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Root uptake of carbon from soil

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This report concerns a study which was conducted for Svensk Kärnbränslehantering AB (SKB). The conclusions and viewpoints presented in the report are those of the authors. SKB may draw modified conclusions, based on additional literature sources and/or expert opinions.

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Abstract

Although plants mainly take up CO_2 from the atmosphere, studies have documented that their roots can absorb dissolved inorganic carbon (DIC) and dissolved organic carbon (DOC) from the soil via roots, accounting for 1–2 % of plant biomass carbon. However, despite these long-standing observations, significant knowledge gaps remain and studies continue to report variability in soil carbon uptake rates and the proportion of soil-derived carbon in plants.

In this report, we present an extensive review of root uptake of carbon from soil by compiling and analysing relevant data both from field and laboratory studies across different plant functional types and comparing the uptake of different carbon forms (DIC and DOC). The fifteen reviewed studies suggested a central value of 2.26 % of carbon from soil (combined DIC and DOC) taken up by plant roots, with a median value of 1.5 %. However, a few studies have shown higher root uptake under field conditions (5–10 %), highlighting the need for further research in different ecosystems to draw more solid conclusions on these values.

Investigation of field and experimental studies showed similar results. These findings suggested consistency of laboratory studies with field data, despite the limitations in isolating root carbon uptake in the field. Moreover, comparable root uptake of DIC (2.2 %) and DOC (2.4 %) were found in the plant roots with median values of 1 % and 0.6 %, respectively. Both DIC and DOC are either adsorbed or absorbed, and while for DIC and small organic molecules passive uptake is suggested, the uptake of larger organic molecules into roots is explained by active uptake. DIC can be fixed, while DOC can be respired indirectly, contributing to the overall energy production and carbon budget. Regarding plant functional types, the rate of uptake was approximately 1.89 % in grass, 2.78 % in forbs and 2.56 % in trees.

However, no significant difference was observed between plant functional types. The reason for a slight difference across different plant categories is not entirely clear but might be associated with environmental conditions and experimental setups between field and laboratory studies, as well as with the low number of studies found for each plant functional type.

Additionally, the data indicated uneven distribution of carbon from soil (DIC and DOC) between roots and shoots in most studies, while only two studies showed an equal distribution. As the overall number of studies reporting uptake rates and contribution of soil-derived carbon forms into plants was still low (15), more studies are needed to refine estimates across different ecosystems and plant functional types and clarify the mechanisms regulating the distribution of soil-derived carbon within plants. This is needed for developing ^{14}C transfer models, which are important for advancing research in radioecology and understanding the movement of radioactive carbon in terrestrial ecosystems.

Sammanfattning

Växter tar huvudsakligen upp koldioxid (CO_2) från luften, men forskning har visat att växtrötter även kan ta upp löst oorganiskt kol (DIC) och löst organiskt kol (DOC) från marken. Denna markbundna kolkälla kan utgöra cirka 1–2 % av växtens totala biomassa. Trots att detta fenomen har varit känt länge finns det fortfarande betydande kunskapsluckor, och studier rapporterar stor variation i hur mycket kol växter faktiskt tar upp från marken.

I denna rapport har vi gjort en omfattande genomgång av både fält- och laboratoriestudier om växters upptag av kol via rötterna. Vi har analyserat data för olika växttyper och jämfört upptaget av DIC och DOC. De femton studier som granskats visar att i genomsnitt tas cirka 2,26 % av växtens kol upp från marken (både DIC och DOC), med ett medianvärde på 1,5 %. Några enstaka fältstudier har dock visat betydligt högre upptag (5–10 %), vilket understryker behovet av mer forskning i olika ekosystem.

Resultaten från fält- och laboratoriestudier var i stort sett överensstämmande, vilket tyder på att laboratorieförsök ger en realistisk bild trots svårigheter att isolera rotupptag i fält. Upptaget av DIC (2,2 %) och DOC (2,4 %) var liknande, med medianvärden på 1 % respektive 0,6 %. Både DIC och DOC kan tas upp passivt (särskilt mindre molekyler), medan större organiska molekyler kräver aktivt upptag. DIC kan användas direkt i växtens kolfixering, medan DOC kan brytas ner och bidra till växtens energiproduktion.

När det gäller olika växttyper var upptaget cirka 1,89 % för gräs, 2,78 % för örter och 2,56 % för träd, men skillnaderna var inte statistiskt signifikanta. Variationen kan bero på miljöfaktorer, experimentella skillnader och det låga antalet studier för varje växttyp.

Slutligen visade de flesta studier att det kol som tas upp från marken fördelas ojämnt mellan rötter och ovanjordiska delar, medan endast två studier visade en jämn fördelning. Eftersom antalet studier fortfarande är lågt behövs fler undersökningar för att bättre förstå upptaget och fördelningen av markbundet kol i växter. Detta är särskilt viktigt för utvecklingen av modeller för ^{14}C-transport, som är centrala för radioekologisk forskning och för att förstå hur radioaktivt kol rör sig i terrestra ekosystem.

Content

1 Introduction

1.1 Carbon cycle

In the atmosphere carbon mainly occurs in the form of carbon dioxide (CO_2). Primary producers, such as plants, take up atmospheric CO_2 for photosynthesis (Calvin, 1962). Although plants mainly take up atmospheric CO_2, it is well-documented that roots can take up small proportion of inorganic carbon (1–2 %) from the soil. This phenomenon has been documented already more than half a century ago in original research studies, including those by Stolwijk and Thimann, (1957) and Skok et al. (1962) and more recent investigations such as Majlesi et al. (2019) and Jyllilä (2022) continue to support this observation. Additionally, several review articles, such as Pérez-Sánchez et al. (2009), Limer et al. (2013), Mobbs et al. (2014) and Thorne et al. (2014), have synthesized findings on this topic, highlighting its broader implications for plant physiology and carbon cycling. However, despite these long-standing observations, significant knowledge gaps remain. Studies continue to report variability in the proportion of carbon from soil taken up by roots, with some suggesting higher contributions than previously estimated (Hwang and Morris, 1992; Tagami and Uchida, 2010; Jyllilä, 2022). Additionally, the factors driving the variabilities such as differences in soil type, microbial interactions, plant species, or environmental conditions are not yet fully understood.

Root uptake of carbon from soil primarily occurs in form of dissolved inorganic carbon (DIC), e.g., carbonate ions in solution, carbonic acid and bicarbonate species (Rasilo, 2013; Limer, et al. 2017). In contrast, particulate inorganic carbon (PIC), which consists of solid carbonate minerals such as calcium carbonate ($CaCO_3$), is not directly available for root uptake. The carbon taken up as DIC may go through transpiration streams within xylem tissues, which drive carbon from the roots to the various parts of plants up to the stomatal cavities (Livingston and Beall 1934; Amiro and Ewing 1992; Bloemen et al. 2013). In addition to DIC, root uptake of soil organic carbon (SOC), particularly in dissolved organic form (DOC) has also been reported in some studies, though its quantitative significance remains uncertain. Particulate organic carbon (POC), in contrast to DOC, is less likely to be directly absorbed by roots due to its larger molecular size. However, microbial decomposition can break down POC into DOC or convert DOC into smaller molecules for uptake. Similarly, under certain soil conditions, PIC can dissolve into DIC, making it available for root absorption. Moreover, in aerenchyma plants, which are often submerged in water, gaseous CO_2 can be taken up by roots and transported up to leaves, facilitating the rapid exchange of gases between belowground and aboveground parts of plants (Takahashi et al. 2014). Soil-derived CO_2 can also be re-assimilated by plant leaves directly in the canopy atmosphere (e.g. Milton et al. 1998). However, this process is not the focus of this report. To maintain consistency, we used DIC for dissolved inorganic carbon and SOC for soil organic carbon, specifically referring to DOC, throughout this report when discussing different soil carbon pools. In this work, the uptake of carbon from soil, refers to all dissolved forms (inorganic and/or organic), as particulate forms are not likely taken up.

