Synthesis

Brown Ground: A Soil Carbon Analogue for the Green World Hypothesis?

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ABSTRACT: For many decades, ecologists have asked what prevents herbivores from consuming most of the plant biomass in terrestrial ecosystems, or "Why is the world green?" Here I ask the analogous question for detritivores: what prevents them from degrading most of the organic material in soils, or "Why is the ground brown?" For fresh plant detritus, constraints on decomposition closely parallel constraints on herbivory: both herbivore and decomposer populations may be controlled by plant tissue chemistry from the bottom up and predators from the top down. However, the majority of soil carbon is not plant litter but carbon that has been consumed by detritivores and reprocessed into humic compounds with complex and random chemical structures. This carbon persists mainly because the chemical properties of humic compounds and interactions with soil minerals constrain decomposition by extracellular enzymes in soil. Other constraints on decomposers, such as nutrient limitation of enzyme production and competition with opportunistic microbes, also contribute to brown ground. Ultimately, the oldest soil carbon persists via transformation into complex molecules that are impervious to enzymatic attack and effectively decoupled from processing by the soil food web.

Keywords: herbivory, decomposition, extracellular enzyme, litter quality, trophic controls.

Terrestrial ecosystems store approximately 3,000 Pg organic carbon (C), far more than the ~700 Pg C as CO_2 in the atmosphere (Jobbagy and Jackson 2000). One-fourth of this organic C is in plant biomass, with the remainder in soils. All of this C embodies energy that heterotrophic organisms could use. Why does so much organic C persist on and in the ground? Possible reasons for the abundance of C in plant biomass were addressed

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by Hairston et al. (1960) in a provocative article that asked, "Why is the world green?" Why is plant biomass so widely distributed, despite the existence of animals and microbes with the capacity to consume or break down all known plant tissues?

Here I ask the complementary question about the far larger pool of organic C in soils: "Why is the ground brown?" Why is so much biological energy turning over so slowly in soils despite the existence and wide distribution of decomposers that could make use of that energy? I start by briefly describing Hairston et al.'s analysis and the continuing discussions that it stimulated and then apply the logic of that analysis and discussion to soil organic C (SOC). I explore additional ways that the breakdown of SOC is constrained relative to the consumption of plant biomass and ask whether they can explain why the ground is more brown than the world is green.

The World Is Green

In essence, Hairston et al. (1960) suggested that there is a lot of plant biomass in terrestrial ecosystems because herbivore populations are controlled by their predators ("top-down" control), and therefore, herbivores cannot consume a large fraction of plant productivity. They argued that since plant biomass and productivity are not controlled by herbivory, they must be controlled by resource availability ("bottom-up" control). This so-called green world hypothesis challenged ecologists to think systematically about the controls on energy transfers between trophic levels (e.g., Fretwell 1977; Oksanen et al. 1981; Polis 1999) and to propose alternative hypotheses to explain the abundance of biomass C in terrestrial ecosystems. One line of thought suggested that predators could constrain herbivores (creating a green world) only when food chains contained an odd number of levels (generally three) (Fretwell 1977, 1987). With four trophic levels, top carnivores could constrain predators, in turn allowing herbivores to flourish and consume plants. Another suggestion was that while there is a large quantity of C in plants, much of it is so well defended and/or so low in quality

as to constrain the growth of herbivores from the bottom up (e.g., Schultz and Baldwin 1982). Many terrestrial plants possess structural defenses such as spines and lignin (Young and Okello 1998), while many others produce chemical defenses like tannins and cyanogenic glycosides that constrain herbivores (Conn 1981). In this hypothesis, the world is green because plants are inedible, not because herbivores are constrained by predation. Clearly, these hypotheses are not mutually exclusive; chemical defenses could slow the growth of herbivores and allow predators to limit their populations.

The Ground Is Brown

Hairston et al. (1960) characterized SOC as a resource that limits detritivores, but they did not ask why there is so much of it. Does grazing on microbes or low-quality organic C in soils constrain rates of decomposition sufficiently to make the ground brown, or do we need to invoke other mechanisms? To answer this question, I need to discuss the differing strategies that herbivores and detritivores use to consume C. Nearly all herbivores mechanically chew or bore into plant tissue, and this is followed by internal digestion and excretion of indigestible material. This strategy means that rates of plant C consumption are limited by the number of herbivores that are ingesting plant biomass. For consumption of SOC, the rate-limiting step is generally considered to be the conversion of polymeric compounds into small molecules that organisms can assimilate (Burns 1982; Sinsabaugh 1994; Sinsabaugh and Moorhead 1994; Schimel and Weintraub 2003). Therefore, I broadly define a detritivore as any consumer of SOC and reserve the term "decomposer" for only those detritivores that carry out the rate-limiting step of SOC decomposition.

