Rhizodeposition of organic C by plants: mechanisms and controls

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Review article

Rhizodeposition of organic C by plants: mechanisms and controls

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Abstract – During their life, plant roots release organic compounds into their surrounding environment. This process, named rhizodeposition, is of ecological importance because 1/ it is a loss of reduced C for the plant, 2/ it is an input flux for the organic C pool of the soil, and 3/ it fuels the soil microflora, which is involved in the great majority of the biological activity of soils, such as the nutrient and pollutant cycling or the dynamics of soil-borne pathogens, for example. The present review first examines the mechanisms by which major rhizodeposits are released into the soil: the production of root cap cells, the secretion of mucilage, and the passive and controlled diffusion of root exudates. In a second part, results from tracer studies (43 articles) are analyzed and values of C flux from the plant root into the soil are summarized. On average, 17% of the net C fixed by photosynthesis is lost by roots and recovered as rhizosphere respiration (12%) and soil residues (5%), which corresponds to 50% of the C exported by shoots to belowground. Finally, the paper reviews major factors that modify the partitioning of photoassimilates to the soil: microorganisms, nitrogen, soil texture and atmospheric CO_2 concentration.

carbon / rhizodeposition / rhizosphere / tracer studies

Résumé – **La rhizodéposition de C organique par les plantes : mécanismes et contrôles.** Au cours de leur vie, les racines des plantes libèrent des composés organiques dans leur environnement proche. Ce processus, nommé rhizodéposition, est d'importance écologique car 1/ c'est une perte de C réduit pour la plante, 2/ c'est une flux d'intrant pour le compartiment de C organique du sol et 3/ il alimente la microflore du sol, qui est impliquée dans la grande majorité de l'activité biologique des sols tels que par exemple le cycle des éléments nutritionnels et des polluants ou encore la dynamique des pathogènes du sol. La présente revue examine en premier lieu les mécanismes par lesquels les rhizodépôts majeurs sont libérés dans le sol : la production de cellules de la coiffe racinaire, la sécrétion de mucilage, la diffusion passive et contrôlée d'exudats racinaires. En second lieu, les résultats d'études de traçage du C (43 articles) sont analysés et les valeurs de flux de C allant de la racine de la plante vers le sol sont synthétisées. En moyenne, 17 % du C net fixé par la photosynthèse est perdu par les racines et il est restitué dans la respiration de la rhizosphère (12 %) et dans les résidus de sol (5 %), ce qui correspond à 50 % du C exporté par les parties aériennes vers le sol. Enfin, l'article répertorie les facteurs principaux qui modifient la répartition des photoassimilats vers le sol : les microorganismes, l'azote, la texture du sol et la concentration en CO_2 de l'atmosphère du sol.

carbone / rhizodéposition / rhizosphère / traçage

1. INTRODUCTION

During their life, plant roots release organic compounds into their surrounding environment. This phenomenon has been studied for more than one century. Indeed, the very complete book of Krasil'nikov [85] reports that root excretion was first evidenced in 1894 by Dyer, who observed the excretion of acidic compounds from the roots of plants. Then, numerous authors identified sugars, organic and amino acids and other compounds in the nutrient solution in which different plants were grown. Krasil'nikov [85] reported that as early as 1927, Minima observed that root excretions of organic compounds by lupine, bean, corn, barley, oat and buckwheat cultivated in Knop's nutrient solution were maximum during the fourth week of growth. Afterwards, these excretions decreased and stopped altogether with plant growth. At the beginning of the 20th century, it was already estimated that root-released compounds yielded 0.6 to 27% of the plant dry weight and studies also demonstrated that greater amounts of substances could be obtained if the nutrient solution was replaced (in [85]).

The release of organic compounds by living plant roots, referred to as rhizodeposition [156] is a process of major importance that is still the subject of investigations for several

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reasons. Firstly, rhizodeposition is an input of organic C into the soil. The soil is the second largest C compartment (1.5×10^{12} t C) after oceans (3.8×10^{13} t C) and before the atmosphere (7.5×10^{11} t C) and plant biomass (5.6×10^{11} t C) (estimates from [152]). Each year, it is estimated that 7.5×10^{10} t of C return to the atmosphere due to soil respiration. Considering that, on average, shoots export to belowground about half of the C fixed by photosynthesis [88], it is of major importance to determine how much of this flux enters the soil organic C pool. This is particularly relevant if the soil is expected to sequestrate C in response to elevation of atmospheric CO_2.

Secondly, rhizodeposition represents a loss of energy for the plant. At first sight, the release of organic C from roots into the soil might figure as a lost pool of reduced C that does not contribute to dry matter production. However, it is well established that rhizodeposits stimulate the biological activity in the rhizosphere, which has important positive feedback for the plant such as enhancing nutrient availability, for instance [77]. However, we still have no idea of the efficiency of rhizodeposition. In other words, would a plant gain extra advantages in terms of mineral nutrition, for example, if it deposited more C into the soil? The response to this question is fundamental with respect to outlooks aimed at engineering the rhizosphere.

