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Why not all productivity leads to carbon sequestration: The role of plant carbon surplus, allocation and the Gadgil effect

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Summary

Increasing plant productivity is considered as the way to maximize carbon (C) sequestration potential of forests. Yet, the changes in the vegetation and soil C stores often exhibit a puzzling divergence. Greater productivity is often associated with smaller, rather than larger, soil C pool. This report reviews plant and microbial processes that elucidate this phenomenon. Different growth-limiting factors affect carbon allocation (the relative sink strength of plants, symbiotic fungi and free-living saprotrophs), biomass chemical composition, its C:N stoichiometry and decomposition differently. The decomposition appears coordinated through (i) detritus chemistry, (ii) asymmetric competition for carbohydrates between mycorrhizal and free-living saprotrophic fungi, and (iii) suppression of some extracellular enzymes by soil acidification under N addition (increased sink strength), but not under elevated CO_2 (increased C supply). The net effect of these interactions is a positive relationship between plant productivity and soil C accumulation in some environments, and a negative one in others.

Introduction

Carbon sequestration in forests may be an important climate mitigation tool (Griscom et al. 2017). Given that human land use has reduced terrestrial C holding capacity by more than 2-fold (Erb et al. 2016), reforestation appears to hold significant potential, even after baseline disturbance regimes are taken into account (Roebroek et al. 2023). However, current efforts often fail to live up to their promise, particularly with regard to accounting for soil carbon (SOC; Green and Keenan 2022, West et al. 2023). Instead, SOC stocks have been declining over recent decades (Bellamy et al. 2005, Xie et al. 2007), apparently due to rising the heterotrophic consumption globally (Bond-Lamberty et al. 2018). Protecting the large SOC pool (3,000 Pg; Walker et al. 2022) requires not only minimizing disturbance of the soil itself (Law et al. 2018, Mäkipää et al. 2023, Mayer et al. 2020, Noormets et al. 2015, Roebroek et al. 2023, Zhou et al. 2006), but also of the ecosystem that has led to its accumulation. It is only through the steady input of new carbon from live roots that SOC pool is maintained, while a part of it is continually turning over. Replacing existing high-biomass low-NPP forests with young high-NPP low-biomass ones, as many climate commitments currently envision (Kirschbaum et al. 2024, Sanderson 2023) would not be able to sustain the SOC pool found in the former, as will be discussed below. Off-site post-harvest storage is beyond the scope of the current discussion.

On-site carbon storage is determined by the balance of photosynthetic carbon inputs and respiratory consumption by plants, microbes, and the entire heterotrophic food chain. Although ecosystem carbon inputs through photosynthesis and emissions through respiration have been investigated extensively and are generally well understood, recent findings about the coupling between them (Mitra et al. 2019, Noormets et al. 2021, Prescott et al. 2020) and the control exerted by microbial processes (Cotrufo et al. 2013, Kohout et al. 2018, Mushinski et al. 2018) compared to that by the environment have brought to light some inconsistencies in current ecosystem carbon cycle models (Lawrence et al. 2019). Central among these is carbon allocation, manifested in the CLM model as the ratio of autotrophic respiration to gross primary production (Ra:GPP; Wieder et al. 2019), and with implications for overall respiration partitioning and the relationship between plant productivity and soil C storage. In this Overview, I will review interactions between plants, their mycorrhizal symbionts, and free-living saprotrophic fungi, that through different growth strategies and sink strengths appear to determine the divergent response of soil C accumulation to increased productivity under different resource availabilities (Terrer et al. 2021). Improved understanding of the mechanistic controls behind SOC dynamics has major implications for multi-objective forest management.

