

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

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## Abstract

Increasing plant productivity is considered as the way to maximize carbon sequestration potential of forests. However, the changes in the vegetation and soil carbon stores often exhibit a puzzling divergence. Greater productivity is often associated with smaller rather than larger soil carbon pool. In the present report, I review 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 carbon to nitrogen stoichiometry, and decomposition differently. The decomposition appears coordinated through detritus chemistry, asymmetric competition for carbohydrates between mycorrhizal and free-living saprotrophic fungi, and suppression of some extracellular enzymes by soil acidification under nitrogen addition (that increases sink strength) but not under elevated carbon dioxide (that increases carbon supply). The net effect of these interactions is a positive correlation between plant productivity and soil carbon accumulation in some environments and a negative one in others.

Carbon sequestration in forests may be an important climate mitigation tool (Griscom et al. 2017). Given that human land use has reduced terrestrial carbon stocks by more than two-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 (Green and Keenan 2022, West et al. 2023). Instead, soil carbon stocks have been declining over recent decades (Bellamy et al. 2005, Xie et al. 2007), apparently because of rising heterotrophic consumption (Bond-Lamberty et al. 2018). Protecting the large soil carbon pool (3000 petagrams; Walker et al. 2022) requires not only minimizing disturbance of the soil itself (Zhou et al. 2006, Noormets et al. 2015, Law et al. 2018, Mayer et al. 2020, Mäkipää et al. 2023, Roebroek et al. 2023) but also of the ecosystem that has led to its accumulation. Soil carbon pool is maintained through the steady input of new carbon from live roots, because a part of the soil carbon is continually turning over. Replacing existing high-biomass, low-productivity forests with young high-productivity, low-biomass ones, as many climate commitments currently envision (Sanderson 2023, Kirschbaum et al. 2024), would not be able to sustain the soil carbon pool found in the former, as will be discussed below. Off-site postharvest 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, Prescott et al. 2020,

Noormets et al. 2021) and the control exerted by microbial processes (Cotrufo et al. 2013, Kohout et al. 2018, Mushinski et al. 2018) compared with 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 Community Land Model as the ratio of autotrophic respiration to gross primary production (Wieder et al. 2019), and with implications for overall respiration partitioning and the relationship between plant productivity and soil carbon 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 carbon accumulation to increased productivity under different resource availabilities (Terrer et al. 2021). An improved understanding of the mechanistic controls behind soil carbon dynamics has major implications for multiobjective 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 the availability of other resources) and carbon status or surplus. Factors (and management techniques) that increase resource availability, such as fertilization

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and competition control, generally do not increase exudates and secondary chemistry, whereas those that increase carbon surplus, such as elevated carbon dioxide and the 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 carbon (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 to 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 (Koricheva et al. 1998, van Groenigen et al. 2014, Augusto and Boca 2022).

## Stoichiometric effects

The response of soil carbon to different productivity-stimulating factors differs based on whether the stimulation increases overall sink strength or merely carbon surplus. Improved nitrogen availability supports soil carbon accumulation (Nave et al. 2009, Janssens et al. 2010, Frey et al. 2014) by increasing plant sink strength and by suppressing saprotrophic late stages of decomposition (see below; Gill et al. 2021) and increasing mineral-associated organic carbon (Yu et al. 2024). In contrast, the improved plant carbon status under elevated carbon dioxide, as well as in faster-growing species and genotypes (Rabearison et al. 2023), leads to declining soil carbon (Tariq et al. 2024) and has been attributed to priming (Gao et al. 2020, Terrer et al. 2021) and microbial community succession and its associated decline in the carbon to nitrogen ratio (the microbial mining hypothesis; Moorhead and Sinsabaugh 2006). Nitrogen-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. Although the initial stimulation of plant growth by carbon dioxide and that by nitrogen is comparable, their opposite effect on the tissue's carbon to nitrogen ratio leads to contrasting changes in decomposition.

## Soil carbon 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 (Sollins et al. 1996, Manzoni and Cotrufo 2024), works through several mechanisms (chemical structure, oxidative state, the Gadgil effect and allelopathy, the organism's carbon status and elemental stoichiometry) that represent the outcome of interactions among 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, in different levels of impact on soil carbon processing, and in an asymmetric competition between them (known as the *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 soil carbon appear stronger than those of primary production or edaphic and climatic drivers (Averill et al. 2014). The Gadgil effect is stronger in ectomycorrhizal than in arbuscular mycorrhizal 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 nitrogen sources (unlike the evolutionarily older arbuscular mycorrhizal fungi, ectomycorrhizal fungi still possess the oxidative and hydrolytic nitrogen-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 ectomycorrhizal 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 the host plants to their mycorrhizal partners declines (at elevated nitrogen levels; Lindahl et al. 2010, Högberg et al. 2021, Keller et al. 2021) and when greater carbon surplus increases exudation, priming, and mineral-associated organic carbon turnover (e.g., at elevated carbon dioxide levels; Kvaschenko et al. 2017, Chari and Taylor 2022, Gunina and Kuzyakov 2022).

## Potential caveats

The evidence presented above suggests that the retention of soil carbon under elevated nitrogen works primarily through acidification-mediated suppression of oxidative enzymes responsible for late-stage decay of lignin and other complex compounds. Although 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 nitrogen in the system, nor does it increase ecosystem-level sink strength or soil acidity. However, rising carbon dioxide does acidify soil much like extra nitrogen does and should be expected to both suppress oxidative enzyme activity and increase the mineral absorption of carbon. Yet, in most elevated carbon dioxide 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 nitrogen leading to higher soil carbon, there are some observations calling into question the persistence of this additional carbon sink. For example, acidification causes nutrient leaching and could make the soil carbon accumulation a transient response, lasting only until the elemental stoichiometry is restored (Manzoni 2017). Second, some studies suggest that ectomycorrhizal fungi may accelerate soil carbon decomposition at elevated nitrogen levels (Frey 2019, Mayer et al. 2023). And third, elevated nitrogen appears to increase soil carbon 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 carbon allocation (including exudation), the controlling factor of soil carbon dynamics (in the absence of other perturbations) may be the phloem transport of carbon and its 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 carbon availability would also decline under drought, with likely changes in the mycorrhiza–saprotroph relationships and predominant carbon 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 (i.e., the 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 (iv) build mineral-associated organic carbon, and chemically complex litter to resist decomposition, promoted by (v) periodic water limitation. In contrast, soil carbon 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 (including good year-round water availability) that result in high plant carbon surplus and abundant and chemically simple exudates that promote the priming of old soil organic matter and increase the turnover of mineral-associated organic carbon. The offsetting effects of atmospheric carbon dioxide (that has been the main contributor to increased productivity in recent decades; Yang et al. 2022) and nitrogen deposition appear to be dominated by carbon dioxide, so that many natural ecosystems experience growing nitrogen deficit (Mason et al. 2022).

The optimal levels of nutrient and water availability at rising carbon dioxide 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 in the present article describes mid-latitude ecosystems (primarily forests). Although other additional factors may affect carbon allocation and sink strength in other climate zones, the principles outlined in the present article appear universal enough to conclude that standard production-centered forestry practices that do not protect soil carbon stores are counterindicated 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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## Author contributions

Asko Noormets (Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing—original draft, Writing—review & editing).

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