In the past decades, many studies have focused on rhizodeposition. Authors have concentrated on determination of C flows from plant roots to soil and on factors that affected them. Results have been reviewed at regular intervals [45, 52, 86, 148, 189]. Briefly, these articles outlined that: 1/ plant roots are able to release a wide range of organic compounds, 2/ there is a great degree of uncertainty about the amounts and the quality of organic C deposited in soil conditions; this comes from the major difficulty of estimating root-derived C in the presence of microorganisms that rapidly assimilate rhizodeposits, and 3/ in soil conditions, many factors are assumed to alter both the amount and the nature of the C compounds released from roots but little is known about how these factors operate.

Our knowledge of rhizodeposition is too incomplete. As a result, the effective outputs of research on rhizodeposition are lacking despite virtual outputs are potentially numerous, such as manipulating C flow to the rhizosphere to alter the microbial dynamics and the related processes (nutrient cycling, organic matter dynamics, pollutant bioavailability, soil-borne pathogen and inoculant dynamics, etc.).

Consequently, two areas of investigations could be suggested. On one hand, new methodologies have to be developed to obtain more reliable estimates of rhizodeposition under various environmental conditions. On the other hand, if a major goal is to manipulate rhizosphere processes through plant ecophysiology and through the quantity and the quality of rhizodeposits, it is necessary to obtain more information about the different mechanisms by which C is lost by roots as well as their regulations by plant genetics and by the environment. The present article concentrates on that latter point. It first reviews literature related to the mechanisms by which major rhizodeposits (in terms of quantity) are deposited into the soil: sloughing-off of root cap cells, secretion of mucilage, passive diffusion of root solutes (exudation) and senescence of epidermal and cortical cells. The article then examines tracer studies (^{14}C) to summarize the main factors that are assumed to affect rhizodeposition. It is attempted to relate their effects to the aforementioned mechanisms of C release from roots. Finally, some outlooks are proposed for future investigations on rhizodeposition.

2. MECHANISMS OF RELEASE OF ORGANIC C FROM LIVING ROOTS

2.1. Sloughing-off of root border cells

Apical meristems of plant roots are covered by a group of cells arranged in layers, the root cap, the surface of which sloughs off as the root tip wends its way through the soil [8]. In mature branched roots, the entire cap itself can be lost as the results of pathogen attacks or as part of a normal developmental process, as it was observed in field-grown maize [173]. The cap initials generate cells that are displaced from the inner zone towards the periphery of the cap where they slough off. During their transit through the cap, the cells first differentiate into statocytes, i.e. gravity-perceiving cells, and then into cells able to secrete mucilage [158]. The separation of cells from the periphery of the cap can easily be observed under a microscope for numerous plant species. In field-grown maize, the detached cells were found alive at some distance from the root tip [174], which indicates that border cells are still viable several days after their separation from the root. Among plants belonging to ten families, the viability of border cells after they separate from the root was demonstrated to be 90% or higher in most cases, except in the *Compositae* sunflower and *Zinnia,* for which most of the border cells were dead when they detached from the cap [53]. Furthermore, in pea, detached cap cells exhibit different gene expression from that of attached cap cells [17]. It is suggested that they play a significant role in engineering the rhizosphere ecology [54] and therefore, the term border cells was proposed instead of the original denomination "slough-off cap cells" [53]. The suggested functions of root border cells are numerous: decrease in frictional resistance experienced by root tips [9], regulation of microbial populations in the rhizosphere by attracting pathogens and preventing them from damaging the root meristem and by promoting growth gene expression in symbiotic microorganisms [53, 54, 55, 198] and protection against heavy metal toxicity such as aluminium [119].

In maize seedlings, the number of cells in the cap ranges from 3 900 to 20 900 [23]. It decreases with root age due to the reduction in the width of root apices [24]. In laboratory experiments, the cap removed artificially is regenerated in 1 to 9 days [8, 23, 158]. The maximum number of cells released daily from the cap is very variable, ranging from a dozen in tobacco to more than 10 000 for cotton and pine, but it is conserved at the species level [55]. In maize, the daily production of cap cells increases from 356 cells·day^{-1} at 15 °C to a maximum of 3608 cells·day^{-1} at 25 °C and declines to 851 cells·day^{-1} at 35 °C [24]. The production of border cells by roots growing in soil is poorly understood. In laboratory experiments, it has been demonstrated that environmental

Table I. Production of root cap cells and mucilage by roots of different plant species.