Fast productivity means fast decomposition

Maximum productivity in production-oriented forestry is achieved through species selection, optimizing resource availability, and minimizing stressors and competition. Invariably, the increase in productivity manifests primarily in aboveground tissues, whereas proportional allocation to fine root and mycorrhizal growth declines (Chen et al. 2013, Feng et al. 2023). Allocation to other processes, like secondary metabolism and exudation may vary, depending on the balance between sink strength (as determined by availability of other resources) and C status or surplus. Factors (and management techniques) that increase resource availability, like fertilization and competition control, generally do not increase exudates and secondary chemistry, whereas those that increase C surplus, like elevated CO_2 and selection of more productive species and genotypes, also tend to increase exudation and carbon-based secondary compounds (Koricheva et al. 1998). Species with the greatest growth potential tend to be shorter lived and chemically simpler (de Jong 1995). Their exudates are more abundant (Guyonnet et al. 2018) and, depending on other growth conditions, can be chemically simpler (Prescott et al. 2020), which would contribute to priming the decomposition of existing organic matter, and increasing the turnover of mineral-associated organic C (MAOC) (Chari and Taylor 2022). The level and chemical composition of secondary defense compounds also affects plants' vulnerability to pests and disease (Brienen et al. 2020). In all cases, the shift toward higher shoot:root ratio also leads to greater aboveground compared to belowground detritus production, which is energetically easier to break down, and exposed to more abundant and diverse decomposer community on the ground surface (Augusto and Boca 2022, Koricheva et al. 1998, van Groenigen et al. 2014).

Stoichiometric effects

The response of SOC to different productivity-stimulating factors differs based on whether the stimulation increases overall sink strength or merely C surplus. Improved N availability supports SOC accumulation (Frey et al. 2014, Janssens et al. 2010, Nave et al. 2009) by increasing plant sink strength and by suppressing saprotrophic late stages of decomposition (see below; Gill et al. 2021), and increasing MAOC (Yu et al. 2024). In contrast, improved plant C status under elevated CO_2, as well as in faster-growing species and genotypes (Rabearison et al. 2023), leads to declining SOC (Tariq et al. 2024), and has been attributed to priming (Gao et al. 2020, Terrer et al. 2021) and microbial community succession and associated decline in the C:N ratio (microbial mining hypothesis; Moorhead and Sinsabaugh 2006). N-driven acidification may also shift the competitive balance in favor of mycorrhizal rather than saprotrophic fungi, given that saprotrophs tend to prefer more alkaline soils than do ectomycorrhizal fungi (Yamanaka 2003), and they rely more on the lignolytic enzymes affected. While the initial stimulation of plant growth by CO_2 and N is comparable, their opposite effect on tissue C:N ratio leads to contrasting changes in decomposition.

Soil C stabilization emerges through symbiotic and competitive interactions

Carbon stabilization in the soil, whether through sorption on mineral surfaces, physical protection in aggregates or chemical recalcitrance (Manzoni and Cotrufo 2024, Sollins et al. 1996), works through several mechanisms (chemical structure, oxidative state, Gadgil effect and allelopathy, organism's C status and elemental stoichiometry) that represent the outcome of interactions between plants, symbiotic fungi and free-living saprotrophic fungi. The differential access of the two fungal guilds to newly assimilated plant carbohydrate supply results in their very different life strategies, impact on SOC processing, and an asymmetric competition between them (known as Gadgil effect; Gadgil and Gadgil 1971). Although there is a range of variability among studies in the magnitude of the effect and the mechanisms are not fully understood (Fernandez and Kennedy 2016), on average, its effects on SOC appear stronger than those of primary production, edaphic and climatic drivers (Averill et al. 2014). Gadgil effect is stronger in ectomycorrhizal (EM) than arbuscular mycorrhizal (AM) communities (Averill and Hawkes 2016), but has been observed in both taxonomic groups (Frey 2019). In addition to the faster growth and faster access to organic N sources (unlike the evolutionarily older AM fungi, EM fungi still possess the oxidative and hydrolytic N-mining enzymes found in their saprotrophic ancestors; Lindahl and Tunlid 2015, Pellitier and Zak 2021), there is also support for potential allelopathic and parasitic interactions that allow EM fungi to outcompete saprotrophs (Fernandez and Kennedy 2016). The competition between symbiotic and saprotrophic fungi shifts in favor of saprotrophs when plants' own sink strength increases and the carbohydrate subsidy from host plants to mycorrhizal partners declines (at elevated N; Högberg et al. 2021, Keller et al. 2021, Lindahl et al. 2010), and when greater carbon surplus increases exudation, priming and MAOC turnover (e.g. at elevated CO_2; Chari and Taylor 2022, Gunina and Kuzyakov 2022, Kyaschenko et al. 2017).