Within the detritivore trophic level, organisms employ three different foraging strategies. Decomposers such as earthworms and enchytraeids use internal digestion to degrade SOC in a manner nearly identical to herbivore consumption of plant material. The second strategy, employed by bacterial and fungal decomposers, involves extracellular digestion. Because these organisms cannot assimilate large molecules, they produce extracellular enzymes that degrade SOC into smaller molecules that can then diffuse across the cell membrane. Finally, a class of microbial detritivores that I will call "opportunists" directly assimilates low-molecular-weight SOC without producing enzymes. Detritivores using all three of these strategies may coexist and compete within the primary consumer level of the soil food web. If SOC decomposition is primarily driven by enzyme-producing bacteria and fungi (Sinsabaugh 1994; Scheu and Setälä 2002), then constraints on foraging with extracellular enzymes should be paramount.

Top-Down Controls

Could predation limit populations of SOC decomposers, leading to brown ground? Overall, predator effects on decomposer populations are highly inconsistent, with frequently observed increases and decreases in decomposer biomass (Coleman et al. 1978; Ingham et al. 1985; Mikola and Setälä 1998a; Wardle 2002). Many detritivores serve as prey for soil micro- and mesofauna, and these predators may consume up to 60% of bacterial production in some soils (Moore et al. 2003). However, predation and faster turnover of detritivore populations usually increase C, N, and P cycling in soils rather than causing SOC accumulation (Cole et al. 1978; Anderson et al. 1983; Ingham et al. 1985; Mikola and Setälä 1998a). Furthermore, if the bacteria consumed by predators are opportunists rather than decomposers, predation would have relatively little effect on SOC stocks. In many soils, fungi play a key role in SOC decomposition, and they are relatively insensitive to top-down control by fungal grazers (Mikola and Setälä 1998b; Wardle 2002; Moore et al. 2003). However, clear top-down constraints on decomposition have been observed. In a desert ecosystem, a trophic cascade suppressed decomposer bacteria and lowered decomposition rates of fresh litter (Santos et al. 1981), and in a microcosm study with agricultural soils, nematode addition decreased long-term C mineralization (Bouwman et al. 1994).

Overall, the evidence for a direct top-down contribution to brown ground appears even weaker than the limited evidence for predation as a driver of the green world. Although this conclusion is based mostly on microcosm data, organisms in microcosms are often chosen for their strong trophic interactions and well-defined trophic roles, and therefore top-down controls are likely to be even weaker in the field. There are, however, several caveats to the conclusion that top-down controls on soil C stocks are weak. First, my analysis excludes the potential role of disease in suppressing decomposer populations because there is not enough information to evaluate this control. In oceanic systems, viruses lyse ~20%–40% of marine bacteria per day (Suttle 2005), yet no studies have examined the fraction of microbial turnover due to viruses in soil. Second, grazing on soil microbes may not lead to brown ground directly, but the associated release of nutrients could stimulate plant growth and increase soil C stocks indirectly through greater plant inputs (Moore et al. 2003). This effect could be minor, however, if sequestration of N in plant and soil organic pools increases microbial N demand and causes a negative feedback to N cycling (e.g., greater fungal : bacterial ratios or higher microbial C : N ratios).

Bottom-Up Forces

The structural and chemical defenses that inhibit plant grazers could also affect decomposers; after all, roughly 85% of terrestrial plant production is not consumed by herbivores and instead enters detrital pools directly (Cebrian 1999). As leaves senesce, low-quality foliage translates into recalcitrant litter for detritivores, with several studies showing that leaf digestibility by herbivores and litter decomposability by microbes are positively correlated (Cornelissen et al. 1999, 2004). In fact, because of the low quality of detrital inputs relative to plant C, detritivores should face more severe bottom-up controls than herbivores. Detrital inputs to soils are rich in plant structural compounds (Reiners 1986) and represent the portion of plant biomass that was not consumed by herbivores. By the time they reach soils, plant materials have been stripped of their most nutritious tissues both by herbivores and the plants themselves, if nutrients have been resorbed during tissue senescence. Any plant material that passes through herbivore guts on its way to the soil has been predigested and may contain higher concentrations of decay-resistant compounds.