Once carbon primarily from atmospheric CO_2, is taken up by plants, it is converted into organic compounds, making it part of the plant organic carbon. Eventually it enters the soil in the form of plant litter, thus, becoming part of the soil carbon pool. After microbial decomposition of organic compounds, some of the carbon is released back into the atmosphere as CO_2, while a portion remains in the soil, where it can contribute to long-term soil carbon storage (Trumbore, 2006; Lange et al. 2015). The carbon in the soil, including that in the soil solution, may be distributed into deep soil layers, groundwater, or aquatic ecosystems as particulate or dissolved organic (POC, DOC) or inorganic carbon (PIC, DIC) (Rasilo, 2013). As mentioned above, a smaller but well-documented pathway is the direct uptake of dissolved soil carbon by plant roots. Carbon transfer and transformation pathways from soil to plants are illustrated in Figure 1-1. Importantly, carbon which was originally derived from the soil and is taken up and stored in plants can end up being transferred into higher trophic levels, being consumed by herbivorous animals or even humans. This is important for nuclear waste management, particularly in the context of geological disposal of nuclear waste where radioactive elements could be accidentally released and migrate through soil into the biosphere and affect the surrounding environment.

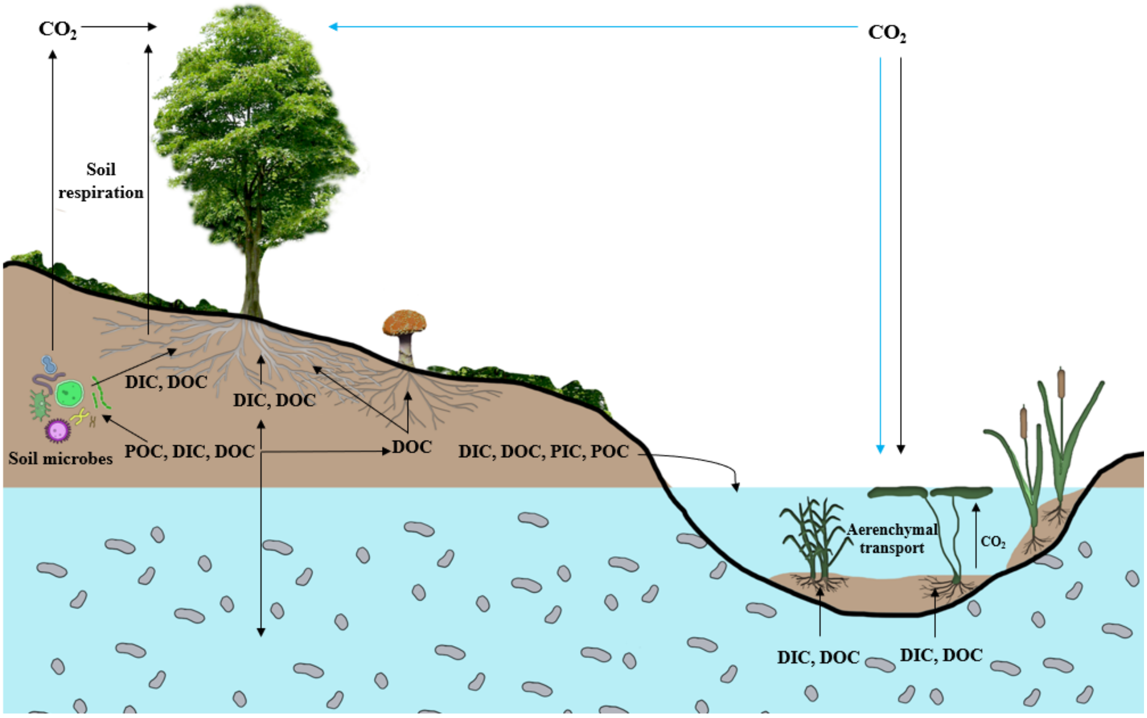

Figure 1-1. *Carbon transfer and transformation pathways from soil to plants. Black and blue arrows indicate the transfer of carbon, derived from the soil/sediment and atmosphere, respectively. The following abbreviations were used: PIC (particulate inorganic carbon), POC (particulate organic carbon), DIC (dissolved inorganic carbon), DOC (dissolved organic carbon).*

1.2 Uptake of carbon from soil relevant to geological disposal of radioactive waste

Nuclear power is considered as an important source of energy for many countries. However, careful management of radioactive waste and spent nuclear fuel is essential in order to avoid any possible adverse effects on the biosphere. Currently, geological disposal is being implemented in countries such as Finland and Sweden as the best approach to dispose of radioactive waste (IAEA, 2009). In this approach, radioactive wastes are stored in deep bedrock down to the depth of hundreds of meters. To evaluate risks of possible releases of radionuclides, e.g., ^{14}C from an underground facility, a safety assessment is required. Potential releases of ^{14}C discharged from radioactive waste repositories (mainly low-level waste) are expected to be in the form of low-weight organic molecules or inorganic carbon (SKB, 2015). Over time, microbial activity and chemical reactions can convert some of these organic ^{14}C into gaseous forms, mostly methane ($^{14}CH_4$) produced by methanogens under anaerobic conditions. As $^{14}CH_4$ migrates upward, it is oxidized to $^{14}CO_2$ by methanotrophs. In the form of $^{14}CO_2$, the carbon is readily available for uptake by plants either through root absorption of $^{14}CO_2$ dissolved in porewater or through photosynthesis of $^{14}CO_2$ transported to surface water (aquatic plants) or atmosphere (terrestrial plants). These processes integrate ^{14}C into the organic carbon cycle, allowing it to be incorporated into plant biomass and subsequently to higher trophic levels. Understanding the mechanisms of ^{14}C migration and uptake into plants and organisms is essential for developing effective waste management strategies and ensuring the long-term safety of radioactive waste disposal in geological repositories.

Although root uptake of carbon from soil is recognized as a minor pathway (only a few percent), compared to the fraction of carbon taken up from the air, it can be quantitatively important in impact assessments where ^{14}C enters surface ecosystems via the discharge of groundwater and/or migration of soil gases. This is because the relative fraction of repository-derived ^{14}C is expected to be higher in soil than in the atmosphere and, thus, root uptake results in a disproportionally high contribution to the uptake of repository-derived ^{14}C in plants (Ota and Tanaka, 2019).