References	Plant	Nature of C	Amount	Units	Comment
[66]	*Zea mays*	Root cap cells	1900	cells/day	Seedling grown in sand: resistance to penetration = 0.3 MPa. For calculations, the root cap cell is considered as a cylinder with a length of 80 µm and a diameter of 21 µm, a density of 1 g/cm^3 and a dry matter/fresh matter ratio of 0.072 [66].
			1.52	µg C/day/root	
		Root cap cells	3200	cells/day	Same conditions as above except the resistance to penetration = 5.2MPa
			2.56	µg C/day/root	
[126]	*Zea mays*	Root cap cells	7	µg DM/mg DM of root growth	
			2.8	µg C/mg DM of root growth	Calculated assuming a C content of root cap cells of 40%
	Convulvus arvensis	Root cap cells	4	µg DM/mg DM root growth	
[55]	*Pinus gossypium*	Root cap cells	10000	cells/day	
[105]	*Vicia faba*	Root cap cells	420–636	cells/day	
[20]	*Zea mays*	Mucilage	34	µg DM/mg DM root growth	
[172]	*Zea mays*	Mucilage	11–17	µg DM/mg DM root growth	Growth in axenic nutrient solution for 28 days
	Triticum aestivum	Mucilage	29–47	µg DM/mg DM root growth	Growth in axenic nutrient solution for 25 days
[15]	*Triticum aestivum*	Root cap cells+Mucilage	3.2–6.4	µg DM/mg DM root growth	
[150]	*Triticum aestivum*	Root cap cells+Mucilage	700	m3/ha	Calculated from the size of the droplet at the root tip
	Zea mays	Root cap cells+Mucilage	1250	m3/ha	Calculated from the size of the droplet at the root tip
[47]	*Arachis hypogea*	Root cap cells+Mucilage	0.13–0.27	mg MS/plant/day	Growth in axenic nutrient solution for 2 weeks
		Root cap cells+Mucilage	0.15	% of root C	

conditions experienced by root tips strongly influence border cell production. For example, an atmosphere with high CO_2 and low O_2 partial pressure inhibits border cell separation in pea during germination whereas later in development, it increases the total number of border cells that accumulate over time [197]. The mechanical impedance experienced by maize roots creates friction that is decreased by the sloughing off of the root cap cell [9]. Consequently, in maize seedlings grown in compacted sand the number of shed cap cells increases exponentially with the penetration resistance from 1 900 cells·day^{-1} (56 cells·mm^{-1} root elongation) for loose sand (resistance to penetration: 0.29 MPa) to 3 200 cells·day^{-1} (750 cells·mm^{-1} root elongation) for compacted sand (resistance to penetration: 5.2 MPa) [66] (Tab. I). The authors estimated that this corresponded to 1.5 and 2.6 µg C per day, respectively.

There is evidence that the number of border cells is also controlled at the genetic level. In pea, the separation of cells from the cap has been shown to be closely correlated to the expression of an inducible gene coding for a pectinmethylesterase, which is thought to solubilize cell wall polymer [183]. Furthermore, there is evidence that cap cells synthesized a factor that accumulates extracellularly and inhibits the production of new cells by the cap meristem without inhibiting cell mitosis in the root apical meristem [54]. Hence, the cap turnover is stopped unless the factor is diluted or unless cells from the periphery are shed. Therefore, in soil, it can be assumed that the production of cap cells is favored on one hand by rain, irrigation and the soil microporosity, which all facilitate the diffusion of the inhibitor away from the cap and on the other hand, by frictional forces that shed the cells from the root tip.

2.2. Secretion of mucilage by roots

A mucilaginous layer has been frequently observed on the root surface of many plants [130] and more particularly at the root tip, where it can form a droplet in the presence of water [150]. There is no clear evidence that the epidermis and the root hairs secrete mucilage [138]. In Sorghum, Werker and Kislev [185] reported small drops of mucilage secreted by root hairs in addition to a fibrillar mucilaginous layer secreted by the epidermal cells. However, the mucilaginous layer observed on these parts of roots may derive from the mucilage secreted by the root cap [174], from the degradation of epidermal cell walls [37] or may be synthesized by rhizosphere microorganisms [149]. However, for most of the plants examined, the mucilage is secreted by the outer layers of the cap cells [136, 146] and it can be seen at the root tip of several plants [117].

The mucilage is composed of polymerized sugars and of up to 6% proteins [2, 146]. The major sugars identified are arabinose, galactose, fucose, glucose and xylose [2, 83]. In maize, the root cap polysaccharide has a molecular weight greater than 2×10^6 daltons, a density of 1.63 $g \cdot cm^{-3}$ [137], a C content of 39% and a C/N ratio of 64 [98].