Another widely recognized bottom-up control that can regulate both herbivore and decomposer populations is nutrient availability. Low foliar nutrient concentrations limit the growth rates of many herbivores (Mattson 1980) and should have a similar effect on multicellular decomposers (Davidson et al. 2004). Recent evidence shows that nutrient availability can also constrain the ability of microbes to degrade C compounds with extracellular enzymes (Allison and Vitousek 2005; fig. 1). Therefore, low N availability can limit the C metabolism of herbivores, multicellular decomposers, and enzyme-producing microbes that process complex compounds that are rich in C but poor in N. This constraint is probably most important for microbes that decompose litter, which is N-poor relative to soil organic matter. In some soils, top-down forces could interact to alleviate bottom-up N limitation if, for example, grazing by predators increases N availability for the decomposers that avoid predation (Ferris et al. 1998).

Overall, there is strong evidence that bottom-up forces control the microbial processing of labile C and plant litter inputs, but this mechanism is not nearly sufficient to explain brown ground. Numerous studies show that decomposition rates correlate positively with measures of litter quality (Melillo et al. 1982; Aber et al. 1990; Aerts 1997), but even the poorest-quality litter largely decays within tens of years. By contrast, most SOC is no longer physically or chemically recognizable as plant material and has turnover times of decades to millennia (Stevenson 1994; Torn et al. 1997; Trumbore 2000). There is also evidence that
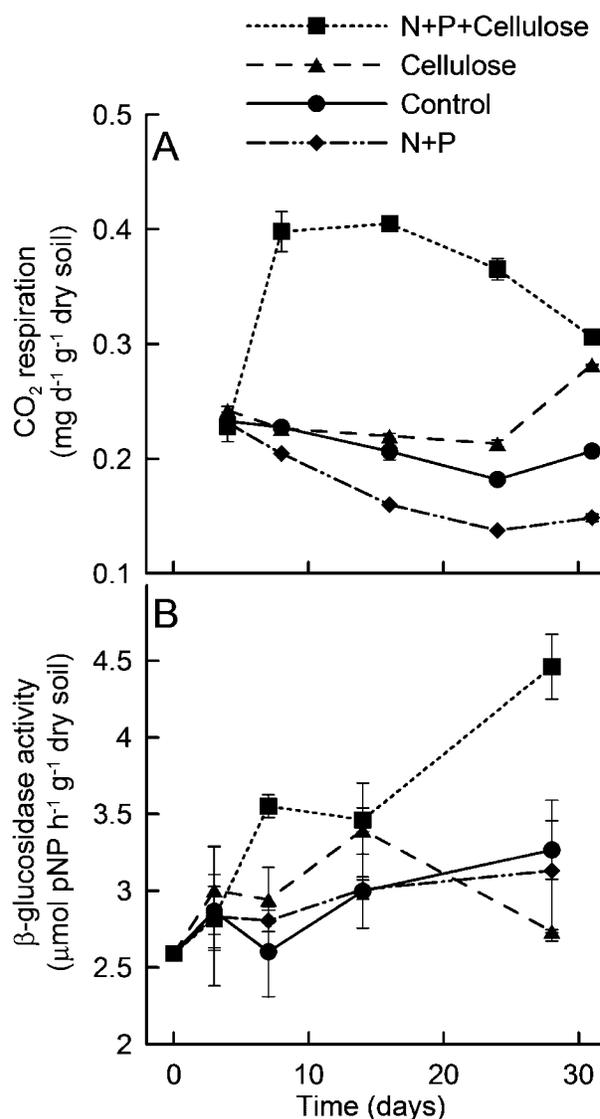

Figure 1: Effect of nutrient addition on soil CO_2 respiration (*A*) and cellulase activity during the decomposition of cellulose (*B*). Adding nutrients in the form of ammonium (N) and phosphate (P) in combination with cellulose significantly increased enzyme activity ($P < .05$, Tukey's HSD post hoc test), which stimulated significantly greater CO_2 release from soil than when cellulose and nutrients were added separately. Data are from incubations with a nutrient-poor Hawaiian soil (Allison and Vitousek 2005).

the effect of added N on decomposition shifts from positive for litter to negative for SOC (Neff et al. 2002). This pattern makes sense because the oldest soil organic material has low C : N ratios and could meet the N demands of decomposers more readily (Stevenson 1994). Thus, the relevance of plant litter quality for brown ground is limited to influencing litter decomposition and to affecting the

fraction of litter inputs that enter slow-turnover pools of SOC (Cebrian et al. 1998).

