

Managing plant surplus carbon to generate soil organic matter in regenerative agriculture

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Soil degradation is a global problem. A third of the planet's land is already severely degraded, and soil is being degraded at a speed that threatens the health of the planet and the civilizations that depend on it (Whitmee et al. 2015). Depletion of soil organic carbon (SOC) resulting from extractive agriculture is a key driver of soil degradation (Lal et al. 2015). Much of this SOC has been released to the atmosphere as carbon dioxide (CO₂), a potent greenhouse gas contributing to ongoing climate change, including extreme weather events. Soil degradation also diminishes water infiltration and retention, biodiversity, watershed functions, and the nutritional value of food. Reversing soil degradation is a top global priority (UNCCD 2017).

Yields of major crops have increased substantially in the last century, primarily through intensive chemical fertilization. However, the greater aboveground plant biomass production resulting from chemical fertilization has usually not led to proportional gains in plant inputs to soil and soil organic matter (SOM) accrual (Khan et al. 2007; Man et al. 2021). Instead, these practices, in concert with other intensive agricultural practices such as intensive tillage, monoculture, application of pesticides, and bare fallows, have caused declines in SOM, increases in greenhouse gas emissions, and pollution of waterways (Loisel et al. 2019). However, adopting regenerative agricultural practices, such as substituting chemical with organic fertilizers like compost or manure, reducing tillage, intensifying and diversifying crop rotations, and cover cropping, often increase SOM (McClelland et al. 2021). The mechanisms underlying the positive effects of regenerative agricultural practices on SOM, however, are not well understood. Elucidating these mechanisms would advance our capacity to design agricultural strategies to reliably enhance agroecosystem SOM content, which would assist in reversing soil degradation

and enhancing soil quality, food security, and climate change mitigation globally (Amelung et al. 2020).

Recent conceptual developments in SOM highlight the direct contribution of microbial products to SOM generation and the key role of soluble plant inputs such as rhizodeposits in generating microbial necromass and SOM. There is now abundant evidence that microbially transformed materials dominate in persistent, mineral-associated organic matter (MAOM) in agricultural soils (Kögel-Knabner 2017), with microbial necromass accounting for more than 50% of the SOC (Liang et al. 2019). Because of the high disturbance and low plant inputs in agricultural systems, MAOM represents the largest component of SOM: over 70% of the SOC of European agricultural topsoils was found in MAOM (Lugato et al. 2021).

The production of microbial biomass, necromass, extracellular metabolites, and MAOM are stimulated by water-soluble plant materials (Haddix et al. 2016; Liang et al. 2017). Living plant roots release 5% to 21% of their photosynthetically fixed C as soluble sugars, amino acids, or secondary metabolites (Huang et al. 2014). Dissolved organic matter from living roots (i.e., exudates and other rhizodeposits) is more efficient than structural litter inputs in forming MAOM (Sokol et al. 2019). The amount and composition of root exudates vary with plant nutritional status (Carvalhais et al. 2011; Tawarayama et al. 2014) and among plant species (Herz et al. 2018; Dietz et al. 2020), and it may therefore be possible to manipulate the abundance and composition of root exudates by modifying the nutritional status or species composition of plants.

Under what conditions do plants exude more C from roots? Prescott et al. (2020) suggested that plants exude more C when their aboveground growth is inhibited but photosynthesis continues, such that the plant generates surplus photosynthetic C, some of which is translocated

belowground. These conditions include inadequate nutrients (nitrogen [N] or phosphorus [P]), water, or temperature, which cause leaf growth to decline while C fixation continues (albeit at a reduced rate), resulting in surplus photo-assimilates. Some of the surplus C-rich metabolites are transported through the phloem, as deficiencies of N and P do not interfere with phloem loading. Depending on the strengths of the various sinks, some of the surplus metabolites end up in roots, where they are further metabolized, and some are used for root growth or stored. Remaining surplus C is exuded directly from roots or metabolized by mycorrhizal fungi, which exude materials they have in surplus. Exudates from roots and fungal hyphae are metabolized by microbes (largely heterotrophic bacteria) associated with their structures (Kaiser et al. 2015), and converted into microbial biomass, necromass, and SOM.