The initiation of mucilage synthesis takes place in the endoplasmic reticulum and completes in the Golgi saccules. The slime is transported to the plasmalemma by the Golgi vesicles. The mucilage is discharged between the plasmalemma and the cell wall by exocytosis [122, 146]. All these processes are energy-dependent. The passage through the cell wall is not systematic and the mucilage can accumulate at the inner wall surface. It is assumed that if both the degree of hydration of the mucilage and the cell turgor are sufficient, the slime moves passively through the cell wall and forms a droplet at the root tip [122]. The passage trough the cell wall is probably due to an increase in the permeability of the middle lamella [92]. Under controlled conditions, the formation of the droplet follows a 3–4 hour cycle [122]. However, in these laboratory experiments, the saturated moisture and the periodic complete removal of the mucilage might have increased the droplet formation. In soil, it can be assumed that conditions might not be as much favorable to the production of such a significant amount of polysaccharide.

The properties of the mucilage secreted by the root cap have been extensively studied. The COO^- groups of the mucilage can bind to cations and in particular, those fixed to clay [50, 67]. Consequently, soil structure is affected and the stability of aggregates is generally increased [29, 170]. Heavy metals also bind to root cap slime [120] and this may play a significant role in the protection of the root tip against their toxicity [119].

The root cap mucilage is able to hydrate extensively. Fully-hydrated mucilage has a water content of 100 000% of dry weight but such a hydration is only obtained in the presence of free water [101]. Indeed, in mucilage collected on nodal roots of maize, the water content (% of dry weight) increases only up to 450% when the water potential of the mucilage increases from –11 MPa to –0.01 MPa [101]. Thus, unless the soil is saturated with water, the root cap mucilage appears as a dry coating over the apex and does not form a droplet as is often observed in vitro [103, 155]. Furthermore, the surfactant and viscoelastic properties of the mucilage [143] might favor the adhesion of root cap cells to the soil particles, and hence their separation from the cap as the root tip moves through the soil. This process is consistent with the rhizosheath observed on roots of grasses [174, 182]. The sheath consists of soil + mucilage and living border cells tightly adhering to the root. The mucilage originates both in the root cap and in microbial syntheses [181]. The sheath is not observed just behind the root tip because the epidermis of this area has a thick complex surface to which mucilage does not adhere [1, 100]. The rhizosheath may function like a biofilm involved in plant nutrition and may have an important role in resistance to drought [181].

The formation of the rhizosheath from root cap mucilage suggests that its mineralization by microorganisms is reduced or very slow. In vitro, root mucilage can readily be utilized by rhizosphere bacteria as a sole source of carbon [83]. Furthermore, in a laboratory experiment, Mary et al. [98] demonstrated that maize mucilage incubated in soil was mineralized at 45% of the added C within 2 weeks. However, in the rhizosphere, mucilage mineralization may be delayed by the preferential use by microorganisms of root exudates, which are more readily available and by the protection of mucilage due to its adsorption on the soil matrix [161].

The amounts of mucilage synthesized in vitro range from 11 to 47 μg MS/mg MS root growth (Tab. I). However, these quantities were determined from roots grown in water or in nutrient solution, which increases the outward diffusion of the mucilage from the periplasmic region and probably stimulates the biosynthesis of the slime [155]. Consistent with this, the estimation of the quantity of mucilage produced in soil based on the size of the droplet surrounding the root cap in vitro might be overestimated: 700 and 1250 m^3/ha for wheat and maize, respectively [150] (Tab. I). At the present time, the amount of mucilage produced in soil remains unknown.

2.3. Root exudation

Excretion of organic compounds from roots was first reported as early as the end of the 19th century. In 1894, Dyer demonstrated the release of acidic substances from roots of barley, wheat and others [85]. The biochemical nature of compounds excreted by roots demonstrates a wide variety: simple and complex sugars, amino acids, organic acids, phenolics, alcohols, polypeptides and proteins, hormones and enzymes [28, 45, 125]. In the literature, the meaning of the term "exudation" may differ significantly. Sensu stricto, exudates were first defined as low molecular weight compounds diffusing passively from intact cells to the soil solution [149]. However, "root exudates" is often used to describe more generally the low molecular compounds released from roots regardless of the process by which they are deposited into the rhizosphere. The main low molecular weight compounds released passively from roots are sugars, amino acids and organic acids. They diffuse passively from the cytoplasm that is commonly three orders of magnitude more concentrated than the soil solution (mM vs. μM, respectively) [125]. For example, in maize roots, average concentrations are 86 mM for sugars [78], 9.5 mM for amino acids [76] and 10–20 mM for organic acids [73]. The lipid bilayer of the plasmalemma is a barrier to free diffusion of solutes because its permeability is reduced,

Table II. Quantities of C in root exudates of different plant species.

