values reported in Table 2 reflects a combination of methodological, geographical and biological variation. Two of the greatest methodological challenges encountered when comparing studies stem from researchers not sampling SOM to the same soil depth [99,100], and not using a uniform approach to estimate and correct for bulk density differences across study sites [101]. The geographic variation reflects differences in grassland productivity and SOM protection driven to a large extent by climate and soil texture [102]. The biological factors that contribute to wide variation in SOC accumulation include the productivity of the grassland species, the degree to which soil microbial populations are nutrient limited [103], and years since conversion to perennial vegetation [102]. Taken together, it is possible to interpret how multiple factors contribute to the broad differences in measured SOC accumulation rates (Table 2). For example, the contrast in low accumulation rates for pasture or restored native grasslands versus higher accumulation rates for bioenergy crops is likely explained by the latter being planted, on average, in more favorable climates, bred for higher productivity, and more commonly fertilized with nitrogen, which not only increases productivity, but can also increase microbial biomass and in turn necromass.

**Table 2.** Summary of field-based estimations of soil carbon accumulation rates in the conversion of annual agriculture to perennial grassland or perennial bioenergy crops.

Study Type	Geographic Areas	Mean C Accumulation t ha <sup>-1</sup> Year <sup>-1</sup>	Depths <sup>1</sup> Sampled (cm)	No. Studies or Sites Included	Reference
Annual crops to perennial pasture or restored native grassland					
Meta-analysis	Central Europe, N. America, Russia	0.72	0–30	273	[89]
Meta-analysis	Russia	0.96	20	45	[90]
Meta-analysis	Tropical to temperate	0.33	5–300	39	[91]
Meta-analysis	Americas, UK, Australia	1.01	NR <sup>2</sup>	23	[92]
Review	N. Midwest USA	0.44–0.5	25	39	[93]
Review	W. Canada	0.59	NR	17	[94]
Chronosequences	Illinois, USA	0.43	100	16	[95]
Review	France	0.50	NR	-	[96]
Review	NR	0.3–1.0	NR	-	[97]
Annual crops to perennial bioenergy crops					
Meta-analysis	NR	1.14–1.88	0–150	23	[98]
Meta-analysis	N. & S. America, Europe				
Miscanthus	S. Africa, Asia	1.09	100	13	[99]
Switchgrass		1.28	100	40	[99]

<sup>1</sup> when a range is reported, it indicates that multiple soil depths falling within the range were included in the study;

<sup>2</sup> NR = not reported.

### Potential Soil Carbon Accumulation with Perennial Grains

The numerous studies documenting SOC accumulation in the conversion of tilled croplands to perennial grasslands have provided a reasonably constrained range of accumulation rates (Table 2). The studies have also highlighted areas of uncertainty that have considerable bearing on the maximum SOC accumulation a given agroecosystem is likely to achieve. Chief among the areas of uncertainty are (1) depth of SOM deposition under different perennial species, and relative stability of deeply deposited SOM; (2) duration of positive net SOM accumulation following conversion from arable land; and (3) percentage of SOM accumulated under the original native ecosystem that can be achieved in the newly established grassland.

To make a rough estimation of how much SOC might be expected to accumulate with a conversion of annual to perennial grains, we used the following equations that included country-specific data from FAOSTAT [78] for land area dedicated to grain crops and SOM levels to 30 cm.

$$C(\text{ha}) = \%SOC \times C_{\text{Lost}} \times C_{\text{Reseq}} \quad (1)$$

$C(\text{ha})$  = potential SOC sequestration per ha in kg,  $\%SOC$  =  $\%SOC$  mass per unit area,  $C_{\text{Lost}}$  = Proportion of soil carbon lost via cultivation,  $C_{\text{Reseq}}$  = Percentage of  $C_{\text{Lost}}$  that can be resequenced.

To calculate potential SOC sequestration per hectare, we multiplied average SOC mass per hectare (data on a country-level basis, derived from FAOSTAT) by a factor representing the proportion of soil carbon lost to cultivation (supplied by us, adjusted for different scenarios). This resulting number, the mass of SOC lost to cultivation, was then multiplied by a factor representing the percentage of SOC lost to cultivation that could potentially be re-sequestered (again, supplied by us, adjusted for different scenarios). This provided us with the mass of SOC per hectare that could potentially be sequestered by conversion from annual to perennial crops.

$$T = C(\text{ha}) \times A \quad (2)$$

$T$  = Total potential soil carbon sequestration in Mg,  $A$  = Area (ha) planted to annual grains per country (cereals, pulses, cotton, annual oilseed).