Generally, the most abundant and oldest constituents of SOC are humic compounds (Campbell et al. 1967; Olk et al. 1995); these humics literally make the ground brown because of their dark coloration. Humics such as humin, humic acids, and fulvic acids are generated through microbial and abiotic synthesis pathways that randomly assemble organic monomers into polymers rich in aliphatic and aromatic substructures (Tan 2003). Thus, nearly all old soil C has cycled through detritivores one or more times and is no longer plant-derived. This material has been consumed and reprocessed without being converted to CO_2 or simple compounds. What characteristics make these reprocessed compounds so resistant to decay? One possibility is that their metabolism yields insufficient energy to support microbial growth. However, the subunits of humics (as well as lignins and tannins) release an amount of energy similar to glucose upon oxidation (NIST 2003; Lide 2004). More likely, the complex, random chemical structure of humic material is responsible for its slow decay. Similar to the polymeric components of plant material, humic compounds can be degraded only by extracellular enzymes that are produced almost exclusively by microorganisms.

There are several reasons why these humic compounds in particular are difficult to degrade enzymatically. First, like many plant tannins (Kraus et al. 2003), humic compounds can directly bind to and inhibit enzymes (Ruggiero et al. 1996; fig. 2), thereby representing a strong bottom-up chemical control on SOC decomposition. This mechanism has been proposed as a partial explanation for the long-term persistence of soil C in northern peatlands (Freeman et al. 2001). Second, randomly structured compounds such as humic acids and plant lignins are generally degraded with oxidative enzymes that may have low catalytic efficiency. For these compounds, microbes cannot afford to produce one specific enzyme for every type of chemical bond that is present (Tate 1987). Instead, natural selection has favored the evolution of oxidative enzyme pathways that are nonspecific and catalyze depolymerization with free-radical mechanisms (ten Have and Teunissen 2001; Claus 2004).

A reliance on these nonspecific enzymes may be a primary reason why some carbon-containing compounds degrade so slowly in soils. The effect of an enzyme is to reduce the activation energy required for polymer degradation—because of the nonspecific reaction mechanism of oxidative enzymes, this activation energy barrier may not be reduced enough to allow efficient degradation of some substrates. These enzymes function by stripping electrons from a nearby substrate or an intermediate compound that later oxidizes the substrate (ten Have and Teu-
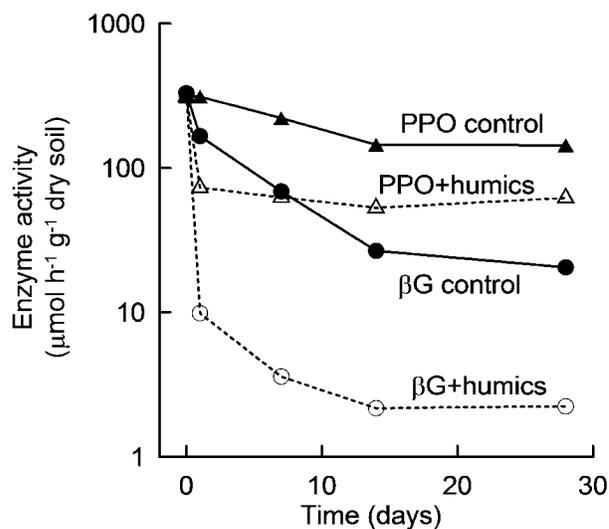

Figure 2: Effect of humic acids on β-glucosidase (βG) and polyphenol oxidase (PPO) activities during soil incubations. Humic acids were incorporated into a nutrient-poor Hawaiian soil at a rate of 15% of soil mass, followed by addition of commercially prepared enzymes. Note the log scale and rapid losses of enzyme activity in the humic acid–amended relative to control soils. S. D. Allison, unpublished data.

nissen 2001). However, substrates with highly random bonding structures may not be able to approach the enzyme active site, thereby limiting the decrease in activation energy. As opposed to hydrolytic enzymes whose active sites have evolved a precise "lock-and-key" fit to common, repeating bond structures, oxidative enzymes are generalists that loosely interact with a diversity of complex substrates with varying degrees of catalytic efficiency. Therefore, I propose that many C compounds persist in soil simply because no enzymes can specifically and effectively catalyze their degradation. This hypothesis is consistent with recent studies showing that the temperature sensitivity of decomposition is higher for low-quality substrates, which may require higher activation energies for degradation (Mikan et al. 2002; Fierer et al. 2005).