1.3 This report

While recent review studies have investigated various aspects of carbon dynamics, including the transfer of radionuclide ^{14}C from soil to plants (notably Limer et al. 2013; Mobbs et al. 2014; Thorne et al. 2014; and Ikonen 2022), these studies did not synthesize the latest available literature on root uptake mechanisms. In fact, the last comprehensive review on the root uptake of carbon from soil dates to the 1930s (Livingston and Bell, 1934), thus, there is a need for an update on this topic. In this report, we conducted an extensive review of the historical and recent international literature to provide an overview of the findings relevant to root uptake of carbon from soil. In this review, carbon from soil refers to the dissolved forms of carbon present in the bulk soil, including DOC and DIC, as the reviewed studies have reported those forms of carbon in soil. However, we used the term 'soil carbon' to refer broadly to both DOC and DIC forms and only specified particular carbon pools when relevant to avoid ambiguity. All the relevant data on field and laboratory studies were compiled and the results were compared among different plant functional types. The main topics that are discussed in this review are 1) the amount of carbon from soil taken up by plant roots, 2) underlying mechanisms, 3) different methods used to study the root uptake of carbon from soil by plants, and 4) recommendations for future studies.

2 Historical remarks

Research on carbon uptake by plant roots initially peaked already during the late 19th century and early 20th century, coinciding with the discovery of photosynthesis and the exploration of fundamental plant growth mechanisms. By the 1920s consensus emerged that the primary source of assimilated CO_2 was the atmosphere, with up to 5 % contributions through roots (Breazeale, 1923). Later in the 1950s, one highly cited study by Russian scientists suggested that up to 25 % of plant carbon was derived from root uptake, suggesting that plant growth can be enhanced through CO_2 fertilization of soils (Kursanov et al, 1952). Thus, interest in the uptake of carbon from soil via roots grew again. However, the findings of the Russian researchers could not be verified, sparking renewed interest, but also skepticism about the role of root-based carbon assimilation.

A second peak in the research started from 1960s, driven by the need to answer fundamental questions related to processes governing plant nutrition, ecosystem dynamics, and agricultural productivity (Skok et al. 1962; Führ and Sauerbeck, 1967). Another highly cited reference (Vuorinen et al. 1989) stated that root uptake of carbon from soil in plants is generally between 1 and 2 %. However, the uptake was not directly measured in this article but only referenced from a previous study of Pelkonen et al. (1985). The authors used Pelkonen et al. (1985) only to contextualize their own results, and to reflect the prevailing view of that era with respect to transfer of carbon from soil into roots. One notable exception from the general behavior of the plants, as discovered in 1984, is *Stylites andicola*, a vascular terrestrial plant that lacks stomata and derives most of its carbon through its roots (Keeley et al. 1984). Native to the high-altitude Andes, *Stylites andicola* is an interesting but rare plant that does not, however, significantly influence global carbon budgets due to its limited geographic range. By 1980s it was also well established that some aquatic plants assimilate large amounts of CO_2 from the sediment via their roots (Søndergaard and Sand-Jensen, 1979). Nevertheless, this review focuses on terrestrial plants due to very limited literature on root carbon uptake of aquatic plants.

Together, the line of research on root uptake of carbon from soil to plants from the 1950s to 1980s contributed significantly to unravelling mechanisms of plant acquisition of carbon from soil, by enhancing knowledge on plant nutrition and root-soil interactions, thereby contributing to food security and sustainable land management. The knowledge was also crucial for modelling global carbon cycles, predicting primary production, and assessing the impact of environmental changes on terrestrial ecosystems.

During the 1990s, the radioecological research community showed increasing interest in carbon uptake from soil by plant roots. This interest was driven by the necessity to understand the mechanisms and implications of carbon uptake and mechanisms from soil, especially in scenarios where radioactive isotopes like ^{14}C could contaminate soils and plants. Specifically, root uptake of C in ^{14}C enriched soil could lead to higher ^{14}C doses in plants than previously assumed (Brix, 1990; Amiro et al. 1991; Sheppard et al. 1991; Amiro and Ewing, 1992; Hwang and Morris, 1992; Milton et al. 1998; Jyllilä, 2022).

From a methodological point of view, the study of carbon uptake from soil by plant roots has evolved significantly, moving from early reliance on radioactive carbon isotopes to safer stable isotopes and refined laboratory techniques. This shift has been facilitated by advancements in analytical techniques, such as isotope ratio mass spectrometry (IRMS), which allows for precise measurements of stable isotopes in plant tissues and soil. Moreover, studies on soil-derived carbon uptake into roots and plants have mostly been conducted in controlled laboratory environments, where carbon sources can be precisely manipulated. However, in recent years, soil-plant systems where the isotope signal differs between soil and plant (e.g., C3: C4 systems, geothermal fields, or recultivated cutaway peatlands; Maljesi et al. 2019, Jyllilä, 2022), have been investigated more extensively, offering valuable insights into the movement of belowground carbon sources into the biosphere.

3 Uptake of carbon from soil in plant roots

The literature in this work was compiled from Web of Science and Google Scholar based on different field and laboratory studies. The focus of this work was to report the proportion of soil-derived carbon taken up by roots relative to the entire plant in terrestrial plant species. Only experimental and field data were compiled in this review and, thus, no modelling studies were included. For studies where the uptake of soil-derived carbon in roots was not directly reported as a proportion of the whole plant (except for Hwang and Morris, 1992, and Enoch and Olesen, 1993), we estimated these values referencing common root/shoot ratios available in the literature. Hence, all the percent values reported here refer to the fraction of carbon derived from soil source (DIC and/or SOC) in the roots relative to the whole plant. Some studies examining the transfer of soil-derived carbon into plants were excluded from these calculations (but are discussed qualitatively, e.g., Ogiyama et al. 2010), as they reported only ^{14}C radioactivity levels in various plant parts without providing specific carbon content data. We also excluded one high uptake rate reported for dissolved organic carbon (DOC) in grass species (23 %; Hu et al. 2022), as it can be criticized for being too artificial due to unnaturally high concentrations of small metabolites and neglecting competition with microbes. However, this study warrants further investigation.

As concluded in the review of 1934, root carbon uptake from soil can be expected to be up to 5 % (Livingston and Beall 1934), which is slightly higher than many others claiming that this process ranges from 1 % to 2 % (Stolwijk and Thimann, 1957; Skok et al. 1962; Schäfer, 1988; Vuorinen et al. 1989; Brix, 1990; Sheppard et al. 1991; Amiro and Ewing, 1992; Milton et al. 1998; Ford et al. 2007; Tagami et al. 2009). An average value of 2 % root uptake of carbon from soil is most often cited in the literature (Stolwijk and Thimann, 1957; Skok et al. 1962; Schäfer, 1988; Brix, 1990; Sheppard et al. 1991; Amiro and Ewing, 1992; Milton et al. 1998; Ford et al. 2007; Tagami et al. 2009; van Dorp and Brennwald, 2009; Tagami and Uchida, 2010). In our review of 15 original studies going beyond the ones mentioned above (Table 3-1), we found on average 2.26 % (± 0.51 standard error of the mean; SEM) of carbon from soil (both DIC and DOC) in the roots relative to the whole plant, which is slightly higher than the commonly cited 1-2 %. However, the median value of the root uptake of carbon relative to the whole plant was 1.50 % as also found by others (Stolwijk and Thimann, 1957; Führ and Sauerbeck, 1967; Amiro and Ewing, 1992; Tagami et al. 2009; Zamanian et al. 2017; Majlesi et al. 2019).

