STØTTET AF
Promilleafgiftsfonden for landbrug

Udredning		SEGES Innovation Crops & Environment	
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Carbon allocation

Carbon allocation represents the exchange of carbon following photosynthetic fixation between aboveground pools (shoot biomass) and the transfer of carbon to the soil or belowground pools. Further, carbon enters the soil as root-derived carbon composed of root exudates and via the mineralization of standing root biomass and from the phyllo-sphere. In simple terms, C exists in roots or microbial biomass, as bioavailable labile organic C, or as more stable C pools (Figure 1; Jansson et al., 2018, 2021).
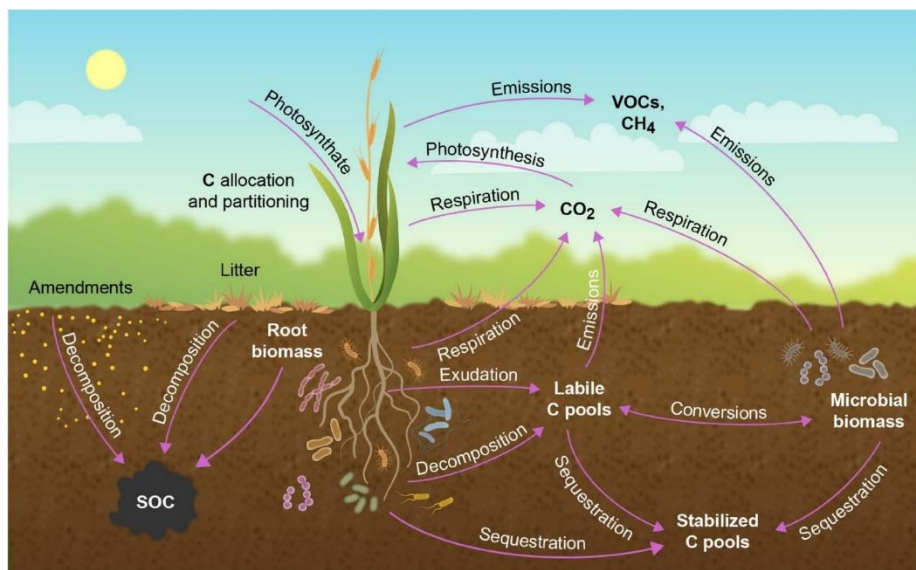
Figure 1. Framework for carbon fluxes in agricultural ecosystems.

Pitfalls in the quantification of root C: Need for soil C modeling.

Root-derived carbon includes both the standing root biomass and rhizodeposition. The latter is characterized as carbon derived from living roots that ranges from low molecular weight root exudates to smaller root fragments (Rasmussen et al., 2019). Specifically, root exudation occurs within hours of photosynthetic fixation and is rapidly utilized by soil microbes. As a result,

it is challenging to capture this important source of root-derived carbon with basic field methods which requires costly advanced isotopic methods for quantification (Peixoto et al., 2022). Further, the carbon derived from the root biomass occurs over progressively longer time periods which can also make it challenging to quantify. However, there are major challenges in adequately quantifying the root biomass that also requires both labor intensive and costly methods that vary among field experiments (Addo-Danso et al., 2016). Some of these methods include root coring, minirhizotrons, ingrowth cores, isotopic labeling, and remote sensing.

To overcome these challenges, soil C modelling approaches have been implemented where root C inputs are estimated from crop yields using allometric functions (Keel et al. 2017). Several different allometric functions have been developed to describe the relationship between soil C input and crop yields (e.g., Bolinder, ICBM, CCB, and C-Tool equations) (for a detailed overview see Keel et al., 2017). However, several influential factors have been documented to influence plant C allocation such as management strategies including plant species, nitrogen fertilization (including fertilizer type), and plant age. Therefore, these findings question the efficacy of using crop yields in the estimation of root C inputs and suggest that these belowground carbon inputs are not proportional to net primary productivity in agroecosystems (e.g., Hirte et al., 2018, 2021; Hu et al., 2018; Heinemann et al., 2023).

Management factors influencing plant C allocation.