To make a theoretical projection of the global potential for SOC sequestration by perennial crops, we multiplied each country's average potential SOC sequestration per hectare by the country's total area planted to annual crops that could hypothetically be replaced one day by perennials, including cereals, pulses, cotton, and oilseed crops, and then adding the sums for all countries.

Table 3 depicts global estimations of potential soil C accumulation in the transition from annual to perennial grain crops based on different assumptions for depth of SOM deposition (30 cm vs. whole profile), duration of positive SOM accumulation (30, 60, 90 years), % of original SOC lost with cultivation (30 or 50), and % of original SOC accumulation possible (70 or 90). Our calculations estimate a potential global accumulation of 13–54 Pg C in grain cropland soils of all countries following conversion to perennial grain agriculture.

**Table 3.** Coarse estimates of soil C accumulation following the conversion of annual to perennial grain agroecosystems using a range of assumptions.

Assumptions	Area	Potential C Accumulation	SOC Accumulation Year <sup>-1</sup> Until Equilibrium Reached		
			30 Years	60 Years	90 Years
Conservative Baseline <sup>1</sup>	Global (Pg)	13	0.42	0.21	0.14
	Average t ha <sup>-1</sup>	11.9	0.40	0.20	0.13
Full profile C accumulation <sup>2</sup>	Global (Pg)	25	0.84	0.42	0.28
	Average t ha <sup>-1</sup>	23.9	0.80	0.40	0.27
50% SOC lost with conversion <sup>3</sup>	Global (Pg)	21	0.70	0.35	0.23
	Average t ha <sup>-1</sup>	19.9	0.66	0.33	0.22
90% of potential Accumulation <sup>4</sup>	Global (Pg)	16	0.54	0.27	0.18
	Average t ha <sup>-1</sup>	15.3	0.51	0.26	0.17
Maximum Accumulation <sup>5</sup>	Global (Pg)	54	1.80	0.90	0.60
	Average t ha <sup>-1</sup>	51.2	1.70	0.85	0.57

<sup>1</sup> conservative baseline assumptions are that 30% of SOC has been lost in conversion to annual agriculture, %SOC values for 0–30cm soil depth, 70% of the lost SOC can be recovered with a conversion back to perennial crop species. <sup>2</sup> assumptions equal to conservative baseline, except C accumulation to 100cm is assumed to be twice that of 30 cm [99,100]. <sup>3</sup> assumptions equal to conservative baseline, except percentage loss of SOC following conversion to annual agriculture is increased from 30 to 50% [4]. <sup>4</sup> assumptions equal to conservative, except soils are expected to accumulate 90% of the SOC lost in conversion to annual agriculture [55]. <sup>5</sup> cumulative change in C accumulation when all three modifications of conservative baseline assumptions are made (full profile, 50% SOC lost, 90% of potential). Overall model based on 2014 FAOSTAT data for country-specific values of land area in annual row crops, SOC to 30 cm. Bulk density (BD) conversions were made using the equation  $BD = 100 / (\%SOM / 0.244) + ((100 - \%SOM) / \text{mineral BD})$  with  $SOM = SOC \times 1.72$  and  $\text{mineral BD} = 1.64$  [89,91].

Only the assumptions resulting in maximum C accumulation (54 Pg) fall within the range of predicted C sinks of 50–78 Pg for cropland soils [4,24]. Using different assumption sets, our calculations estimate SOC accumulation rates ranging from 0.13 to 1.70 t ha<sup>-1</sup> year<sup>-1</sup>. This range of values is similar to the empirically measured range of SOC accumulation rates of 0.33–1.88 t ha<sup>-1</sup> year<sup>-1</sup> from grassland and bioenergy studies (Table 2). Possibly the least realistic assumption we make in our modeling exercise was a linear 90-year time span for approaching SOM steady state. This assumption resulted in low rates of C accumulation per year, and contrasts with most studies that suggest C accumulation rates reaching a maximum in the first few decades following conversion to perennials, and then declining substantially by year fifty [54,55,89,91].

