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Plant surplus carbon underlies belowground carbon fluxes

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I propose that patterns of belowground carbon flux observed under various environmental conditions can be largely explained by plant production of 'surplus carbon'. Under common environmental conditions such as moderate deficiencies of water, nitrogen or phosphorus, high light, low temperatures, or elevated atmospheric carbon dioxide concentrations, plant leaf cells produce more photo-assimilates than they are able to use for primary metabolism, and so have surplus fixed carbon. Accumulation of surplus carbohydrates can damage leaf cells and so must be either transformed to other compounds or removed from the leaf. Active carbohydrate sinks are essential for the transport and removal of surplus C. Moderate deficiencies of N or P do not interfere with phloem loading, so much of the surplus C can be transported through the phloem, eventually reaching the roots. Active sinks for surplus carbon in roots include phosphorylated and non-phosphorylated respiration, conversion to starch, transfer to mycorrhizal fungi, or carboxylation to malate which is exuded or taken up by bacteria both inside and outside the root. These active sinks prevent metabolite accumulation and feedback inhibition of photosynthesis. The foundational benefit of belowground C fluxes and transfers to root-associated organisms may be assisting with the removal of surplus fixed carbon.

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Leaf growth (cell division and elongation) declines at an earlier/lesser stage of nutrient deficiency than does photosynthesis.

Therefore:
Under mild nutrient deficiencies, plant leaf cells produce more photo-assimilates than they are able to use for primary metabolism (and growth), and so have ‘surplus carbon’.

In natural ecosystems, plants are often deficient in N or P.

Do plants often have surplus carbon?

Plants often have surplus carbon

The green plant may indeed be a pathological overproducer of carbohydrates.
(Harper 1977)

Plant C reserves are rarely even close to depletion during periods of high demand.
(Körner 2003)

The growth of trees is not C-limited.
(Millard et al 2007)

In CO_2-rich environments, plants do not reduce C uptake as much as expected - they simply '**pump more C through their body**' and emit much of the surplus fixed C back into the atmosphere via respiration, especially soil respiration. (Körner)

Accumulation of surplus carbohydrates can cause photo-oxidative damage to leaf cells and so *must be either transformed to other compounds or removed from the leaf* (Lambers and Oliveira 2019).

Transport and removal and of surplus C is made possible by active carbohydrate sinks.