The key to regenerating SOM may, therefore, be maintaining plants under conditions in which they produce surplus photosynthates and release them from their roots or through root associates such as mycorrhizal fungi. The surplus C framework (Prescott et al. 2020) suggests that this could be achieved by maintaining N, P, or water availability at levels at which plants are vigorous but slightly deficient in one factor, such that not all photosynthates are assimilated into aboveground tissues. This contrasts with high rates of N and P addition, which increase the aboveground sink for photosynthates and reduce fluxes of

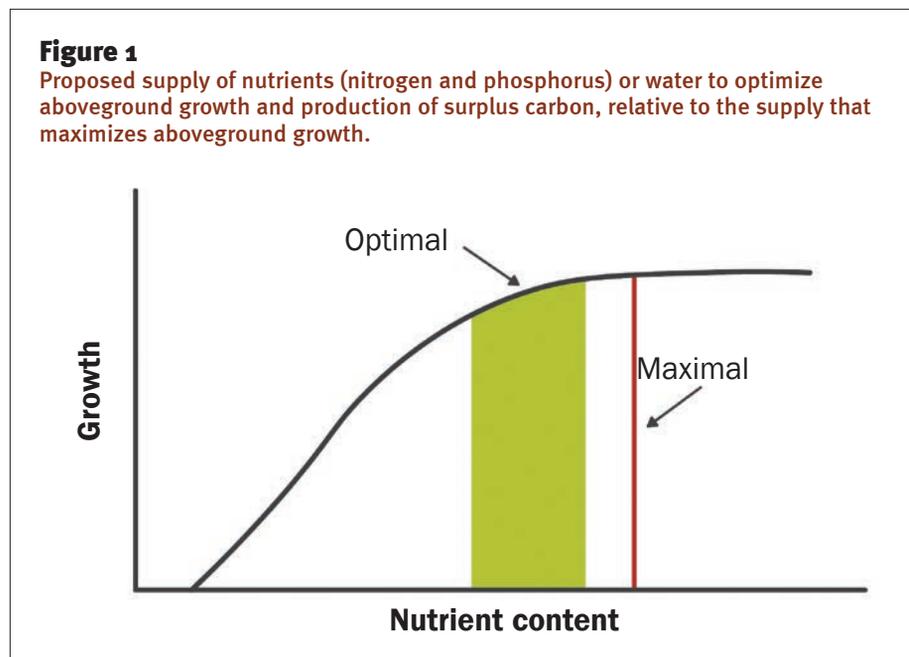
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Received September 20, 2021.

C to roots and soil. Nitrogen fertilization has been shown to reduce belowground C allocation (Pausch and Kuzyakov 2018), root:shoot biomass ratios (Bonifas et al. 2005; Hirte et al. 2018), quantities of root exudates (Dawson et al. 2000; Kaštovská et al. 2017) and other plant-derived labile C compounds in the soil (Man et al. 2021), and transfer of plant-derived C from mycorrhizal hyphae to soil bacteria (Gorka et al. 2019). In contrast, mild deficiencies of N or P can enhance root growth (particularly root length [Lynch et al. 2012]). Likewise, moderate drought (but not extreme drought [Preece and Peñuelas 2016]) can increase root exudation (Karlowsky et al. 2018; Williams and de Vries 2020), rhizodeposition (Meier et al. 2020), and mycorrhizal abundance (Kundel et al. 2020). The key to producing crops without degrading soil may therefore be to determine the levels of nutrient and water availability that support high rates of photosynthesis and aboveground growth but also slightly constrain the aboveground sink for photo-assimilates, such that a portion is transported belowground to support the soil ecosystem. We suggest the following three principles to guide adaptation of agricultural practices for this purpose:

Principle 1. Manage Availability of Nitrogen, Phosphorus, and/or Water to Maintain a Continuous Flux of Soluble Carbon Belowground to Support Soil Organisms. Providing N or P in amounts slightly below the level that maximizes aboveground growth results in the production of surplus photosynthates, some of which are transported belowground and a portion are released as root exudates (Prescott et al. 2020). The *optimal* rate of nutrient supply is that which supports high aboveground plant growth while also maintaining a continuous supply of root exudates to promote soil microbial biomass and SOM formation (figure 1). The *optimal* amount of N or P is less than that which generates maximum aboveground biomass. Substituting synthetic fertilizers with organic fertilizers also assists in supporting root growth and exudation (Zhang et al. 2019).