References	Plant	Amount	Units	Compounds	Comments
[5]	*Hordeum vulgare*	76–157	µg/plant/day	Exudates	Depending on mechanical constraint, 21 days of growth
		0.2–0.4	% root DM/day	Exudates	Calculated from original data
		5–9	% root DM		
[51]	*Brassica napus*	16–21	µgC/plant/day	Total C	Sterile and non sterile roots, calculated from original data
[52]	*Acer saccharum*	2.7–6.7	% root DM/day	Exudates	Defoliated-control, calculated from Smith (1971)
	Agropyron smithii	0.01	% root DM/day	Reducing sugars	Defoliated/control, effect of temperature, calculated from Bokhari and Singh (1974)
[84]	*Zea mays*	0.03–0.06	% root DM/day	Sugars	Sterile and non sterile roots, 23 days of growth
		0.03–0.04	% root DM/day	Organic acids	Idem
		0.001	% root DM/day	Amino acids	Idem
		0.02–0.03	% root DM/day	Sugars	Three levels of K tested, nitrate+ammonium, 23 days of growth
		0.01–0.07	% root DM/day	Organic acids	Idem
		0.0005–0.0007	% root DM/day	Amino acids	Idem
		0.001–0.002	% root DM/day	Sugars	Three levels of K tested, nitrate, 25 days of growth
		0.016–0.019	% root DM/day	Organic acids	Idem
		0.0004–0.001	% root DM/day	Amino acids	Idem
[140]	*Triticum aestivum*	121–153	µg C/cm root growth	Exudates	Sterile, nutrient solution: 2 or 4 day replacement
		196–226	µg C/mg DM root growth	Exudates	Sterile non sterile nutrient solution: 2-day replacement
		576–1174	µg C/mg C root growth	Exudates	Nutrient solution: 2 day replacement, sterile-inoculated with *Pseudomonas putida*
				Exudates	
[75]	*Zea mays*	0.1–1.2	% root DM/day	Exudates	Calculated from original data, sterile, no or daily changes of nutrient solution, 10-day culture
		1.22	µg C/root tip/h	Exudates	Standard values for model simulation
		0.24	µg C/cm of root /h	Exudates	Idem

especially for charged compounds compared with neutral molecules. However, the protons excreted by the H^+-ATPase provide an electrochemical gradient for the diffusion of anions [73]. Transient defects in the plasmalemma can also significantly increase its permeability, as suggested for amino acids [21].

Membranes of plant cells bear sugar and amino acids proton-coupled ATPase transporters that mediate assimilate imports into cells [19]. Hence, it is not surprising that in vitro, plant roots are able to actively take up sugars and amino acids from a solution [76, 78, 154, 160, 194]. The consequence of this influx on net exudation may be important in axenic nutrient solution but in soil, the evidence is less obvious. Indeed, microorganisms are also very efficient competitors for the uptake of sugars and amino acids [25, 74, 128, 175]. The injection of labeled compounds into the rhizosphere indicated that plant capture was of minor importance compared with microbial uptake of glucose and of charged or uncharged amino acids [129, 131, 153]. Therefore, it is not known if the plant can tune the net exudation in non-sterile soil by altering the influx of sugars and amino acids.

In maize, the spatial examination of exudation indicates a greater efflux of solutes close to the root apex [102, 104]. This does not seem to relate to variability in the plasmalemma permeability nor to the spatial repartition of transporters, which is uniform along maize roots [76, 78]. The greater exudation behind the root apices is consistent with the concentration gradients of sugars and amino acids inside the root [73] and with the diffusion through the apoplast of sugars from the phloem to the apical meristems [74], diffusion that is supported by experimental and theoretical evidence [16].

The amount of C exuded has been expressed in a wide range of units. Table II gives some estimates reviewed from the literature for plants cultivated in nutrient solution. Due to the re-sorption of exudates by plant roots, these values have to be considered with caution if extrapolations to soil conditions

are the aim. It can also be seen that the proportion between sugar, amino acids and organic acids varies greatly, especially between sugars and organic acids. The relative proportions of sugars and amino acids exuded reflect quite correctly the relative concentrations in root tissues for these solutes.

Besides the passive diffusion of solutes, plants are able to respond to environmental conditions by altering their excretion of organic compounds. For example, in response to environmental nutrient stress such as P or Fe deficiencies, anion channel proteins, embedded in the plasmalemma, significantly increase the passive efflux of carboxylates (malate, citrate and oxalate) whose complexing properties facilitate nutrient mobilization by the plant [73, 124, 125]. The chelating properties of organic acids are also a central mechanism involved in rhizosphere detoxification, as demonstrated in aluminium-tolerant plants [7, 41, 93]. Apart from organic acids, many other compounds are released by plant roots in response to the environment. The most studied are phosphatases excreted by roots in P-stressed plants [40, 118], phytosiderophores released in Gramineous plants and which are involved in micronutrient acquisition [27, 176] and some phenolics such as flavonoids, which play an important role in symbiosis establishment [186]. A comprehensive review covering these compounds is available in [125]. There is a lot of evidence that both the amount and the nature of root exudates are very variable according to the physiological status of the plant and to the plant species [35, 45, 125]. Therefore, it can be assumed that the controlled release of particular exudates in response to sensed environmental stimuli is probably a major mechanism that allows the plant to face unfavorable rhizosphere conditions such as nutrient deficiencies, toxicities or proliferation of pathogenic microorganisms.