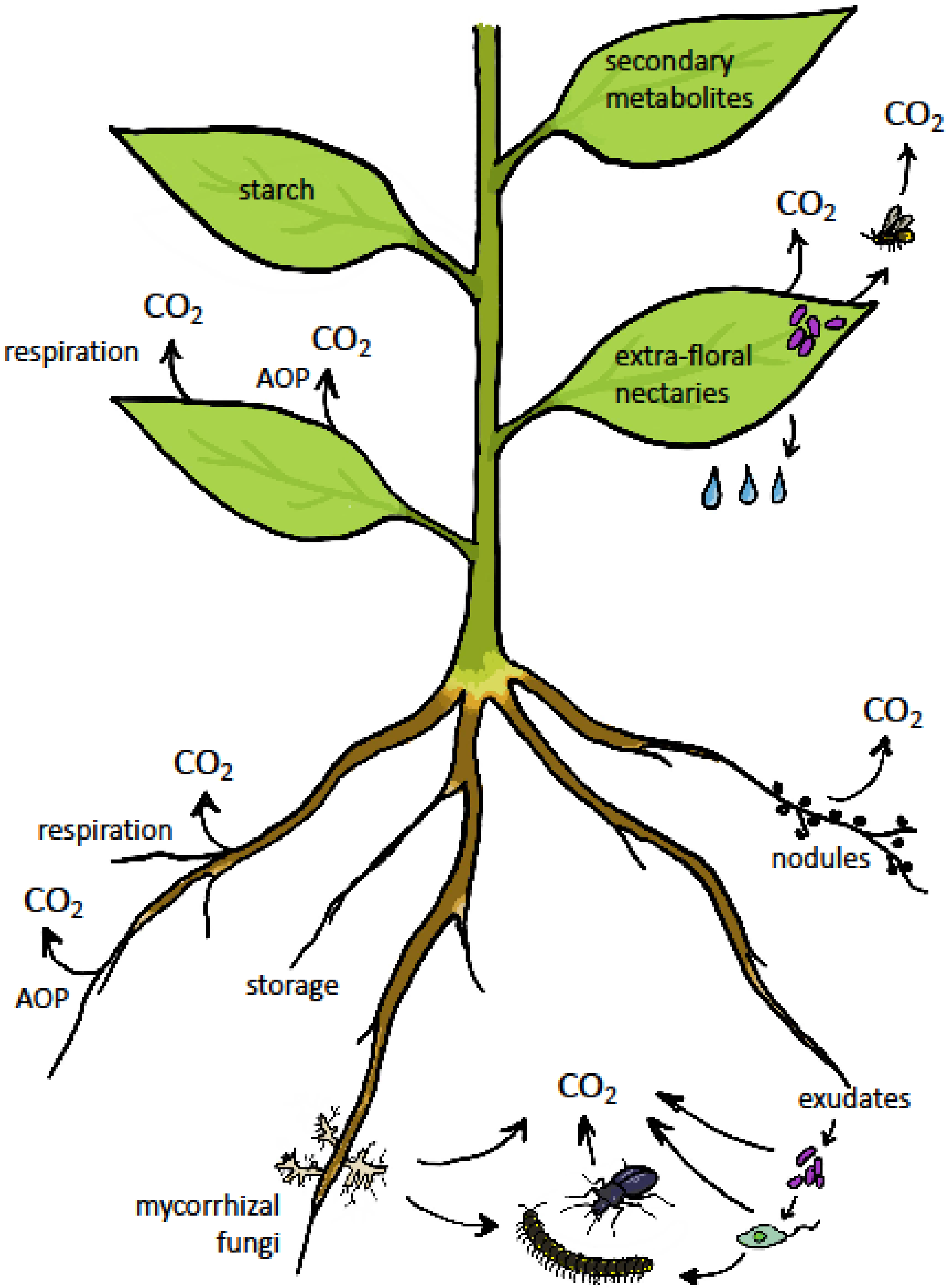
Active carbohydrate sinks prevent feedback inhibition of photosynthesis.

Activities of these sinks increase under the same conditions that result in generation of surplus C

(mild-moderate deficiencies of N, P or water, and high light and CO_2).

Active sinks for surplus carbohydrates

- starch
- secondary metabolites
- extra-floral nectaries
- volatile organic compounds
- aphids, ants
- alternative oxidase pathway
- root exudates
- mycorrhizal fungi
- soil organisms – food web
- understory trees
- living stumps



Prescott, C.E. 2022. Sinks for plant surplus carbon explain several ecological phenomena. Plant & Soil https://doi.org/10.1007/s11104-022-05390-9