Potential caveats

The evidence presented above suggests that the retention of SOC under elevated nitrogen works primarily through acidification-mediated suppression of oxidative enzymes responsible for late-stage decay of lignin and other complex compounds. While the enhancement of sink strength appears to further contribute to the effect by keeping exudation low, it may be of secondary importance. Competition control that is used for improving nutrient availability for the crop plants, does not increase the amount of N in the system, nor ecosystem-level sink strength and soil acidity. However, rising CO_2 does acidify soil much like extra N, and should be expected to both suppress oxidative enzyme activity and increase mineral absorption of C. Yet, in most elevated CO_2 studies, the extra exudates and priming of old organic matter appear to dominate over any such suppression (Terrer et al. 2021).

While existing studies almost universally support the idea of elevated N leading to higher SOC, there are some observations calling to question the persistence of this additional C sink. For example, acidification causes nutrient leaching and could make the SOC accumulation a transient response until the elemental stoichiometry is restored (Manzoni 2017). Second, some studies suggest that EM fungi may accelerate SOC decomposition at elevated N levels (Frey 2019, Mayer et al. 2023). And third, elevated N appears to increase SOC accumulation primarily in ecosystems with high lignin litter, but less in systems with low-lignin litter (Gill et al. 2021).

Finally, as the priming effect depends on the stoichiometric balance of different elements and plant belowground C allocation (including exudation), the controlling factor of SOC dynamics (in the absence of other perturbations) may be the phloem transport of C and exudation to the soil. Phloem transport is, in turn, likely determined by the plants' growth dynamics (regulated by both genetic and environmental factors) and water availability. As phloem transport is coupled to overall plant water status (Sevanto 2014), it can be hypothesized that soil C availability would also decline under drought, with likely changes in the mycorrhiza-saprotroph relationships and predominant C processing pathways. Indeed, experimental drought suppresses heterotrophic respiration and increases ecosystem net carbon balance (Noormets et al. 2021).

Conclusions and recommendations for forest management for carbon sequestration

Thus, for maximum long-term carbon retention in both plants and soil, the ecosystem must include (i) (ecto)mycorrhizal fungi that would suppress later stages of decomposition by constraining saprotrophic fungal activity (Gadgil effect), (ii) slightly acidic soil that would also suppress oxidative enzymes produced by saprotrophs, (iii) moderate exudation of organic acids or amino acids to support mycorrhizal symbionts and build MAOC, and (iv) chemically complex litter to resist decomposition, promoted by (v) periodic water limitation. In contrast, SOC decomposition would be accelerated in ecosystems with (i) fast-growing species that produce easily decomposable litter and simple exudates that prime decomposition, (ii) short harvest cycles that necessitate frequent site entry and high soil disturbance that also promotes decomposition, (iii) novel species that do not match existing soil microbiome, (iv) too high fertilization rates that suppress mycorrhizal associations, and (v) nutrient limitation under otherwise favorable growth conditions (incl. year-round good water availability) that result in high plant C surplus and abundant and chemically simple exudates that promote priming of old SOM and increase the turnover of MAOC. The offsetting effects of atmospheric CO_2 (that has been the main contributor to increased productivity in recent decades; Yang et al. 2022) and N deposition appear to be dominated by CO_2, so that many natural ecosystems experience growing N deficit (Mason et al. 2022).

The optimal levels of nutrient and water availability at rising CO_2 levels and with different community structures (including with determinate and indeterminate-growing species) still need to be elucidated. It should also be noted that most of the information referenced here describes mid-latitude ecosystems (primarily forests). While other additional factors may affect C allocation and sink strength in other climate zones, the principles outlined here appear universal enough to conclude that standard production-centered forestry practices that do not protect SOC stores are counter-indicated for climate mitigation. If both biomass production and climate mitigation are targeted in the same ecosystem, the management decisions will inevitably face fundamental trade-offs.

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