Principle 2. Incorporate Leguminous Plants. Soil microbial biomass produc-



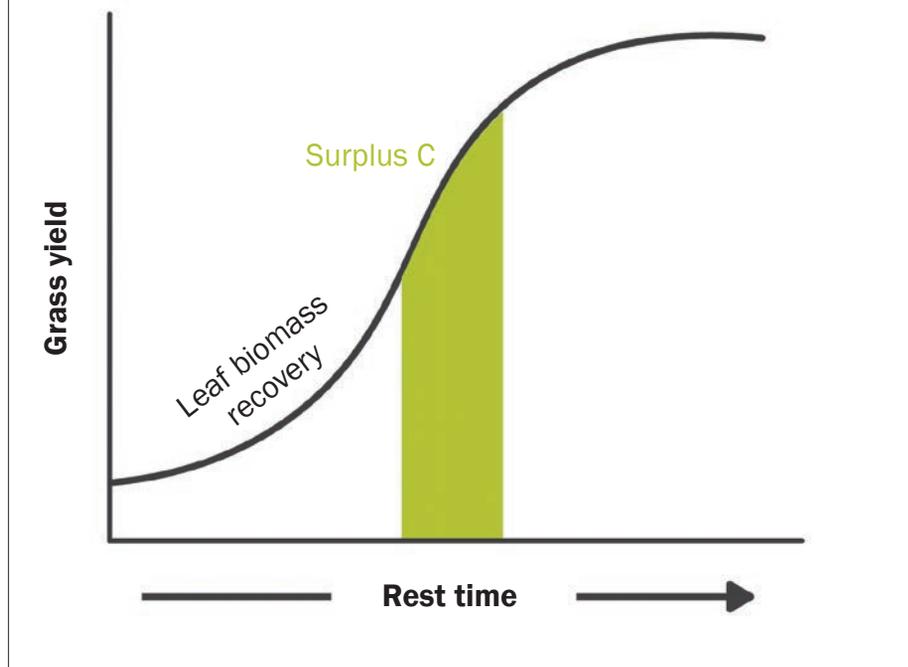
tion requires substantial quantities of N in addition to labile C. Soil microbes and SOM have low C:N ratio relative to plant litter (Paul 2007), and N-rich microbial products such as amino sugars are important precursors of MAOM (Kopittke et al. 2020). Available N increases microbial C use efficiency, microbial biomass, and MAOM stocks (Cotrufo et al. 2013; Mosier et al. 2021). Applying chemical N fertilizers can counteract the beneficial effects of heightened N availability on MAOM generation by reducing belowground C flux in plants. However, including leguminous plants in agricultural systems provides both C and N in soluble forms and in the rhizosphere, where they are likely to generate soil microbial biomass and SOM. Root exudates from leguminous plants have higher concentrations of N-rich compounds such as amino acids and ammonium (NH_4) than other types of plants (Fustec et al. 2010). Upon release into the rhizosphere (or hyphosphere in mycorrhizal plants), N-rich exudates are rapidly incorporated by soil microbes (deNeergard and Gorissen 2004), which stimulates production of new microbial biomass, necromass, and SOM (Kopittke et al. 2020). Exudation of N-rich compounds may also inhibit degradation of existing SOM by reducing the liberation of oxidative enzymes to “mine N” from SOM (Bengston et al. 2012). Greater

stocks of SOC are often found beneath leguminous plant species (Drinkwater et al. 1998; Gregorich et al. 2001), and forage grasses and legume mixes are a traditional practice for maintaining soil fertility (Franzliebbers 2012). Release of exudates rich in both C and N should be maximal when plant aboveground growth is limited by P, such that both C and N are in surplus (Cardenas et al. 2021). Therefore, management of plant P supply (figure 1) could be key to optimizing aboveground growth and release of C- and N-rich exudates into the soil.