2.4. Senescence of root epidermis

Behind the root tip, epidermal cells differentiate either into hair cells (trichoblast) or non-hair cells (atrichoblast). Root hairs are involved in anchorage, in water and nutrient uptake and in symbiosis [62, 138]. In recent years, extensive research has detailed the genetic control of root hair development, especially in *Arabidopsis* (reviewed in [42, 151]). From a study carried out by Dittmer [32] on 37 species belonging to 20 angiosperm families, the size of root hairs is quite constant within a given species but is very variable between species. Root hairs are typically 80–1500 µm long and have a diameter of 5–20 µm. The root hair zone is on average 1 to 4 cm long [62]. The literature gives evidence that root hair density is also very variable between plants: 1 to 180 hairs·mm^{-1} of root, 70 to 10 800 hairs·cm^{-2} of root (Tab. III). Furthermore, environment strongly influences root hair development. For example, low levels of minerals, especially P and nitrate [79, 94], mechanical constraint, low O_2 partial pressure or high temperatures stimulate root hair formation. Similar effects can be observed when roots are exposed to ethylene, which suggests that ethylene could be involved in the regulation of root hair development by environmental factors [115].

There is little information about the lifespan of root hairs. Based on the loss of the nucleus, it was estimated that the longevity of root hairs was 2–3 weeks in wheat, barley and maize [38, 64]. However, microscopic examinations indicate some cytoplasm lyses in 4-day-old hairs in maize [38]. Thus, despite the fact that the cell wall can persist for several weeks or months [62], the lifespan of root hairs is probably shorter, i.e. 2–3 days. If root hairs are considered as cylinders that have a dry weight:fresh weight (DW:FW) ratio of 0.072, a density equal to 1 g·cm^{-3} and a C content of 40% DW, the calculation of the hair density of a 50 hairs·mm^{-1} root indicates that small hairs (80 µm in length, 5 µm in diameter) correspond to 2.2 ng C·mm^{-1}root whereas large hairs (1500 µm in length, 20 µm in diameter) are equivalent to 680 ng C·mm^{-1}root. Medium-size hairs (500 µm in length, 10 µm in diameter) correspond to 56 ng C·mm^{-1}root. Theoretically, these amounts of C should be deposited into the soil after the hair death. However, to our knowledge, it is unknown if the cytoplasm material is released into the soil or recycled within the root tissue.

Although it is not a general rule, there are numerous reports that cells from the root epidermis senesce [28]. For instance, in maize, the senescence is extensive proximal to the region where the late metaxylem matures [184]. The senescence can even concern cortical cells. Nuclear staining with acridine orange showed that senescence of cortical cells concerns the old parts of the roots but some work has also indicated the absence of a nucleus in the cortex of young roots in cereals [38, 59, 64]. However, the impermeability of the cell wall to the stain may cause an artefact that biases the evaluation of the cell vitality [184]. Thus, it would be necessary to gain more information about (1) the lifespan of the root epidermis (including root hairs) and of the root cortex in soil conditions, and (2) the fate of the intracellular content of the senescing root cells.

2.5. Relative proportion of rhizodeposits

Due to the very different units used to express the quantities of C from rhizodeposits, comparisons are difficult. However, from Table I, it is reasonable to estimate that border cells represent 1–3 µg C·mg^{-1} DM of root growth, or 1.5–2.5 µg C·day^{-1}·root^{-1}. On average, mucilage ranges from 2–20 µg C·mg^{-1} dry matter (DM) of root growth, assuming a C content of 39% DM. In comparison, Table II indicates mean exudation values of 150 µg C·mg^{-1} DM of root growth, 0.2–7% root DM/day. These calculations suggest that exudation releases almost 10–100 times more carbon than border cells and mucilage. As calculated previously, the death of root hairs with a medium size and density would deposit 56 ng C·mm^{-1} root. If root hair decay concerns 1 cm of root per day, which is reasonable, the amounts deposited are 3 orders of magnitude less than exudation.

3. FACTORS AFFECTING C FLUXES TO THE RHIZOSPHERE

Factors affecting the release of C from roots into the soil are numerous and have been extensively reviewed, e.g. [28, 45, 52, 148, 189]. The literature shows that the total amounts of organic C deposited in the rhizosphere can vary greatly according to the plant ecophysiology. This can be explained as follows. Both the environment and the plant genetics and

Table III. Root hair density in different plant species.