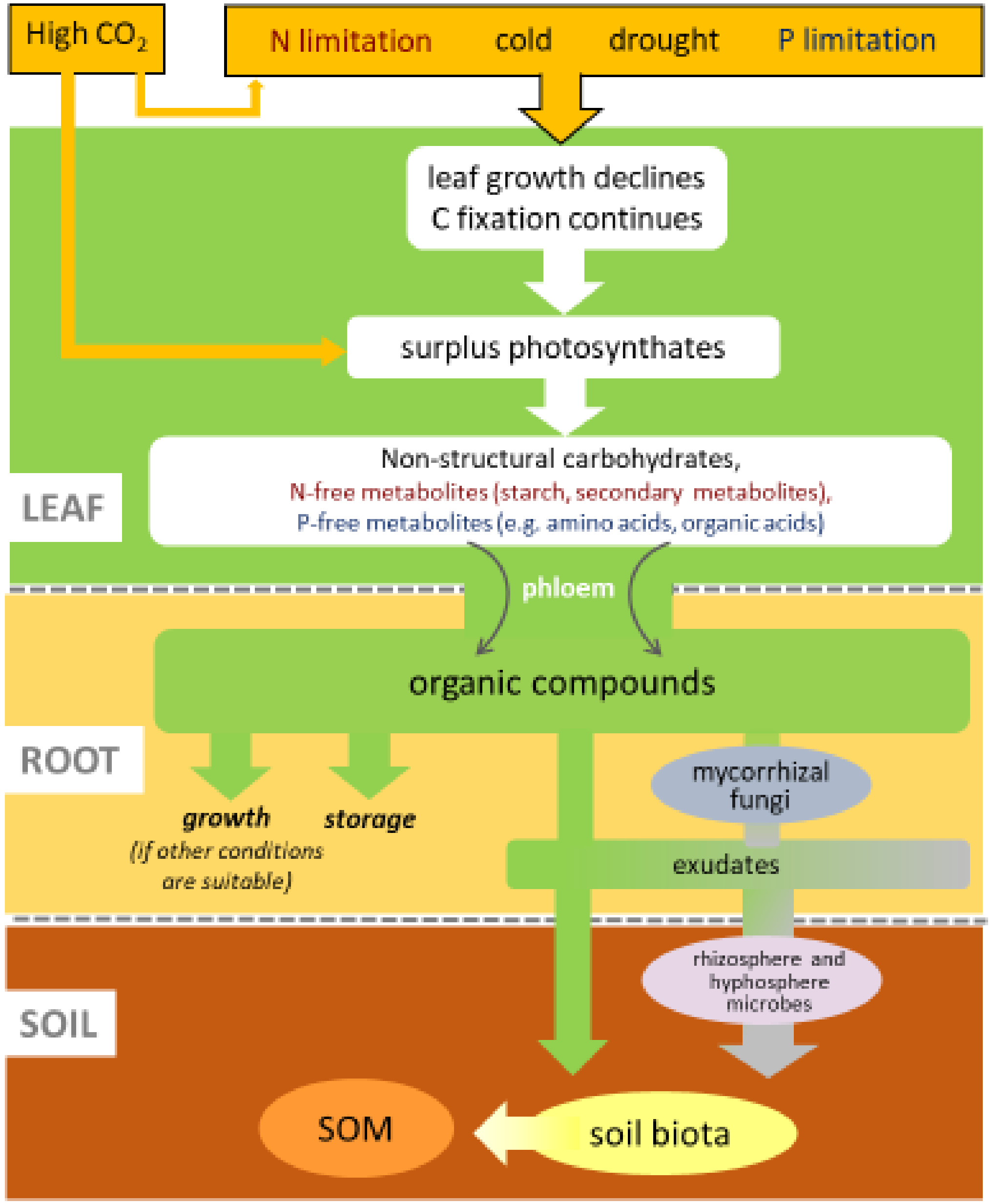
The Surplus Carbon Hypothesis

Under common environmental conditions plant leaf cells produce more photo-assimilates than they are able to use for primary metabolism and growth, and so have ‘surplus carbon’

Such conditions include: mild–moderate deficiencies of water, nitrogen or phosphorus, high light, low temperatures, or elevated atmospheric carbon dioxide concentrations