A corollary to this hypothesis is that the chemical structures of the oldest soil compounds are extremely diverse, with the same structure repeating infrequently over microbial spatial scales. If humic compounds were to contain chemical bond structures that repeated frequently, selection would favor the evolution of specific enzymes to degrade those structures, as in the case of cellulose-degrading enzymes (Beguin 1990). Instead, nonspecific and less efficient oxidative enzymes appear to be the evolutionary solution to the challenge of degrading random chemical structures. Such structures preclude the evolution of targeted enzymes because too many different enzymes would

have to be produced to make degradation efficient (Tate 1987; Insam 1996). Therefore, humic SOC is protected by its random chemical structure for hundreds to thousands of years despite the high abundance and energy content of the resource.

Because a large fraction of SOC can be degraded (albeit slowly) only by oxidative enzymes, oxygen limitation can also contribute to brown ground. In high-latitude peat-lands, oxygen limitation is a major constraint on SOC decomposition (Freeman et al. 2001). Additionally, oxygen limitation can indirectly inhibit the breakdown of complex C by curtailing aerobic respiration and the growth and enzyme production of soil decomposers (McLatchey and Reddy 1998). Low-oxygen conditions are quite common across many soil types due to the formation of anaerobic microsites (Silver et al. 1999), temporal variation in soil water content (Sierra and Renault 1998), and soil aggre-gation processes (Sexstone et al. 1985), suggesting that oxygen limitation of decomposition is probably common in localized regions of spatially heterogeneous soils.

Competition

In addition to top-down and organic matter controls on decomposer populations, competition within the detriti-vore trophic level could also contribute to brown ground. Recent advances in microbial ecology have inspired a greater appreciation of the functional diversity of microbial communities. Some detritivores, particularly bacteria, may be opportunistic consumers of labile, dissolved SOC and contribute little to complex SOC decomposition. Within the fungal community, basidiomycetes are one of the few taxa with lignin-degrading capabilities (Kirk and Farrell 1987), while other fungi may target cellulose as a substrate for decomposition (Lynd et al. 2002). This differentiation could lead to brown ground if the decomposition of re-calcitrant SOC substrates depends on specialized microbes that are poor competitors or where microbially produced antibiotics inhibit more efficient decomposers.

Increasing evidence suggests that some decomposer fungi compete poorly under N deposition. Studies in hard-wood forests of the north central United States show that C mineralization rates decline and SOC stocks increase in forest stands that produce recalcitrant litter, while the op-posite response occurs in stands producing more labile litter (Carreiro et al. 2000; Waldrop et al. 2004*b*). A prob-able explanation for this pattern is that decomposers of recalcitrant litter compete poorly under high-N conditions and produce fewer oxidative enzymes, while decomposers of labile litter and their enzymes are stimulated under N deposition (Waldrop et al. 2004*a*). In this case, changes in litter decomposition by fungi appear to alter the parti-tioning of litter C into soil pools that contribute to brown ground.

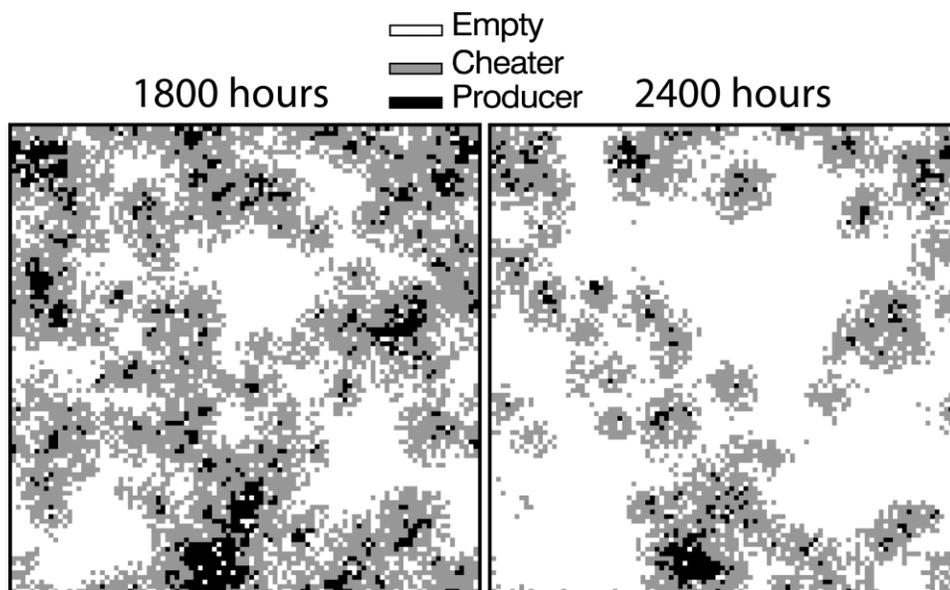In soils where SOC degradation depends on microbes that forage with extracellular enzymes, degradation and