Table 3-1 summarizes the root uptake of soil-derived carbon across different plant functional types (grasses, forbs, woody plants), including information on the carbon form (DIC/DOC), the methods used, and whether and how atmospheric uptake of carbon was prevented. The table provides details for both field and laboratory studies, showing various proportions of carbon uptake, and highlights also transfer of carbon from roots to shoots. For instance, only two studies reported a relatively equal distribution of carbon between roots and shoots (Stolwijk and Thimann, 1957; Schäfer, 1988), while others found an uneven distribution. Several studies did not directly measure root-to-shoot transfer (Tagami et al. 2009; Tagami and Uchida, 2010; Majlesi et al. 2019; Jyllilä, 2022). The prevention of atmospheric uptake of carbon, derived from soil, was achieved mostly by using airtight sealed systems (chambers) or a steady flow of air. This ensures that the carbon measured and analyzed is directly linked to the uptake of carbon pools via roots, rather than re-assimilation of atmospheric CO_2. However, some studies did not provide this information (Brix, 1990; Sheppard et al. 1991; Majlesi et al. 2019; Jyllilä, 2022).

The average root uptake of carbon from soil reported under field and laboratory conditions was similar, being 2.20 % (± 0.77) and 2.30 % (± 0.69), respectively (Figure 3-1). The median values were also similar, showing 1 % and 1.50 % root uptake of carbon from soil under field and laboratory-based studies, respectively. Applying independent-samples t-test, no significant differences were observed between the methods. Similarly, no significant differences were observed between ^{14}C- and ^{13}C-based studies or between hydroponic and soil-based systems in controlled environments (data not shown). However, the results of the field studies showed greater variability (as observed by larger scatter in Figure 3-1) and, in some studies, a higher uptake of carbon from soil by roots compared to the laboratory data, even though the average uptake was higher in the laboratory studies. The highest values of root uptake in the field were mostly evident in fruit and flowering plants (5.40 %) and trees (6.83 %) in a geothermal field in Iceland (Jyllilä, 2022). Such uptake rate in this study may be attributed to the high concentrations of soil CO_2 in volcanic and geothermal areas. Field studies also often use “natural” tracers, where whole soil system carries a different isotope signature than the plants, thus, all carbon species are “labelled” and can be taken up (e.g. DIC and SOC). Both direct root absorption and indirect uptake (via leaf re-assimilation of soil-derived $^{14}CO_2$) contribute to carbon uptake in most cases (except for Milton et al, 1998), with indirect leaf uptake often representing a larger fraction. Milton et al. (1998) found in a field study where plants were transferred to the discharge area of a nuclear waste management field (with some potted plants having no root contact with the contaminated soil and others with contact), that ^{14}C uptake by leaves was up to 5 % through re-assimilation, whereas root uptake contributed minimally (0.1 %).

While field conditions more closely simulate natural ecosystems, their suitability for isolating root carbon uptake and, thus, for modeling carbon uptake is limited. However, despite these limitations, laboratory studies were consistent with field data, as no significant difference in root carbon uptake was found. This is likely due to the high variability, the still limited number of studies particularly from the field and the range observed across both. Overall, the uptake of carbon from soil into roots was quite variable and ranged from 0 to 10 %. Among the laboratory studies, Führ and Sauerbeck (1967) and Hwang and Morris (1992) reported the highest root uptake, being 5 % and 10 %, respectively.

In general, similar proportions of root uptake were found among different plant functional types, as one-way ANOVA showed no significant differences across the plant types. Root uptake of carbon from soil was lowest from Figure (1.89 % ± 1.17) followed by trees (2.56 % ± 1.5) and forbs (2.78 % ± 0.65) (Figure 3-1), but again, no significant differences were found due to the overall low number of plant-specific studies. The median values showed 0.75 % of root uptake for grass, 1.25 % for trees and 2 % for forbs. The reason for a small difference across different plant categories remains unexplained, but variations in species-specific uptake mechanisms, the environmental parameters and experimental setups under field and laboratory conditions may be contributing factors. Vapaavuori and Pelkonen (1985) observed that the growth of trees (willow) increased even by up to 31 % when grown hydroponically in sodium bicarbonate ($NaHCO_3$) solution. However, uptake was not measured directly and the growth can, thus, be related to indirect effects of the high bicarbonate concentration (e.g., changes in pH, increased NO_3 at elevated DIC concentrations in the roots zone (Cramer et al. 1996); therefore, this study was excluded from our calculations.

In another study, a biomass increase was observed in tomato plants (*Solanum lycopersicum*) grown in soil with higher DIC concentrations. Direct uptake measurements indicated that less than 5 % of the carbon originated from DOC, which could not account for the significantly higher biomass growth (Tagami and Uchida, 2010). Thus, physiological changes and interactions driven by increased CO_2 levels likely played a significant role in promoting plant growth. Nevertheless, our findings indicated the highest root uptake in the forbs, which was not significantly different to the other analyzed plant functional types.

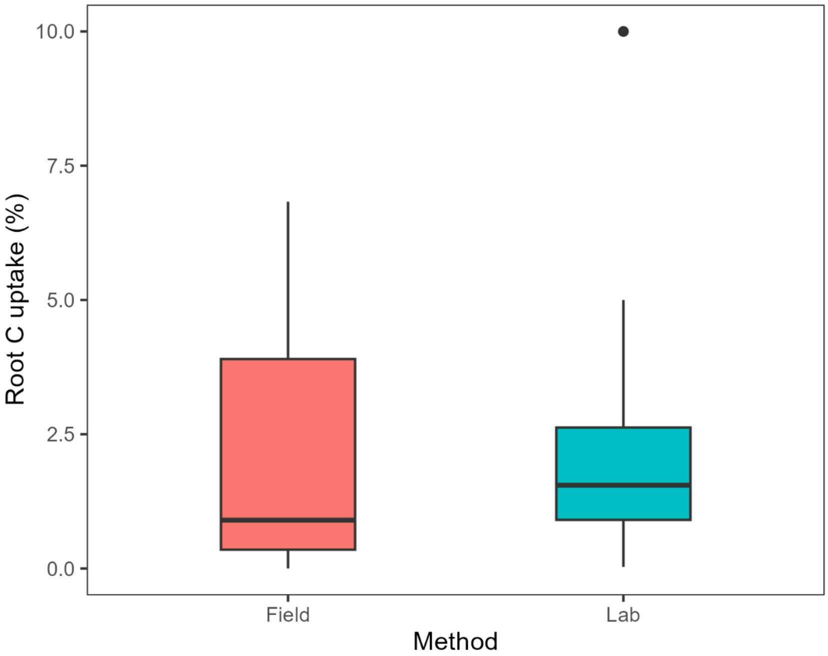

Figure 3-1. *Uptake of carbon from soil in plant roots (%) in field (n= 11) and laboratory studies (n= 14). The lower and upper hinges in each boxplot correspond to the 25th and 75th percentiles. The upper whisker in each boxplot extends from the hinge to the largest observation no further than 1.5 × IQR from the hinge (where IQR is the inter-quartile range or distance between the 25th and 75th percentiles), and the lower whisker extends from the hinge to the smallest observation at most 1.5 × IQR of the hinge. The lines in the boxes indicate the median values and the dot outside the boxplots represent an outlier.*