Surplus C is generated under mild–moderate deficiencies

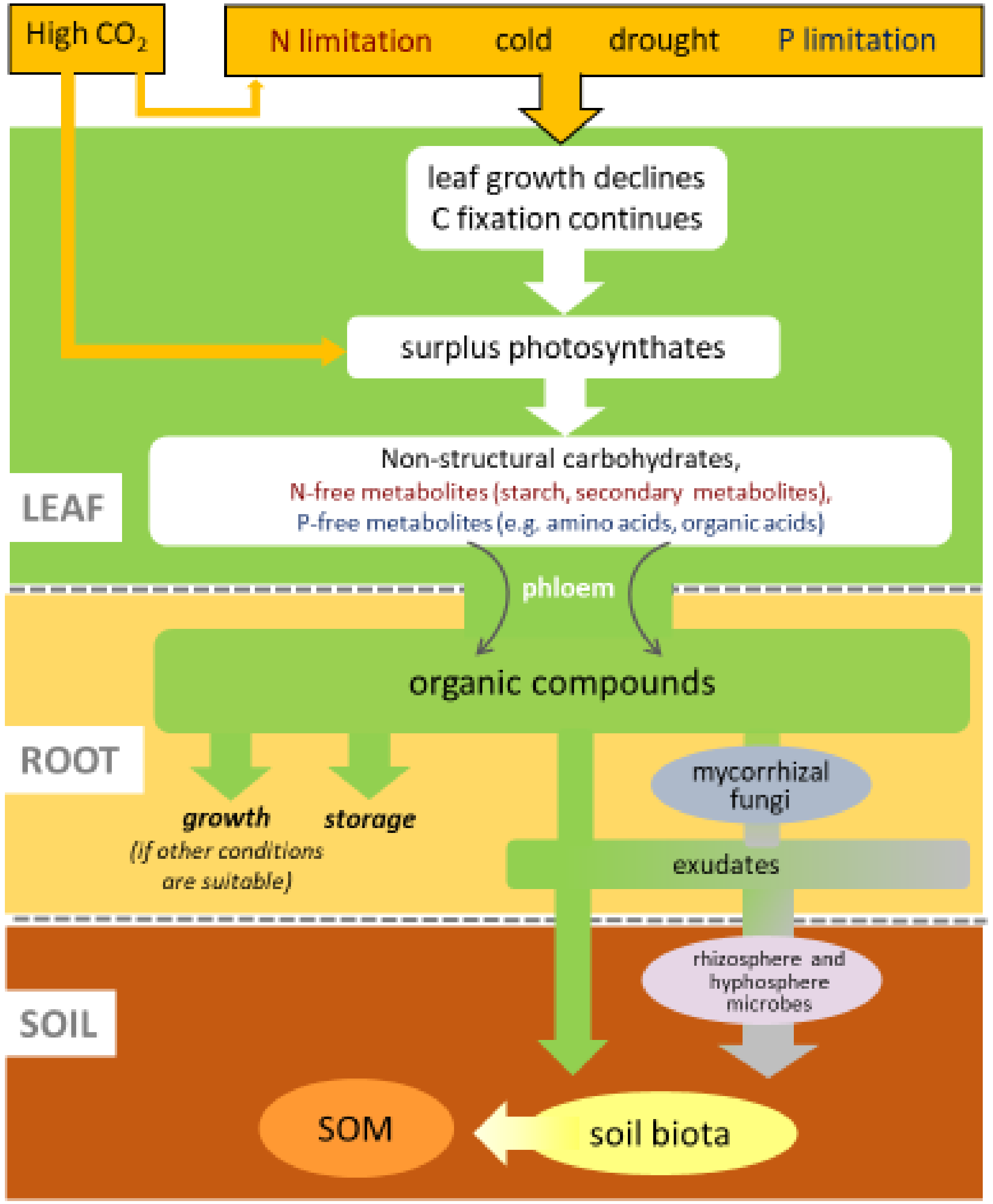
- not extreme or prolonged



Plant Surplus Carbon

Implications for belowground C flux and plant biomass allocation

Prescott et al. 2020. Surplus carbon drives allocation and plant–soil interactions. Trends in Ecology and Evolution https://doi.org/10.1016/j.tree.2020.08.007