References	Plant	Root radius (cm)	Root hairs (mm^{-1} root)	Root hairs (cm^{-2} root)	Root hair length (mm)
[39]	*Triticum aestivum*	8.50×10^{-3}	38	7115	1.27
	„	8.00×10^{-3}	25	4974	0.74
	„	7.50×10^{-3}	24	5093	0.49
	Hordeum vulgare	8.50×10^{-3}	30	5617	1.1
	„	7.50×10^{-3}	27	5730	0.52
	„	7.50×10^{-3}	31	6578	1
	„	8.00×10^{-3}	30	5968	0.64
Föse (1991) [79]	*Spinacia oleracea*	1.07×10^{-2}	71	10561	0.62
	Brassica napus	7.30×10^{-3}	44	9593	0.31
	Lycopersicon esculentum	1.00×10^{-2}	58	9231	0.17
	Triticum aestivum	7.70×10^{-3}	46	9508	0.33
	Allium cepa	2.29×10^{-2}	1	69	0.05
	Lolium perenne	6.60×10^{-3}	45	10851	0.34
	Phaseolus vulgaris	1.45×10^{-2}	49	5378	0.2
[99]	*Arabidospis thaliana*		53–63		
[14]	*Elymus pycnathus* (L.)				
	Main root		44		0.37
	1st order branching		7		0.32
	2nd order branching		3.5		0.32
	Puccinellia maritima (L.)				
	Main root		20		0.51
	1st order branching		11		0.47
	2nd order branching		5		0.5
	Spartina anglica (L.)				
	Main root		21		0.17
	1st order branching		10		0.24
	2nd order branching		5		0.25
[193]	*Agropyron cristanum*				
	Main root		71		0.19
	Branchings		181.6		0.153

physiology can influence (1) the flux of C from each root to the rhizosphere, which is related to the root functioning, and (2) the size and the morphology of the overall root. Therefore, any attempt to model rhizodeposition will have to consider the plant ecophysiology. The aim of this part of the paper is to examine tracer studies to analyze the main factors that affect rhizodeposition. To reach that goal, we analyzed the partitioning of net fixed C between the plant-soil pools from ^{14}C tracer experiments. The main factors examined are plant age, microorganisms, soil texture, soil nitrogen and atmospheric CO_2 concentration. There are of course numerous other factors that alter rhizodeposition. They are not detailed in the present study because no sufficient data from ^{14}C-labeling experiments were available. Among them are light intensity [61], photoperiod [169], temperature [97], soil pH [108], anoxia [110] and defoliation [65, 135].

Tracer experiments were chosen because studies are numerous and because the expression of results in terms of partitioning coefficients of net fixed C is a common basis for the majority of articles. Indeed, in non-tracer experiments, the comparison between studies is difficult or impossible because the classification of rhizodeposits is not uniform between articles (soluble, insoluble, sugars, total C, etc.) and because results are expressed in a wide range of units [167]. Among tracer experiments, labeling of photoassimilates with ^{14}C is the most commonly-used technique to study C flow to the rhizosphere. Other isotopes have also been used for labeling experiments, such as ^{11}C and ^{13}C and C flows to the soil can

also be studied using the natural abundance of ^{13}C. All these techniques have been reviewed elsewhere, e.g. [86, 106, 121] and will not be detailed here.

The present study examines experiments in which plant shoots were exposed to ^{14}C except [132] in which ^{13}C was used as tracer. The exposition of shoots to the tracer was either as a pulse (a few minutes to several hours) or as a permanent exposition from germination until sampling. These two procedures are referred to as pulse or continuous labeling. Briefly, pulse labeling experiments are very useful for obtaining information on C fluxes in relation to the plant ecophysiology, but due to the brief exposition of the plant to the tracer, this technique fails to provide reliable C budgets, which can be assessed by continuous labeling. Moreover, from a technical point of view, continuous labelings differ from pulse-chase experiments in that they are cumbersome, expensive and hardly applicable in field situations [106]. However, Warembourg and Estelrich [178] compared 298-h and 78-day-long labelings in *Bromus erectus*. They concluded that reliable estimations of C fluxes to the rhizosphere can be obtained from an intermediate strategy consisting of repeated short-term labelings of a few days each.

The tracer experiments reviewed for the present study expressed results as ^{14}C-partitioning coefficients, i.e. percentages of the net fixed C allocated to C compartments. The compartments are shoot and root C, CO_2 from rhizosphere respiration (root respiration + the rhizomicrobial respiration, i.e. microbial respiration derived from rhizodeposition) and C in soil residues. The respective partitioning coefficients are SHOOT, ROOT, RR and RES. We also investigated partitioning of ^{14}C between belowground compartments as percentages of labeled C exported by shoots. These partitioning coefficients are ROOTBG, RRBG and RESBG. Articles for which ^{14}C partitioning was not complete were discarded. Data were analyzed with SAS V 8.02 for Windows (Microsoft), The SAS Institute Inc., Cary, NC, USA.