Plant species (Crops vs. Grasses)

The amount and partitioning of recently fixed carbon belowground varies between annual crops and grasses (Figure 2). The larger carbon input belowground from grasses is in part based on the perennial nature of grasses that require a greater investment in the root system for continual regrowth each year and following grazing or cutting. Further, the domestication of crops to attain higher yields through various management strategies reduces belowground

allocation in favor of retaining carbon in the aboveground biomass (Kuzyakov & Domanski, 2000; Pausch and Kuzyakov, 2018).
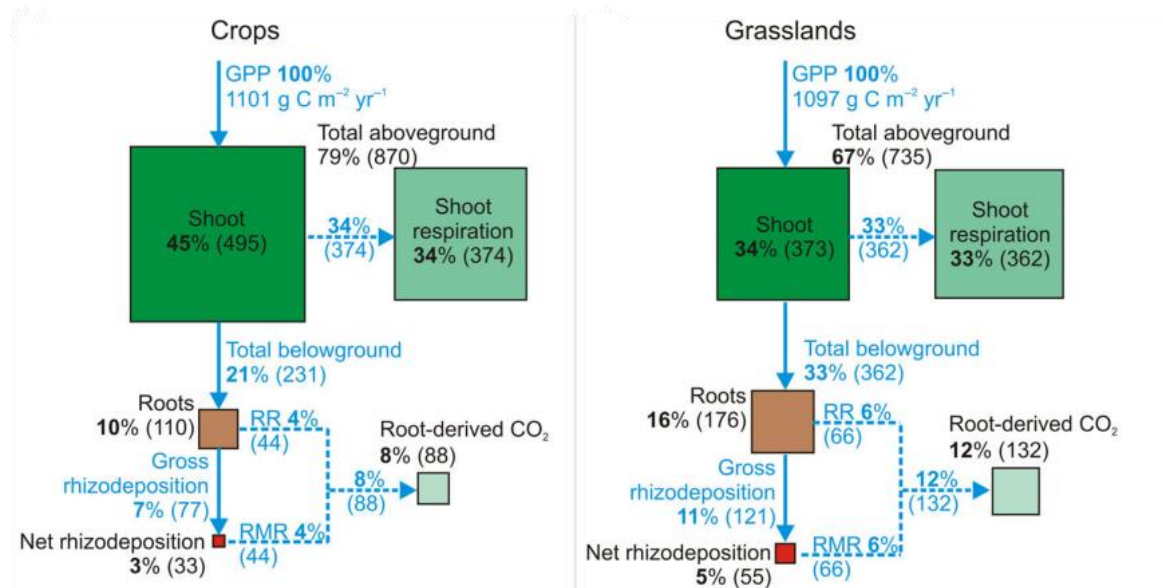

Figure 2. Overview and examples of C allocation patterns for crops and grassland species (Pausch and Kuzyakov, 2018). The percentage values (generalization) shown were calculated as averages of all collected data. For crops, 20 studies including 99 data sets, and for grassland species, 16 studies with 128 data sets were used. Based on gross primary production (GPP), absolute values of C partitioning (examples) for crops and grasslands are shown in parentheses (g C m^{-2} year^{-1}).

Plant age

Plant age and developmental stage directly impact the allocation of C belowground. Specifically, young crops allocate proportionally more C to roots as compared to older plants with higher allocation to the shoots (Figure 3). This also results in reduced root exudation in response to changing allocation patterns in older plants but an enhanced contribution from root turnover (Pausch et al., 2013). The pattern of C allocation differs between crops and grasses. Specifically, the point at maximum belowground allocation for crops occurs around 50 days after planting followed by a steep decrease. On the contrary, there is a consistent increase (around 100 days) for grass species followed by a more gradual decline with plant age. These considerable

differences are associated with the perennial nature of these grassland species requiring continual growth over several years (Warembourg and Estelrich, 2001).
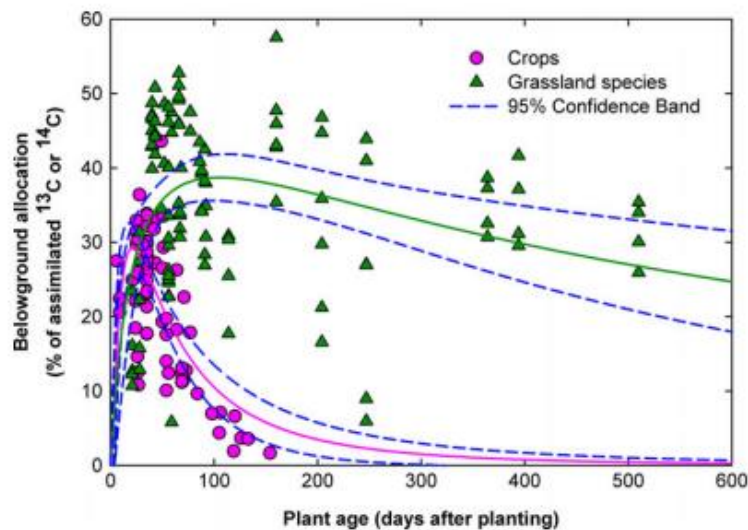
Figure 3. Total ^{13}C or ^{14}C allocation of recent assimilates to all belowground pools for crops and grassland species depending on plant age (Pausch and Kuzyakov, 2018).