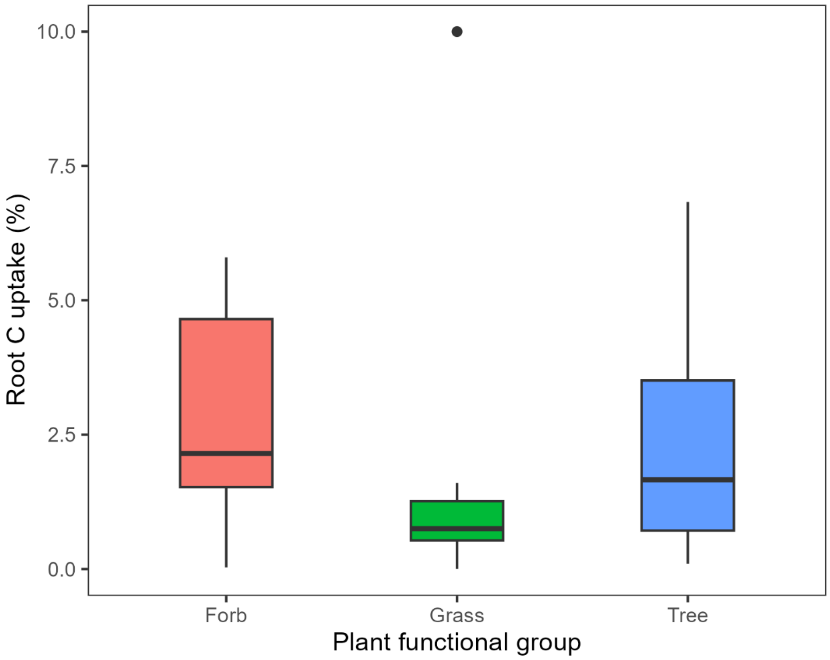

Figure 3-2. *Uptake of carbon from soil in plant roots (%) as a function of plant functional types, forb (n= 10), grass (n= 8) and tree (n= 4). The lower and upper hinges in each boxplot correspond to the 25th and 75th percentiles. The upper whisker in each boxplot extends from the hinge to the largest observation no further than 1.5 × IQR from the hinge (where IQR is the inter-quartile range or distance between the 25th and 75th percentiles), and the lower whisker extends from the hinge to the smallest observation at most 1.5 × IQR of the hinge. The lines in the boxes indicate the median values and the dot outside the boxplots represent an outlier.*

Table 3-1. Summary of published data on root uptake of soil-derived carbon across plant functional types (grasses, forbs, woody plants, nitrogen fixers, and succulents), including information on carbon form (DIC = dissolved inorganic carbon, DOC = dissolved organic carbon), method applied, additional notes relevant for uptake of ^{14}C from soil to roots and whether or not atmospheric uptake of soil-derived carbon was prevented. Literature data are sorted in ascending order, starting with the oldest publication year. The value in parenthesis indicates the median value of root uptake into plants.

Field/Laboratory	**Plant Functional Type**	**Plant**	**Method**	**DIC/DOC**	**C form**	**Proportion of carbon from soil taken up via roots of total plant carbon (%)**	**Notes**	**Prevention of atmospheric uptake of soil- derived carbon**	**Reference**
Laboratory	Forb	Pea (*Pisum sativum var. Alaska*)	Plant roots were submerged in a solution containing the inorganic ^{14}C compounds	DIC	$^{14}CO_2$ and ^{14}C-labelled bicarbonate	**2.7**	Transportation of carbon from roots to shoots and equal distribution of ^{14}C radioactivity between roots and shoots	Flushing atmospheric CO_2 at a constant rate	Stolwijk and Thimann, 1957
	Grass	Barley (*Avena sativa, var. Segrehaver*)				**1.15**			
Laboratory	Forb	Cocklebur (*Xanthium pensylvanicum Wallr.*)	The plants were grown in a chamber, where roots were immersed in a nutrient solution and $^{14}CO_2$ was bubbled into the solution	DIC	$^{14}CO_2$	**0.03**	Around 65 % to 84 % of the total activity was found in the roots, indicating that a substantial amount of the absorbed carbon was retained in the root system	Roots were isolated in a chamber system to prevent atmospheric CO_2 interference and labelled CO2 was filtered out to remove any residual CO_2 before released into the air	Skok et al. 1962
Laboratory	Forb	Sunflower (*Helianthus annuus*)	Plants were grown in a nutrient solution containing labelled organic material	DOC	^{14}C-labelled humus	**1.6**	Likely the majority are not fixed but only adsorbed and kept in the root epidermis or on the roots	Constant aeration of free-air CO_2 to remove carbon from root respiration	Führ and Sauerbeck, 1967

Field/Laboratory	Plant Functional Type	Plant	Method	DIC/DOC	C form	Proportion of carbon from soil taken up via roots of total plant carbon (%)	Notes	Prevention of atmospheric uptake of soil- derived carbon	Reference
		Radish (*Raphanus sativus*)				**5**			
		Carrot (*Daucus carota*)				**3.6**			
Laboratory	Grass	Wheat (*Triticum aestivum*)	Application of $H^{14}CO_3^-$ to root system of wheat plant in hermetically sealed pots	DIC	CO_2 and bicarbonate	**0.33**	After applying $H^{14}CO^-_3$ to the root system, incorporation of HCO_3 was observed in the sugar-, starch-, and fiber-fraction. The transfer of carbon from roots to shoots was found in form of bicarbonate	Airtight sealed pots to isolate the plant roots and soil from the atmosphere	Schäfer, 1988
Laboratory	Grass	Common reed (*Phragmites australis*)	The plants were grown in a stock solution containing $KHCO_3/NaH^{14}CO_3$ as dissolved inorganic carbon	DIC	$KHCO_3/NaH^{14}CO_3$	**0.6**	The uptake of DIC in roots from interstitial water was insignificant (up to 1 %). The activity was higher in nodes than leaves, being the highest in rhizomes. ^{14}C moves upwards as CO_2 within the hollow stems of the plant	No specific information was provided to prevent the atmospheric uptake of soil-derived C but growing plants in a chamber under controlled airflow environment seemed to prevent the C flow from the soil into the atmosphere	Brix, 1990