Figure 3: Grid data from a spatially explicit model of microbial growth and enzyme production (EnzModel). Cheaters that do not produce enzymes compete with enzyme-producing microbes that degrade a complex organic substrate. In this simulation, the degradation of the substrate declines as cheaters surround and suppress enzyme producers over time. EnzModel parameters and outputs are described in an article by Allison (2005).

interception of enzymes or reaction products could impede decomposition. Proteases are abundant in soils and may reduce enzyme concentrations, thereby reducing the decomposition of other soil compounds (Renella et al. 2002). Because extracellular enzymes are rich in labile C and especially N, opportunistic "cheaters" may exploit secreted enzymes by colonizing areas adjacent to enzyme producers, further impeding decomposition (Allison 2005). Although microbes are known to grow rapidly on plant exudates in the rhizosphere (Cardon et al. 2002), the possibility that microbes intercept the exudates of other decomposers requires further investigation.

New theoretical evidence does provide support for the hypothesis that competition with opportunists could suppress SOC mineralization by enzyme-producing decomposers. Simulation modeling suggests that with sufficient interference from cheaters, enzyme producers can suffer localized extinctions, resulting in low enzyme production and reduced decomposition (Allison 2005; fig. 3). Plant roots, opportunistic bacteria, or even facultatively opportunistic decomposers could act as cheaters and inhibit decomposition in soils. Although empirical evidence for cheater suppression of decomposition is scarce, enzyme-producing and cheater strains of yeast have been identified (Velicer 2003) and could be used as a model system for addressing this possibility.

Physical Effects

Soil chemical and physical properties may also lead to C accumulation by inhibiting enzyme-substrate interactions. For example, barriers to diffusion, chemical or physical shielding of substrates, and alternative fates for enzymes and substrates can impede enzyme foraging by bacterial and fungal decomposers (Ekschmitt et al. 2005). Thus, greater enzyme production may not always drive higher rates of C degradation (Schimel and Weintraub 2003). In arid soils with low water potential, extracellular enzymes and labile C compounds are likely to remain near the locations where they are produced because water films are thin and diffusion paths are tortuous (Stark and Firestone 1995). Frozen soils have a similar effect on diffusion, thereby limiting interactions between enzymes and substrates (Mikan et al. 2002). Soil aggregation also physically protects organic C from degradation by restricting the diffusion of enzymes, substrates, and reaction products (Sollins et al. 1996). Exudates from soil microbes, such as glomalin production by arbuscular mycorrhizal fungi, further enhance physical protection and C storage by stabilizing soil aggregates and increasing C inputs (Rillig et al. 1999).

Positive relationships between soil mineralogy/texture and C storage have been shown repeatedly (Oades 1988)
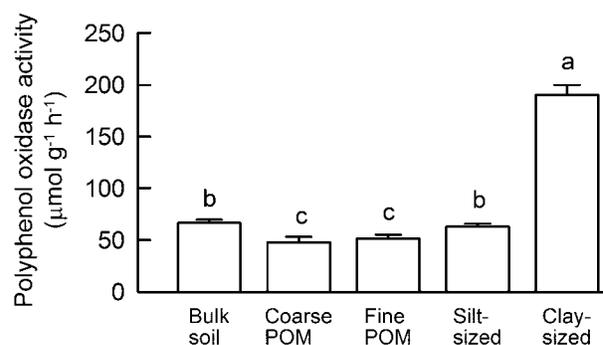