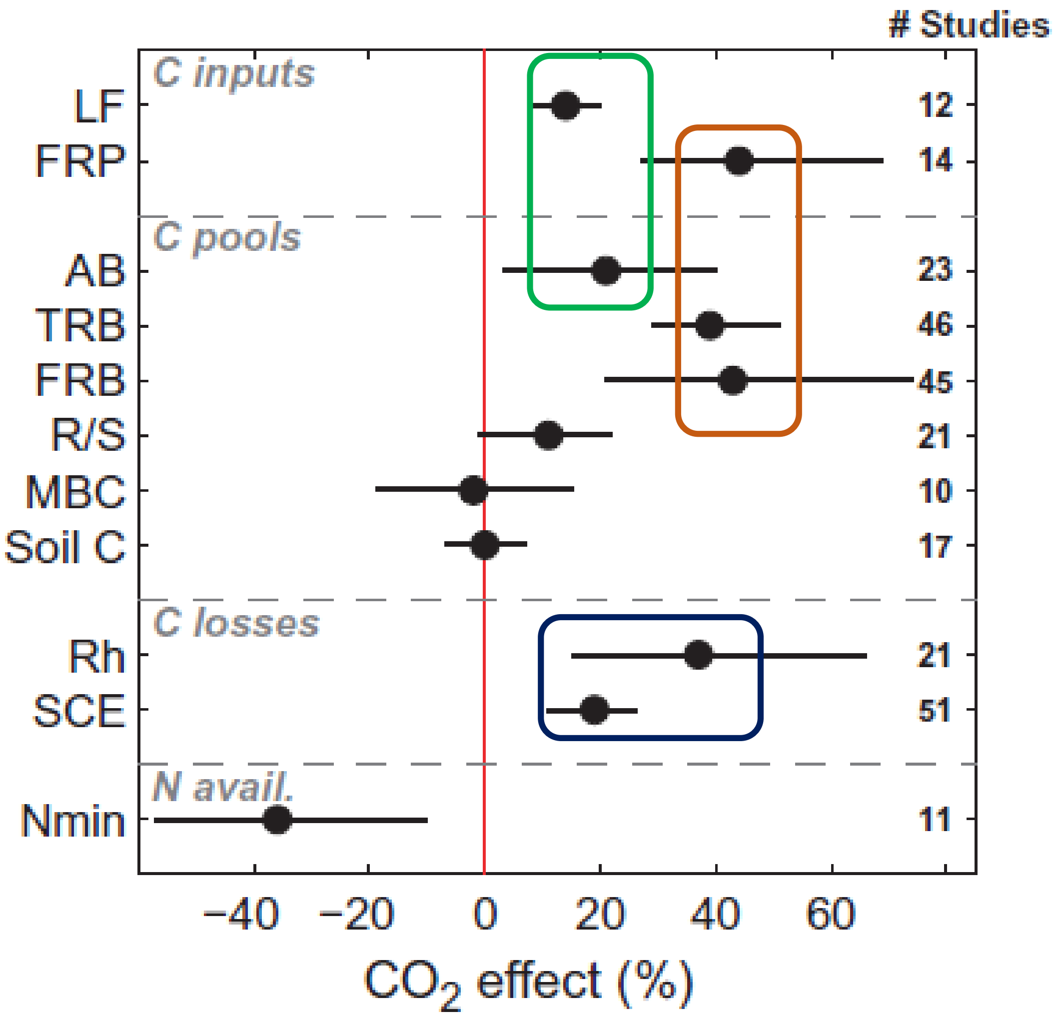


Belowground C flux as % of total:

will increase with:
- elevated CO_2
- low temperature
- moderate drought

will decrease with:
- addition of N or P
- addition of water

Prescott et al. 2020. Surplus carbon drives allocation and plant–soil interactions. Trends in Ecology and Evolution https://doi.org/10.1016/j.tree.2020.08.007



Meta-analysis of 131 manipulation experiments

Elevated CO_2 induced a C allocation shift towards below-ground biomass compartments.