#### 4. The Role of Diversity in Improving SOM

Discussions of SOM dynamics in this paper have primarily focused on the importance of perennial vegetation in soil development. However, plant diversity is also an important consideration. Ecologists have firmly established that single species or monoculture plantings of a crop will eventually decline in productivity due to pathogen load or insect herbivory [104–106]. Growing different plant functional groups together (e.g., legumes and grasses) can also result in greater productivity due to niche partitioning or complementarity [107]. To the extent that NPP translates into belowground organic matter production, diversity in perennial cropping systems is predicted to affect SOM stocks and rates of accumulation [108].

Crop diversity can also affect SOM through its effect on the quality of organic matter entering the soil. For example, Ampleman and colleagues [109] compared SOM accumulation in stands dominated by C<sub>4</sub> grasses with more diverse forb-grass prairie mixtures. Soils planted to >66% C<sub>4</sub> grasses showed a decline of 0.31 t C ha<sup>-1</sup> year<sup>-1</sup> over 33 years, whereas the soils planted to forb dominated and forb-grass mixes increased in SOC at the rate of 0.56 and 0.27 t ha<sup>-1</sup> year<sup>-1</sup>, respectively. One explanation for this and similarly low rates of SOC accumulation in other settings is that soil microbial populations are limited by nutrients, especially N [92]. When soil nutrient availability is insufficient to meet the stoichiometric ratios of the microbial biomass, many plants appear to be able to induce mineralization of nutrients held in SOM by priming the rhizosphere with labile carbon exudates [109]. While this can induce a flush of microbial activity, it is different from stimulating large microbial populations with more stoichiometrically-balanced inputs which can lead to the accumulation of necromass and ultimately physio-chemically stabilized SOM [103,110].

#### 5. Conclusions

SOM is widely expected to play a central role in efforts to transition agriculture from an industrial model where high volumes of energetically expensive and environmentally damaging inputs are required to achieve a high volume of outputs, to an ecosystem model, where adequate food is produced within sustainable energy and biogeochemical boundaries of the planet [23,29,36,111]. Yet in spite of its agreed upon importance, SOM has proven difficult for farmers to build. Few grain-producing agroecosystems feature SOM levels that match the native ecosystems that preceded them. Why is this the case? While many questions still exist, ecosystem science has advanced a great deal in identifying the factors that regulate SOM formation and mineralization. Two processes that contribute greatly to the accumulation of SOM are the allocation of plant productivity belowground by roots [50], and the stabilization and protection of organic compounds in soil aggregates [51]. Perennial vegetation promotes both of these processes. Indeed, perennials are essential for soil and ecosystem development to progress in almost all native terrestrial ecosystems [36]. In contrast, annual crops allocate a smaller amount of biomass belowground and they have historically required tillage which breaks apart soil aggregates and induces microbial mineralization of SOM.

Most approaches to increasing cropland SOM either strive to increase organic matter inputs (adding cover crops, breeding deep-rooted annuals, amending with biochar) or decrease soil disturbance (no-till), but the nature of annual crop production makes it difficult to address both

processes. In basic terms, this explains why SOM levels in annual grain agriculture rarely match levels attained by native ecosystems. Ecosystem theory, and empirical evidence from ex-arable grasslands and bioenergy crops suggest that perennial grain crops will facilitate SOM accumulation and soil development similar to what occurs in native ecosystems [36]. There are many challenges to achieving such a “natural systems agriculture”. For example, it is not yet clear how farmers will facilitate succession or stand replacement in shifting from one perennial crop to another without inducing large losses of SOM from tillage [112]. Challenges notwithstanding, an agriculture based on diverse perennial crops has great potential for improving SOM contents and achieving goals of ecological intensification and climate change mitigation in agriculture.

Working on the ecological sustainability of agriculture addresses an essential part of rectifying the food system as a whole, but other parts of the whole need attention as well [113]. For example, progress will be limited as long as government subsidies promote large-scale industrial production of a few annual grain crops [88]. The consolidation of corporations that market seeds and other inputs as well as corporations that purchase and process grain can also profoundly restrict systemic changes in the food system. Moreover, global governance and economic structures will need to align in order to advance changes in food systems that are embedded in much larger socio-economic systems [114].

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