Principle 3. In Pastures, Maintain Grass in the Portion of the Growth Phase in which Leaves Generate Surplus Carbon. Harnessing surplus plant C to enhance SOM regeneration might also be achieved by managing grazing times in perennial pastures. In unfertilized pastures, plants probably generate surplus photosynthate during the later portion of the active growth phase (Phase 2), when leaf biomass has recovered and photosynthesis rates are high (figure 2). It may therefore be possible to optimize aboveground biomass and belowground C flux by maximizing the time that grass spends in the active growth phase. This would entail prohibiting grazing while grass is in the recovery period (Phase 1), but grazing prior to the onset of Phase 3 in order to maintain high rates of photosynthesis. Indeed, maximizing the

Figure 2

Proposed period of time in which grass is in the portion of the active growth phase in which leaves generate surplus carbon (C).



length of the “rest” period between grazing events is one of the central tenets of regenerative grazing (Spratt et al. 2021) and underlies the positive effect of adaptive multipaddock (AMP) grazing systems on SOC stocks (Teague et al. 2010; Byrnes et al. 2018). Increased root exudation and rhizosphere microbial biomass has been reported where grazing intensity is moderate and followed by a rest period (Hamilton and Frank 2001; Sun et al. 2017). The positive effects of AMP grazing on SOC stocks may therefore be related to the production and exudation of plant surplus C during the rest period. The positive effect of AMP grazing on soil MAOM stocks is also positively related to stocks of N in the pastures (Mosier et al. 2021). Intensive N fertilization of pastures could compromise long-term soil fertility by reducing belowground fluxes of labile C and reducing the proportional abundances of fungi and gram-positive bacteria, which contribute more than gram-negative bacteria to SOM (Tandon et al. 2019). However, including legumes, which exude both C and N, would promote production of microbial biomass and MAOM. The large increase in microbial populations in

the rhizosphere of grasses in the presence of urine from grazing animals (Dawson et al. 2000) further emphasizes the important interactions between available C and N in the rhizosphere that generate microbial biomass and MAOM.

LINKS BETWEEN PLANT SURPLUS CARBON AND REGENERATIVE AGRICULTURAL PRACTICES

The three suggested mechanisms for managing plant surplus C and N to encourage SOM generation are closely aligned with the principles of regenerative agriculture (table 1). The complementarity of these approaches suggests that the beneficial effects of regenerative practices in restoring SOM may be at least partly attributable to their role in promoting the production of plant surplus C and N and their release belowground (figure 3).

Withholding one of the resources that limit aboveground growth in order to allow flux of plant surplus C to the soil will result in lower crop yields than those attained through intensive fertilization or irrigation or both. However, enhanced SOM levels and plant-microbe-soil associations will improve soil structure and

fertility, water infiltration and retention, and nutrient cycling and retention (Lal 2020), which should safeguard long-term agroecosystem productivity and resilience (figure. 3). Fertilization can increase plant susceptibility to drought, through higher transpiration or reduced root:shoot ratios (Van Sundert et al. 2021; Kübert et al. 2019). Compared with a conventional high-fertilization system, low-input maize (*Zea mays* L.) cropping systems in which soil fertility was maintained by leguminous cover crops and compost had greater SOC (Drinkwater et al. 1998), root length density (Pallant et al. 1997), and abundance of arbuscular mycorrhizal fungi (Douds et al. 1993). Long-term average yields were similar, and the low-input system outperformed the conventional system in years of drought (Lotter et al. 2003). In another low-input system that incorporated legumes and manure, OM was greater and more evenly distributed, and maize rooted deeper in the soil compared with a high-fertilizer-input system (Lazicki et al. 2016). Crop yield was similar or greater in the low-input system than in the high-input system. Judicial use of fertilizers, as practiced in regenerative agriculture, has additional benefits in reduced input costs, nitrous oxide (N₂O) emissions, and pollution of waterways.

ENHANCING THE EFFECTIVENESS OF REGENERATIVE AGRICULTURE THROUGH MANAGEMENT OF PLANT SURPLUS CARBON: A RESEARCH AGENDA

We have proposed plant surplus C as a mechanism through which crops could be managed to promote SOM generation with minimal loss of yield. Several hypotheses associated with this proposed mechanism warrant investigation.