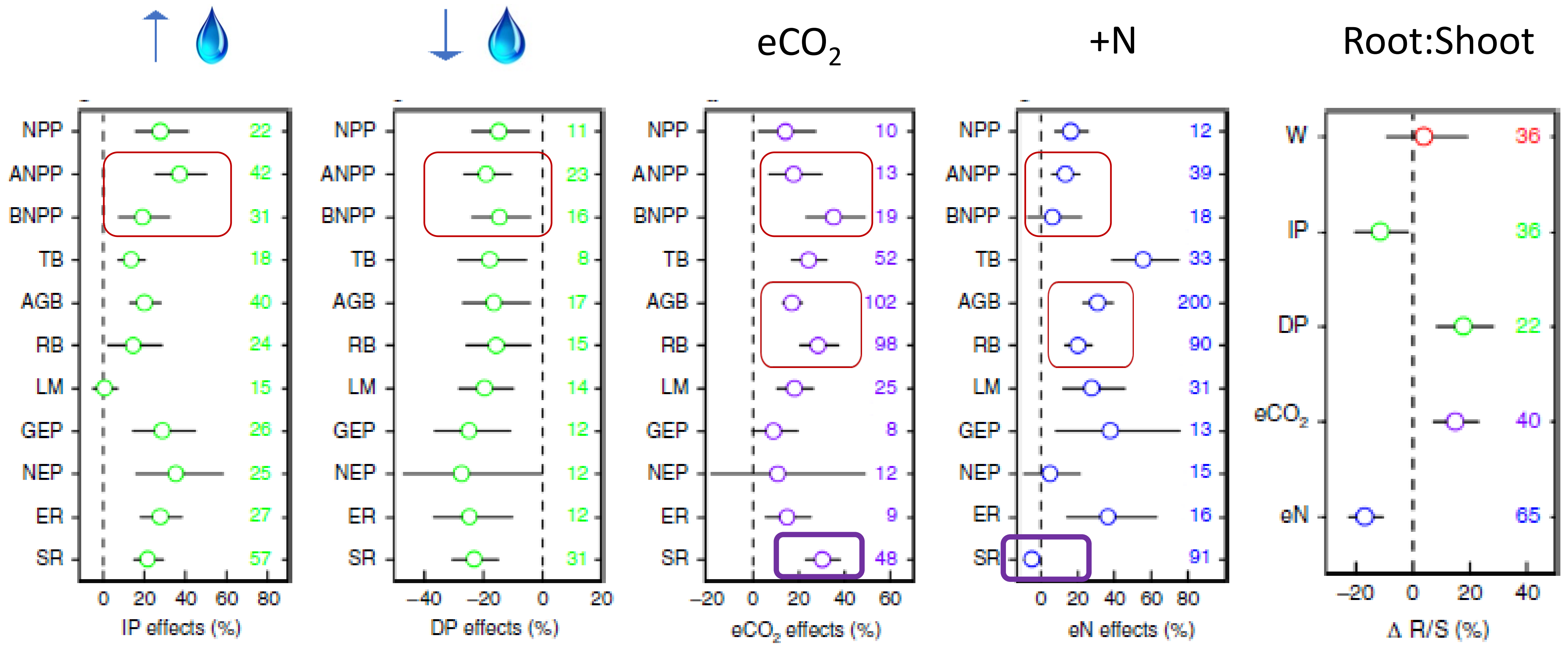
Soil CO_2 efflux and heterotrophic respiration increased.

Effects reversed by N addition.