Figure 4: Polyphenol oxidase activity in different physical fractions of Illinois grassland soils. POM = particulate organic matter. The highest enzyme activity occurs in the clay-sized fraction, which also contains carbon with the greatest mean residence time, suggesting that enzymes and substrates are immobilized on mineral surfaces. Data from Allison and Jastrow (forthcoming). Bars with the same letter are not significantly different at $P < .05$ (Tukey's post hoc HSD test).

and help drive the physical protection of SOC (Sollins et al. 1996; van Veen and Kuikman 1990). Ultimately, physical protection depends on factors that block interactions between organic substrates and enzyme active sites at the molecular level. Although mineral sorption often stabilizes enzymes against degradation (Tietjen and Wetzel 2003; Kelleher et al. 2004), mineral-bound compounds are unable to diffuse, thereby reducing the encounter rates between enzymes and substrates. Even if substrate does diffuse to bound enzymes, the active site may be blocked so that enzymatic catalysis is reduced, as evidenced by reductions in the activities of some mineral-sorbed enzymes (Gianfreda et al. 1992). Conversely, mineral-bound C substrates may be physically prevented from entering the active sites of mobile enzymes (Sollins et al. 1996). In addition to large surface areas that facilitate sorption, many soil minerals also contain mesopores or physical structures that can trap small organic compounds and exclude degradative enzymes (Mayer et al. 2004; Zimmerman et al. 2004). In extreme cases, substrates, enzymes, and microbes may all be present in a soil but so strongly bound to mineral surfaces that substrate degradation is minimal and enzymatic products are unlikely to reach microbes (fig. 4). This scenario may help to explain why the C associated with reactive clays can be tens of thousands of years old (Torn et al. 1997).

Soil minerals can also interact with humic compounds synergistically to increase C storage (Tan 2003). Humic compounds may strongly sorb to mineral surfaces where they become further stabilized against degradation (Cornejo and Hermosín 1996). These mechanisms are evident in tropical soils that are enriched in reactive clay minerals and stabilize organic C by immobilizing degradative en-

zymes and humic compounds (Zech et al. 1997). Despite warm temperatures and a favorable moisture regime for decomposition, tropical evergreen forest soils store 20% of global soil C (Jobbagy and Jackson 2000) largely because of mineral stabilization mechanisms.

Although physical factors such as frosts and droughts can reduce foraging by herbivores on plants, the physical constraints on extracellular enzyme foraging do not have obvious analogues aboveground. Therefore, soil minerals and limitations on molecular-level diffusion represent additional constraints on C processing that are absent from the green world but strongly enhance brown ground.

Conclusions

Like the green world, brown soils may result from trophic controls on consumer populations or chemical control by plant tissues (table 1). Thus, the influence of top-down and bottom-up ecological forces extends beyond annual plant net primary production to whole-ecosystem C balance. However, these mechanisms alone cannot account for brown ground because at any given time, SOC from fresh plant inputs represents a relatively small fraction of the total SOC pool. During decomposition, plant detritus is transformed into random chemical structures that have long residence times in the soil. The formation of these compounds represents a leak from actively cycling SOC pools into a resistant, dead-end pool of SOC, which is effectively decoupled from the soil food web. In an ultimate form of resource control, large amounts of SOC persist via transformation into compounds that are virtually impervious to enzymatic action.

Other critical differences between soils and plants also help to explain the predominance of brown ground. In contrast to the internal processing of plant biomass by herbivores, a significant and perhaps overwhelming fraction of SOC is degraded by free-living microbes that pro-

duce extracellular enzymes. Microbial enzymes and substrates can be easily lost due to diffusion, interception, degradation, or sorption. These processes should either limit decomposition directly or reduce the biomass of microbial decomposers, thereby contributing to brown ground. Although decomposers could limit enzyme diffusion through production of cell-bound enzymes, soil C degradation would still be limited because these enzymes could not interact with distant substrates. Unlike plants in the green world, soils also contain minerals and aggregate structures that act as physical obstacles to the enzymatic degradation of organic compounds. Together with the chemical structure of humic polymers, these constraints largely explain why the ground is more brown than the world is green.

Acknowledgments

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Table 1: Constraints leading to the green world and brown ground

Constraint	Contribution to green world	Contribution to brown ground
Predation and disease	Moderate	Minor/uncertain
Competition	Minor	Uncertain
Nutrient limitation	Moderate	Moderate
Plant structural and secondary compounds	Major	Moderate
Reprocessing of soil C into humic compounds	None	Major
Mineral compounds/barriers to diffusion	None	Major
Oxygen limitation	None	Moderate

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