Field/Laboratory	Plant Functional Type	Plant	Method	DIC/DOC	C form	Proportion of carbon from soil taken up via roots of total plant carbon (%)	Notes	Prevention of atmospheric uptake of soil- derived carbon	Reference
Field	Forb	Radish, (*Raphanus sativus L.*)	Inorganic $^{14}\mathrm{C}$ ($^{14}\mathrm{C}$-$\mathrm{CO_3}$) was applied to the soil as a solution of sodium bicarbonate, which was then mixed into the soil	DIC	Carbonate species	**0.6**	The study also labelled DOC (synthetic organic chemical) in addition to DIC and shows that DIC is taken up more effectively by plants compared to organic carbon	Field experiment. No specific information was provided to prevent the atmospheric uptake of soil-derived C. Re-assimilation of $^{14}\mathrm{CO_2}$ is possible and also discussed	Sheppard et al. 1991
		Bean (*Phaseolus vulgaris*)							
Laboratory	Forb	Bean (*Phaseolus vulgaris*)	Nutrient solution culture, using $\mathrm{NaH^{14}CO_3}$ tracer	DIC	Carbonate species	**1.5**	Plant uptake of C via the roots was independent of the photosynthetic rate and, in most cases, could be predicted bv knowing the transpiration rate and the nutrient solution concentration. The transfer of carbon from roots to shoots occurred passively through the transpiration stream	Adjusted airflow cuvette system under controlled environment to prevent the C flow from the soil into the atmosphere	Amiro and Ewing, 1992
Laboratory	Grass	Saltmarsh cordgrass (*Spartina alterniflora*)	Submerging the belowground tissues in $\mathrm{NaH^{14}CO_3}$ culture solution as well as injection of $^{14}\mathrm{CO_2}$ into the lacunar space	DIC	Carbonate species	**10**	The authors state that approximately 10 % of the carbon comes from the utilization of DIC and internal fixation of $\mathrm{CO_2}$, which includes both $\mathrm{CO_2}$ from the air and DIC. The study does not provide an exact separation of	The primary focus was not on prevention of atmospheric C but isolation of root system, using sealed plant chamber with silicone rubber helped to prevent	Hwang and Morris, 1992

Field/Laboratory	**Plant Functional Type**	**Plant**	**Method**	**DIC/DOC**	**C form**	**Proportion of carbon from soil taken up via roots of total plant carbon (%)**	**Notes**	**Prevention of atmospheric uptake of soil- derived carbon**	**Reference**
							these sources. Further, the study indicates that the labeled carbon taken up by the roots is transferred to the leaves and other aboveground tissues, although a substantial portion remains in the roots	the C flow from the soil into the atmospheric	
Field	Fern	Native ostrich ferns (*Matteuccia struthopteris*)	Small plants were planted into the ^{14}C discharge zone of a radioactive waste management area	DIC and DOC	$^{14}CO_2$	**0.1**	The ^{14}C is mostly taken up by leaves in form of $^{14}CO_2$ (re-fixation; up to 5 %). The transfer of C taken up by roots to shoots was very small compared to atmospheric C (0.1 %)	By comparing potted plants (which had limited root access to the contaminated soil) with planted ones (which rooted directly into the soil) the root-vs-air uptake of ^{14}C was assessed	Milton et al. 1998
	Tree	Cedar *(Thuja occidentalis "Smargd)*							
Laboratory	Tree	Loblolly pine *(Pinus taeda)* seedlings	Isotopically labeled soil DIC was applied in the irrigation water to measure uptake of soil DIC in the plant. The treatment solution contained 4 mM $CaCO_3$	DIC	^{13}C labelled DIC	**0.92**	A slight but non-significant increase was observed in both, the relative C gain in the whole plant (0.92 %) and in the root (1.6 %) by the contribution of soil DIC in NH_4^+ fertilized seedlings. Only minor fraction of C was transferred from roots to shoots	The plants were grown in a sealed system with controlled flushing of CO_2	Ford et al. 2007

Field/Laboratory	**Plant Functional Type**	**Plant**	**Method**	**DIC/DOC**	**C form**	**Proportion of carbon from soil taken up via roots of total plant carbon (%)**	**Notes**	**Prevention of atmospheric uptake of soil- derived carbon**	**Reference**
Field	Grass	White rice (*Oryza sativa*)	Stable carbon isotope ratios ($\delta^{13}C$ values) and total carbon concentrations in rice grains and associated soil samples were collected and analyzed throughout Japan	DIC and DOC	^{13}C/ ^{12}C natural abundance	**1.6**	The δ values for white rice and soil showed a weak correlation, suggesting a potential carbon supply from soil to rice. But differences in δ values between soil and plants were small, posing challenges in data interpretation	Natural isotopic tracers were used to separate the C contribution between soil and atmosphere in the plants. Both direct and indirect uptake of C derived from soil was, thus, considered	Tagami et al. 2009
Field	Grass	White rice (*Oryza sativa*)	Stable carbon isotope ratios ($\delta^{13}C$ values) and total carbon concentrations in rice plants and associated soil samples, as well as upland plants and their soil samples, were collected and analyzed throughout Japan	DIC and DOC	^{13}C/ ^{12}C natural abundance	**0.6**	Using natural abundance can be challenging for this purpose of source separation. Different processes, such as photosynthesis, respiration, and decomposition, can cause fractionation of carbon isotopes	Natural isotopic tracers were used to separate the C contribution between soil and atmosphere in the plants. Both direct and indirect uptake of C derived from soil was, thus, considered	Tagami and Uchida, 2010
	Forb	Upland field crops (tomato, eggplant, cucumber, cabbage, radish, carrot, onion, potato, sweet potato, wheat, barley, legumes, radish, leek)				**5.8**			

Field/Laboratory	Plant Functional Type	Plant	Method	DIC/DOC	C form	Proportion of carbon from soil taken up via roots of total plant carbon (%)	Notes	Prevention of atmospheric uptake of soil- derived carbon	Reference
Laboratory	Forb	Gromwell (*Buglossoides arvensis*)	^{14}C labelling of HCO_3^- in carbonate free (sand) and carbonate containing soil (loess) in a controlled growth chamber	DIC	$^{14}CO_2$ in the atmosphere and Na2 $^{14}CO_3$ in soil solution	**1.6**	The shoots also showed significant incorporation, but the roots had the highest incorporation of labeled carbon, reflecting their role in HCO_3 uptake. A significantly higher percentage (around 6.3 %) of fruit carbonate in is derived from lithogenic carbonates	The plants were sealed with cotton and petroleum jelly. The setup provided an airtight seal to prevent the exchange of CO_2 between the atmosphere and the soil solution	Zamanian et al. 2017
Field and laboratory studies	Grass	Reed canary grass (*Phalaris arundinacea* L .)	Use of natural abundance of ^{14}C in a depleted cutaway peatland and application of isotope mixing model to track the proportion of soil-derived C in the plants	DIC/DOC	$^{14}C/^{12}C$	**0.9**	No foliar uptake of carbon from soil was observed despite the availability in the canopy, possibly because of open canopy	Field experiment without separation of direct and indirect uptake of carbon from soils. However, ^{14}C signal of the soil was only detected in the roots (not in the leaves)	Majlesi et al. 2019
	Tree	Scots pine (*Pinus sylvestris* L.)				**2.4**			
Field	Forb	*Ranunculus sp.*, *Taraxacum sp.* and *Fragaria sp.*	The proportion of C was determined in the plants using natural isotopic difference (^{13}C) between geological and biological sources in a geothermal field by	DIC	CO_2, $^{13}C/^{12}C$	**5.4**	The transfer of carbon from soil varied from 0 to 13 % in the leaves of different species. However, no direct measurement of root-to-shoot transfer was reported	Field experiment without separation of direct and indirect uptake of carbon from soils	Jyllilä, 2022
	Tree	*Sorbus sp.* and *Picea sp.*				**6.83**			
	Lower plant	*Equisetum sp.*, lichen and moss				**0**			