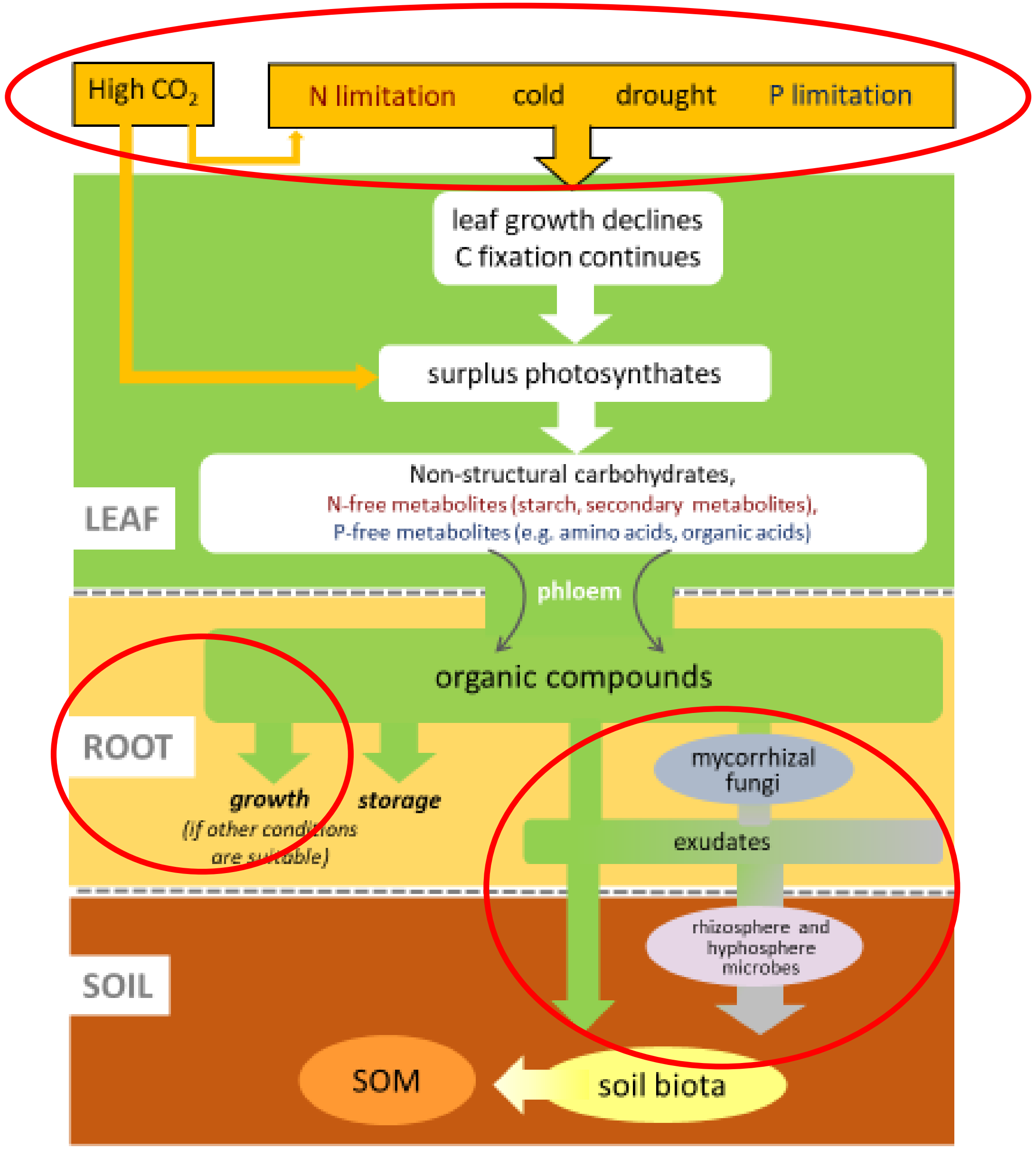
Figure 1. Overall CO_2 effects on soil C inputs, C pools, C losses and N availability. The effects on litterfall (LF), fine root production (FRP), above-ground biomass (AB), total root biomass (TRB), fine root biomass (FRB), root-to-shoot ratio (R/S), microbial biomass C (MBC), soil C content (soilC), heterotrophic respiration (Rh), soil CO_2 efflux (SCE) and net N mineralization (Nmin) are indicated as percentage response to elevated CO_2. Overall means and confidence intervals (CIs) are given, which means a significant CO_2 effect is apparent when the zero line is not crossed. The number of studies used for the analysis is indicated above the *x*-axis.

Dieleman et al 2010. Soil [N] modulates soil C cycling in CO2-fumigated tree stands: a meta-analysis. Plant Cell & Env 33: 2001-2011.

Changes in net primary productivity (NPP) and its above- and belowground components (ANPP and BNPP), total, aboveground and root biomass (TB, AGB and RB), litter mass (LM), gross and net ecosystem productivity (GEP and NEP), and ecosystem and soil respiration (ER and SR) induced by increased precipitation, decreased precipitation, elevated CO_2 and elevated N. Changes in root-to-shoot ratios (ΔR/S).



Song et al 2019. A meta-analysis of **1,119** manipulative experiments on terrestrial carbon-cycling responses to global change



Plant Surplus Carbon

Conceptual framework linking environmental constraints to plant growth with biomass allocation and belowground C fluxes