Nitrogen fertilization

As nitrogen (N) is often limited, increasing the N availability through fertilization has been shown to alter the C allocation pattern (Pauch and Kuzyakov, 2018). Specifically, fertilization studies with perennial ryegrass (*Lolium perenne*) showed a negative correlation between the belowground allocation of recently assimilated carbon with increasing N fertilization. It is suggested that the higher availability of N reduced belowground carbon input to maximize resource utilization. For instance, a higher proportion of carbon is retained in the shoots to increase biomass yield. Further, within a Swiss long-term field trial with both maize and wheat grown under different farming practices documented a similar conclusion (Figure 4; Hirte et al., 2018). Irrespective of a higher biomass with increasing fertilization in the conventional treatment, the proportion of C allocated belowground were similar between organic and conventional farming for both maize and wheat.
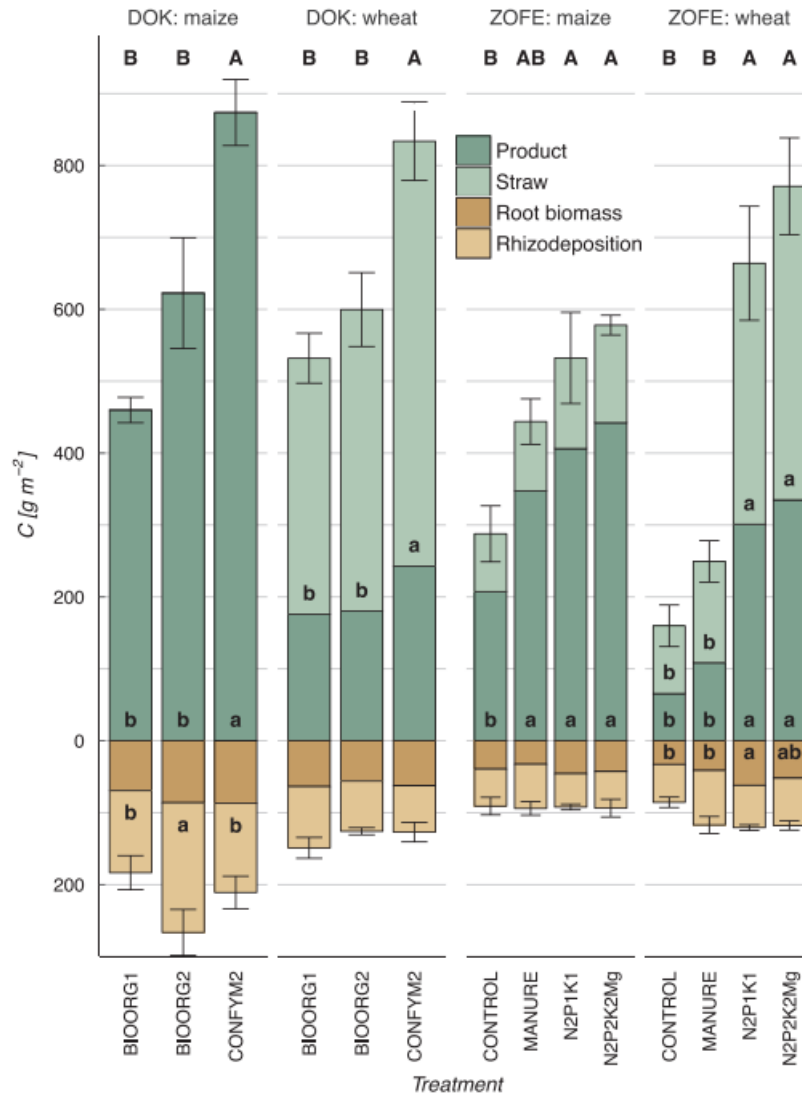
Figure 4. Below and above ground plant C of field-grown maize and wheat at harvest in different treatments of the DOK and ZOFE long-term field trials. Product refers to total above ground biomass of silage maize (DOK) or grain yield of grain maize (ZOFE) and wheat. Error bars: SEs of total below and above ground C (4 field replications). Different letters (lower case: root biomass, rhizodeposition, product, and straw C; upper case: total below and above ground C) denote significant ($p < 0.05$) differences in least squares means of C pools between treatments within crops and sites (missing letters: no differences) (Hirte et al., 2018).