Field/Laboratory	**Plant Functional Type**	**Plant**	**Method**	**DIC/DOC**	**C form**	**Proportion of carbon from soil taken up via roots of total plant carbon (%)**	**Notes**	**Prevention of atmospheric uptake of soil- derived carbon**	**Reference**
	Grass	*Poa sp.*	two-pool isotope mixing model			**0**			
Mean ± SEM (Median)						**2.26 ± 0.51 (1.5)**			

In this report, we also compiled and compared data relevant to the uptake of DIC and DOC. Interestingly, the data revealed similar uptakes of DIC and DOC in the plants, being 2.2 % ± 0.61 and 2.4 % ± 0.66, respectively (Figure 3-2). However, it is important to note that the median values showed slightly higher uptake of DIC, being 1 % compared to 0.6 % for uptake of DOC. Applying independent-samples t-test revealed no significant difference between DIC and DOC uptake. Traditionally, it is believed that plants prefer to take up DIC, such as bicarbonate (HCO_3^-), carbonate (CO_3^{2-}), and carbon dioxide (CO_2) dissolved in water. This is because of the fact that typically DOC in soil needs to be first broken down by soil microorganisms and turned from organic compounds into the forms (DIC) that plants can easily take up. However, it is also possible that simpler DOC compounds can be directly taken up and metabolized by plants. Some studies demonstrate that plants can take up organic nitrogen forms which co-occur with carbon compounds, indicating a widespread capacity to absorb organic molecules directly from their environment (Kielland et al. 2006). However, these studies primarily focus on organic nitrogen uptake, leaving the contribution of associated carbon to the plant's carbon budget largely unquantified. In this context, the study by Hu et al. (2022) is again noteworthy, reporting a 23 % incorporation of small organic metabolites in grass species. Despite methodological limitations (high concentration of organic molecules, lack of competition with microbes), this study underscores the potential for plants to absorb organic carbon forms, enhancing their overall carbon assimilation processes. However, when competition with microbes is considered, Kuzyakov and Jones (2006) found a low sugar absorption capacity of roots of maize. The uptake potential of DOC requires further research, particularly to unravel the underlying mechanisms, as discussed below. The DOC values reported here were extracted based on five studies only (Führ and Sauerbeck, 1967; Milton et al. 1998; Tagami et al. 2009; Tagami and Uchida, 2010; Majlesi et al. 2019). This is crucial for accurate interpretation of the values.

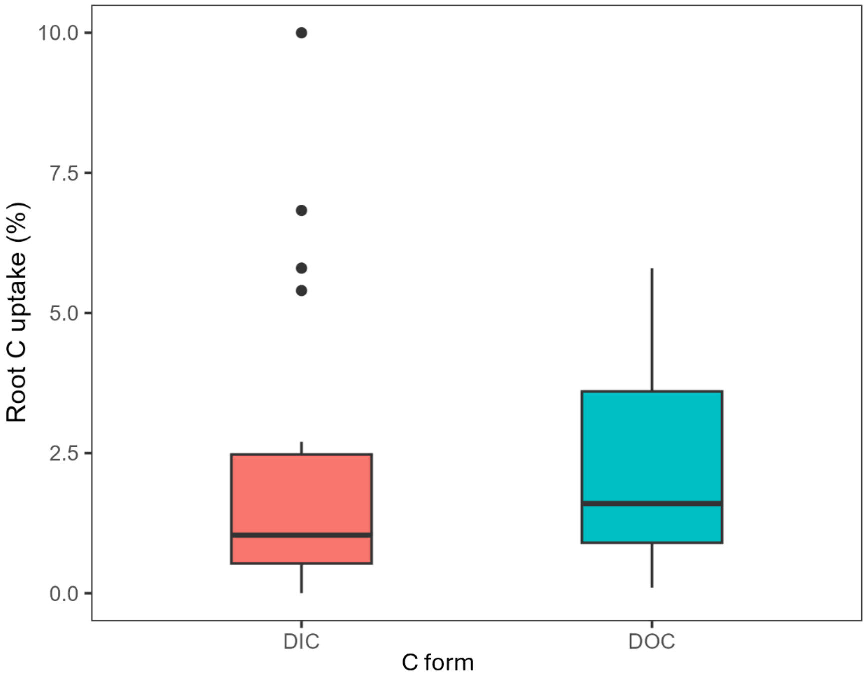

Figure 3-3. *Root uptake of carbon from soil (%) relative to the whole plant as a function of C forms, DIC (n= 20) and DOC (n= 9). The lower and upper hinges in each boxplot correspond to the 25th and 75th percentiles. The upper whisker in each boxplot extends from the hinge to the largest observation no further than 1.5 × IQR from the hinge (where IQR is the inter-quartile range or distance between the 25th and 75th percentiles), and the lower whisker extends from the hinge to the smallest observation at most 1.5 × IQR of the hinge. The lines in the boxes indicate the median values and the dots outside the boxplots represent outliers.*

4 Forms and underlying mechanisms relevant to root uptake of carbon from soil

4.1 Uptake of soil-derived carbon via roots: mechanisms and uptake pathways

We also reviewed the mechanisms underlying the uptake of carbon from soil into roots and conclude based on the literature that DIC can be taken up in gaseous form or aqueous solution in the form of carbonate ions (HCO_3^- and H_2CO_3) (Öquist et al. 2009). The pH plays a role in the form of inorganic carbon uptake from aquatic media. At low pH (5-5.5), dissolved carbon dominantly prevails in the form of CO_2, which is preferably taken up, while at higher pH (7 and higher), bicarbonate is mostly available and taken up slower since it is energetically less favorable and needs to be catalyzed to CO_2 before fixation (Vuorinen et al. 1989). Brix (1990) also reported that CO_2 is the dominant form of carbon in the root systems rather than bicarbonate. In whichever form it is taken up or absorbed, CO_2 needs to be dissolved in water before reduction may occur. The uptake is most probably passive via the water uptake, but also active transport mechanisms have been reported (Stolwijk and Thimann, 1957; Pastenes et al. 2014, Zamanian et al. 2017). Passive transport is supported by studies which have reported that root uptake is predicted by transpiration rate and nutrient solution concentration (Amiro and Ewing, 1992; Zamanian et al. 2017). Additionally, diffusion plays an important role in passive uptake, particularly when concentration gradients exist between the soil solution and the plant root, facilitating the movement of carbon from soil into plant roots (Sánchez-Cañete et al. 2017).