An alternative interpretation

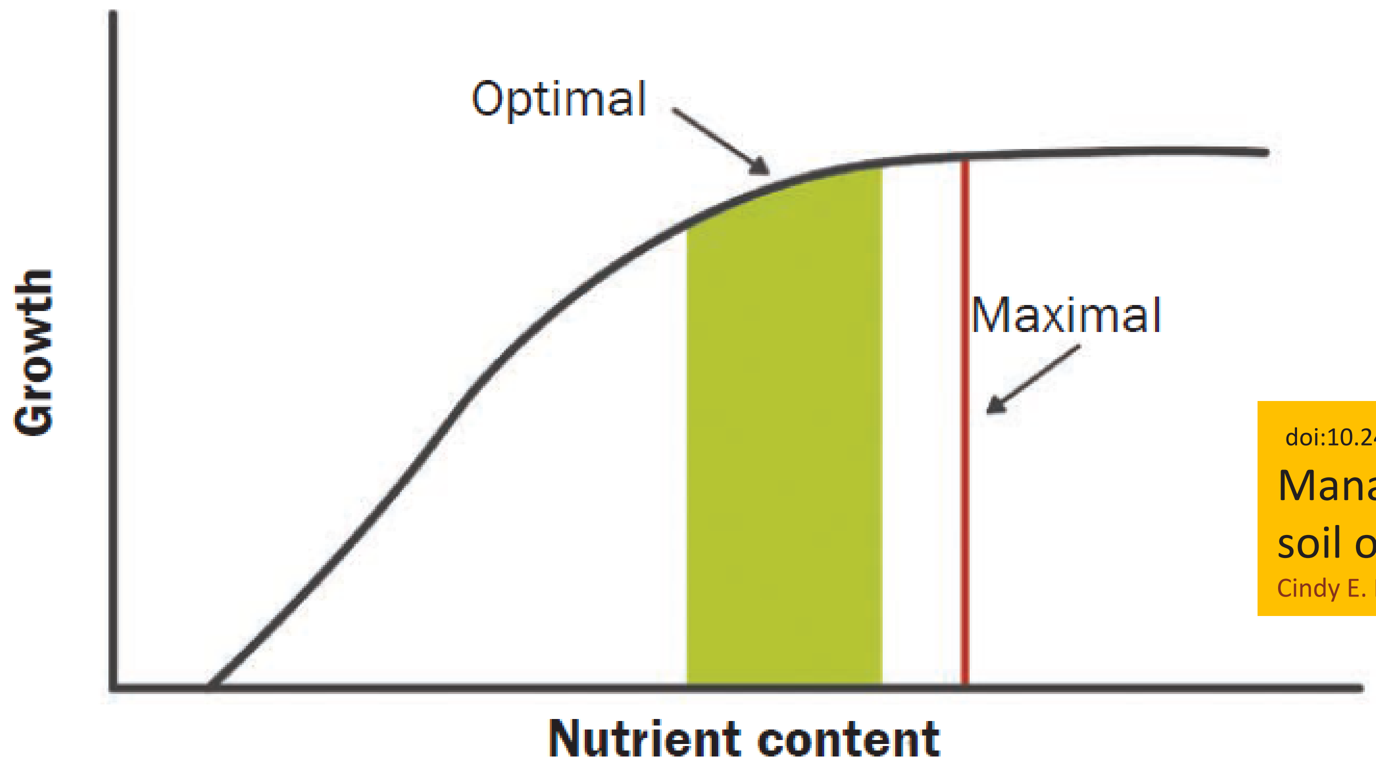
Increased belowground C allocation in response to deficiencies of nutrients or water are usually interpreted as ‘investments’ by the plant to secure more.

An alternative interpretation of the evidence is that plant metabolic processes necessarily differ according to availability of nutrients and water, and this is reflected in many ways, including fluxes of C between aboveground and belowground components.

Differences in C fluxes and ‘allocation’ among plants growing under different environmental conditions may be metabolic consequences, rather than ‘investments’ by the plant to secure additional resources.

Can we optimize the amount and proportion of C allocated belowground?

Figure 1
Proposed supply of nutrients (nitrogen and phosphorus) or water to optimize aboveground growth and production of surplus carbon, relative to the supply that maximizes aboveground growth.



doi:10.2489/jswc.2021.0920A

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

Cindy E. Prescott, Yichao Rui, M.Francesca Cotrufo, and Sue J. Grayston

Dieleman et al 2010 Soil [N] modulates soil C cycling in CO2-fumigated tree stands: a meta-analysis. Plant Cell & Environment 33: 2001–2011. https://doi.org/10.1111/j.1365-3040.2010.02201.x

Harper 1977 Population Biology of Plants.

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Lambers & Oliveira 2019 Plant Physiological Ecology.

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