We propose that there are “sweet spots” with respect to availabilities of plant resources within which plants are actively photosynthesizing but aboveground sinks for photosynthate are constrained by availability of N, P, or water, and that this condition promotes belowground transport and exudation of C-rich labile compounds. This could be tested by simultaneous measurements of C-fixation, aboveground and belowground biomass production, and root exudation in plants

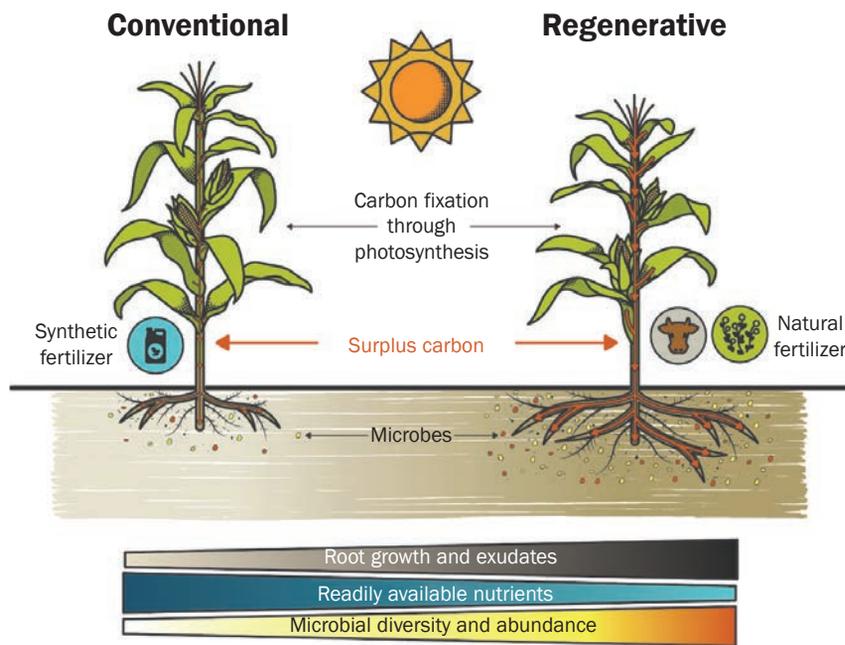
Table 1

Suggested principles for promoting generation of soil organic matter through the production and release of plant surplus carbon (C), and regenerative agricultural principles relevant to each principle.

Surplus C principle	Regenerative agricultural principles
Provide nutrients and water in amounts that optimize aboveground yield and belowground C flux	Use fertilizers and irrigation judiciously; use organic amendments; maintain living roots
Include plants with nitrogen (N)-fixing associates that release exudates rich in C and N	Incorporate legumes in crop mixtures, cover crops, rotations, and pastures; increase crop diversity
Maximize time grass is in the portion of the active growth phase in which leaves generate surplus C	Extended rest period through adaptive multipaddock grazing

Figure 3

Regenerative agricultural practices maintain belowground fluxes of plant surplus carbon that support soil microbes and generate soil organic matter.



maintained at different levels of resource availability (N, P, water, and temperature).

The suggestion that exudation of C and N from legumes could be increased through manipulation of plant P supply should be tested by measuring root exudate production and composition at various rates of P supply.

Influences of exudates from different functional groups of plants on soil microbial communities should be examined by tracing the fate of root exudate “cocktails” from mixtures of plants through soil microbial communities and into SOM pools.

Root exudation from cover crops may be considerable during cold or dry periods, given that both cold and dry conditions constrain plant growth more than photosynthesis and lead to surplus C production (Prescott et al. 2020). Root exudates from cover crops should be quantified, characterized, and tracked through the soil food web and into SOM to more fully assess the contribution of cover crops to SOM generation.

A central tenet of regenerative agriculture is that these practices increase the flow of sugars from plant roots, and that this can be accomplished by *maximizing* rates of photosynthesis. Instead, the key may be to

encourage high rates of photosynthesis *but limit the aboveground sink for carbohydrates* so that a proportion of the photosynthate is transported belowground. These proposed mechanisms could be distinguished by measuring root exudation under conditions in which photosynthesis rates are equivalent, but aboveground sinks for photosynthate are constrained or unconstrained.

In conclusion, it may be possible to grow crops without degrading soils by simultaneously promoting both aboveground yield *and* C fluxes belowground. Consideration of conditions in which plants generate surplus C could assist in optimizing agricultural practices to accommodate both crop production and restoration of soil health.

ACKNOWLEDGEMENTS

The authors thank Jack Dempsey, Casey Lapham, and Infantree Branding Agency for their assistance with graphical design. Y. Rui was financially supported by a USDA National Institute of Food and Agriculture, Agriculture and Food Research Initiative grant (2020-67019-31160) and funding from William Penn Foundation and Towards Sustainability Foundation.

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