DOC uptake is less well understood, with mixed evidence regarding its mechanisms. While passive uptake of small organic molecules is possible (Wu et al. 2010), active transport is more frequently suggested, as demonstrated in Hu et al. (2022), where organic compounds promoted root growth and potentially contributed to the carbon budget. However, studies often highlight the challenges of distinguishing true DOC uptake from adsorption onto root surfaces or microbial decomposition into DIC near the roots (Führ and Sauerbeck, 1967; Ogiyama et al. 2010). Führ and Sauerbeck (1967) suggested that only small molecules, such as fulvic acids, could penetrate root epidermal layers, while larger organic molecules remained adsorbed on root surfaces.

4.2 Carbon transport from roots to shoots and utilization

While CO_2 is primarily fixed into carbohydrates in the leaves through photosynthesis and then transported downwards, it is suggested that the small portion of carbon taken up by roots can support this process through the activity of phosphoenolpyruvate (PEP) carboxylase enzyme in non-photosynthetic tissues like roots (Jackson and Coleman, 1959; Hwang and Morris, 1992). Other fractions of carbon taken up by the roots are transported to the stems and leaves via the xylem tissues, which are important for efficient transport of water and nutrients and provide structural support in overall physiology and survival of plants (Livingston and Beall 1934; Amiro and Ewing 1992; Bloemen et al. 2013). Many studies reviewed here report an upward transport, with highly variable results. Some indicate that the majority of the carbon taken up by roots from the soil remains in the roots (e.g., Skok et al. 1962; Ford et al. 2007), while others report an equal distribution of ^{14}C between the roots and aboveground plant compartments (e.g., Stolwijk and Thimann, 1957; Schäfer, 1988; re-assimilation of $^{14}CO_2$ being excluded in most cases). After transportation of carbon to upper parts of plants, a proportion of the carbon is transpired as CO_2, while the rest is incorporated into sugars and other organic compounds through photosynthesis in the leaves to support plant growth and biomass (Hoch 2014).

4.3 Comparative studies of DIC and DOC uptake

It is commonly believed that the means of carbon transfer from soil to plants is largely by the uptake of DIC as well as to a smaller extent by DOC from the soil solution, groundwater stream, and irrigation water through root absorption and/or diffusive processes (Sheppard et al. 1991; Pérez-Sánchez et al. 2009; Hoch, 2014; Doulgeris et al. 2015). However, as shown here, the potential for uptake of DOC species is relatively high for plants, though results are variable. Five studies cited here report different rates of organic carbon uptake via roots, ranging from higher to minimal impact. Kuzyakov and Jones (2006) investigated the transfer of glucose via roots and concluded that the capture of carbon from decomposing organic matter in soil has an insignificant impact on the plant's carbon budget unless the plant is non-photosynthetic. Führ and Sauerbeck (1967) suggested that up to 5 % of organic carbon sources were found in the root relative to the whole plant, using ^{14}C-labelled humus substances. However, it was difficult to distinguish the proportion of ^{14}C, which was really taken up into living root tissue, from the proportion which was simply held by the roots via adsorption and precipitation reactions, as discussed above. In another study by Sheppard et al. (1991), where both DOC and DIC uptake was observed, 0.6 % of the carbon in plants was derived from labelled bicarbonate and far less from a ^{14}C-labelled synthetic organic compounds. The study also discusses the differences in behavior and mobility between inorganic and organic carbon, implying that inorganic carbon is more accessible for plant uptake. In another study by Ogiyama et al. (2010) the amount of carbon from soil in plants was reported, but it was suggested that the ^{14}C-labelled acetic acid breaks down in the culture solution by soil microorganisms, attached to the roots and that ^{14}C is finally taken up in inorganic carbon form. Field-based studies using natural tracers (^{14}C, ^{13}C) where the isotopes are homogeneously distributed in the soil in both DIC and DOC species, reported relatively high uptake of ^{14}C in the roots relative to the whole plant; 2.4 %- 6.83 % in trees (Maljesi et al. z<A 2019; Jyllilä, 2022) and 5.4 % in forbs (Jyllilä, 2022). However, no evidence of direct uptake of DOC was reported in these studies. While Hu et al. (2022) suggested that organic compounds can stimulate root growth by 23 %, Wu et al. (2010) found minimal uptake of pharmaceuticals. On the other hand, also significant growth stimulation was reported for DIC: the study by Vapaavuori and Pelkonen (1985) showed a 31 % increase in biomass growth with higher CO_2 concentration in soil, although it is unclear whether this carbon originated from DIC or whether changes in soil conditions caused increased the growth. Thus, this study is not included in our calculations.

In this context, also the role of mycorrhiza needs to be briefly discussed. Mycorrhizal fungi, which colonize most plant roots, are crucial for nutrient uptake and stress protection (Smith and Read, 2008). These fungi obtain carbon from plants and transfer nutrients to them, benefiting both partners and contributing to soil structure (Miller and Jastrow, 2000). While most research has focused on carbon transfer from plants to fungi, some studies suggest fungi may also contribute to soil organic carbon uptake by plant roots. For example, Bago et al. (2000) found that carbon transfer from fungi to roots could be reversible. Mycorrhizal fungi are also associated with organic nitrogen uptake, which contain carbon compounds as mentioned above (Smith and Read, 2008; Näsholm et al. 2009). A study by Majlesi et al. (2019) showed that trees with higher mycorrhizal colonization (93 %) absorbed more carbon than a grass with lower colonization (43 %). While these results suggest a link between mycorrhizae and carbon uptake, further research with diverse species is needed to confirm the role of mycorrhizae in carbon uptake from soil. Overall, our data suggests that DOC, especially small compounds, is taken up by plants similarly to DIC. Though there are exceptions, the uptake rate is not higher than 2.50 % for both.

5 Final remarks and future recommendations

In this work, the literature data relevant to the root uptake of carbon from soil (DOC/DIC) relative to the whole plant were compiled and analyzed by categorizing the methodology (e.g., field vs. laboratory studies), plant functional types and carbon forms (DIC vs. DOC). Overall, the findings suggested a central value of 2.26 % of carbon from soil (combined DOC and DIC) in plant roots with a median value of 1.5 %. However, a few studies showed 5-10 % root uptake under field conditions, which highlights the need for more research in different ecosystems to draw a more solid conclusion on these values. Moreover, various methods, plant functional types and carbon forms demonstrated similar results as no statistically significant difference was observed across the categories, suggesting that these factors do not substantially affect the uptake rate, and that more research is needed as the overall number of studies reporting the proportion of root carbon uptake from soil in plants was relatively low.

Caution should be taken on interpretation of data related to DOC uptake by plants as only in five studies direct uptake of DOC was examined, with mixed results. Henceforth, more experimental studies on root uptake of DOC excluding microbial degradation of organic carbon are recommended. Moreover, a systematic review on root uptake of carbon from soil among different plant functional types is important for understanding the underlying mechanisms of root uptake. Research on the transfer of carbon from roots to shoots, as well as studies on mycorrhizal colonization, is also crucial, as these mechanisms are poorly understood, and also this review could only speculate about the mechanisms since evidence is still lacking. Ultimately, understanding the contributions of DIC and DOC to plant carbon budgets is vital for advancing our knowledge of plant-soil carbon interactions and ecosystem carbon cycling. Future research should focus on elucidating the processes governing DOC absorption, particularly for small organic molecules, to enhance our understanding of how these carbon forms are integrated into plant carbon dynamics.

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