Farming system: organic vs. conventional

The root C allocation within the topsoil in organic, no-till, and conventional farming across 24 winter wheat fields in Switzerland found higher root C inputs in organic compared to conven-

tional soils irrespective of yield (Hirte et al., 2021). Specifically, the root C allocation was significantly higher in organic farming as illustrated by an increase in root biomass (+40%) and root-shoot ratios (+60%) compared to conventional farming within the topsoil (Figure 5). Further, there was no effect of deeper soil layers (i.e., between 25-75 cm) and with no-till. Three management factors in the topsoil were found to explain most of the variation between the root biomass across organic and conventional farming systems. These included (1) weed biomass; (2) mineral N fertilization amount; and (3) soil organic carbon. It was suggested that weeds, which are higher in organic farming occupy the same niche creating competition resulting in the proliferation of the winter wheat roots to acquire resources (Kiær et al., 2013). Further, the lower mineral N availability in response to a reduced fertilization intensity in the organic system resulted in a higher root biomass (Chirinda et al., 2012; Hu et al., 2018).
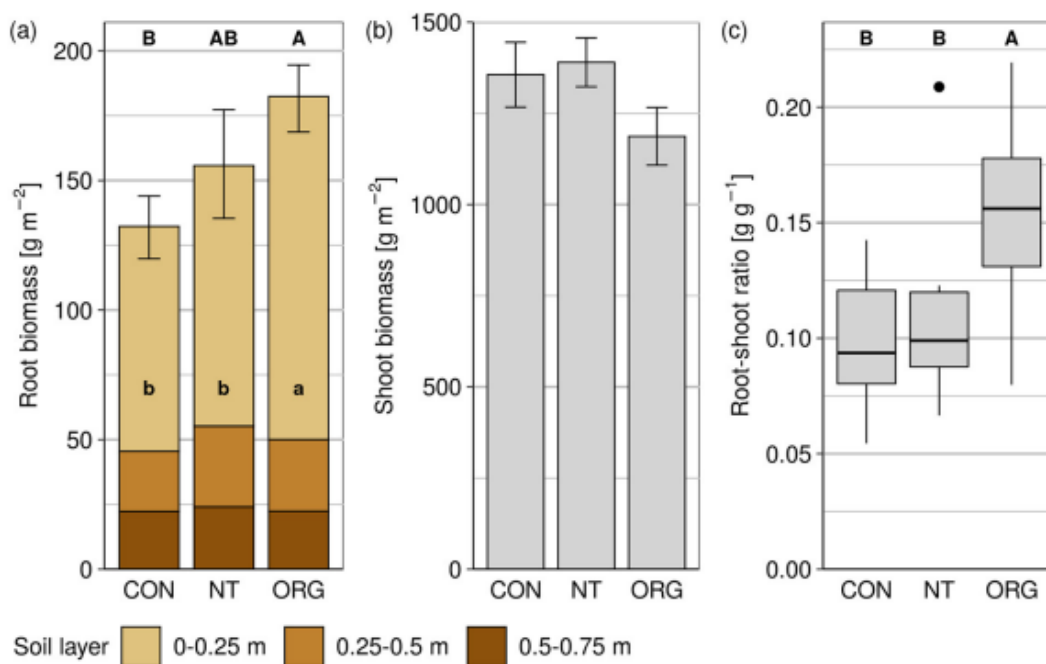
Figure 5. Root biomass in the top (0–0.25 m), intermediate (0.25–0.5 m), and deep (0.5–0.75 m) soil layers, wheat shoot biomass, and root-shoot ratios in conventional (CON), no-till (NT), and organic (ORG) winter wheat fields at flowering in Switzerland (n = 8 sites; average of 4

field replications each). Error bars refer to standard errors of total root (0–0.75 m) and shoot biomass of 8 sites. Different letters denote significant differences between estimated marginal means of root biomass in the individual soil layers (lower case letters) and total root biomass and root-shoot ratios (upper case letters) at $p < 0.05$ (Tukey HSD) (Hirte et al., 2021).

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