3.1. Data overlook

There were 43 articles examined. A given article presents as many sets of ^{14}C-partitioning coefficients as experiments/treatments. For example, an article that examines the effect of nitrogen fertilization (+N and -N) and of elevated CO_2 (elevated and ambient) will provide 4 sets of coefficients. Hence, the total number of coefficient sets analyzed was 237 (Tab. IV). There are more data for pulse labelings than for continuous labelings (137 sets of coefficients vs. 100, respectively) although the number of articles analyzed is comparable, around 20. Whatever the labeling procedure, the maximum contribution of an article to the total number of coefficient sets is 12–26% (data not shown).

The data show that tracer experiments focus on a restricted number of plants (Tab. IV). There are 1.5 times more data for annual plants than for perennials. Among annuals, *Triticum aestivum, Hordeum vulgare* and *Zea mays* represent 88% of the coefficient sets and among perennials *Lolium perenne* represents more than 35% of the coefficient sets. More than 65% of the coefficient sets concern *Lolium perenne* and *Bromus erectus*. Data on *Bromus erectus* were drawn from a single article. Examination of plant age indicates that the great majority of the data concerns the juvenile stage of development (Tab. V). In continuous labeling experiments, the mean is 37 days and the median 28 days. In pulse labeling studies, the mean is 146 days and the median is 87 days but the coefficient of variation for the mean is two times greater that that in continuous labelings. The difficulty of maintaining an atmosphere with a constant $^{14}CO_2$ activity and constant CO_2 concentration [180] can greatly contribute to explain the fact that continuous labeling focused on younger plants compared with pulse-chase studies. Indeed, in pulse labeling experiments, late development stages such as flowering and grain filling have been investigated [81, 107, 164].

Table VI outlines that the partitioning coefficients from continuous labeling studies are normally distributed except the RES and RESBG coefficients (^{14}C in soil residues), the distributions of which are skewed to low values (data not shown). This means that the majority of the data are low and few coefficients extend to greater values. The root sampling procedure may provide a possible explanation for the non-normality of these coefficients. Indeed, it is very difficult to separate, by hand picking/sieving, the fine roots from the soil and a variable proportion of them may be left in the soil, artificially increasing the values of the RES and RESB coefficients. Moreover, the washing of roots extracts some soluble ^{14}C, which can also overestimate labeled soil residues [163]. In pulse labeling experiments, none of the partitioning coefficients are normally distributed (Tab. VI). The distribution of PA coefficients has a low Kurtosis (data not shown). For the other coefficients, once again, data are skewed to the low values. The non-normality of the distribution of the partitioning coefficients in pulse-chase experiments can be explained by the non-standardization of the labeling procedures. Among the studies, both the exposition of shoots to $^{14}CO_2$ and the chase period are very variable in length (Tab. V). The length of time of the labeling ranges from 20 minutes to 720 hours (data not shown) with a median of 6 h and a mean of 108 h. The length of the chase period, that is, the time elapsed between the labeling and the sampling, is probably the key point that affects assimilate partitioning. In the articles reviewed, the chase period ranges from 30 minutes to 504 hours (data not shown) with a mean and a median equal to 145 h and 48 h, respectively (Tab. VI). This indicates that in general, the chase period is short, which could lead to an incomplete partitioning of ^{14}C and to an overestimation of the ^{14}C recovered in shoots and an underestimation of C flows to belowground. This is supported by the greater mean SHOOT coefficient in pulse labeling studies compared with continuous labeling studies (64 versus 57, Tab. VI). Conversely, a long chase period may increase the labeled carbon retrieved in the rhizosphere respiration and decrease the ^{14}C in the soil residues.

The mean partitioning coefficients for SHOOT, ROOT, RR and RES determined from pulse and continuous labeling experiments are 64, 20, 12 and 5% and 57, 22, 14 and 7%, respectively. This indicates that shoots export almost half of the net fixed C to belowground [88]. In average, among the net C allocated belowground, half is retained in root tissues, a third is lost as root+rhizomicrobial respiration and more than 15% is retrieved as soil residues. It is interesting to note that in pulse-chase experiments, SHOOT coefficients for annual

Table IV. Number of partitioning coefficient sets reviewed for different plant species. A partitioning coefficient set consists of the percentages of the tracer allocated to shoots, roots, rhizosphere respiration and soil residues.

Annual (A) /Perennial (P)	Plant	Labeling (*)	References	Partitioning coefficient sets			
				Number	Total/species	% of total relative to labelling	% of total
A	*Triticum aestivum*	C	[6], [11], [91], [96], [97], [112], [113], [164]	45		56.3	
A		P	[46], [81], [132], [133], [165], [166], [187}, [190]	30	75	49.2	53.2
A	*Hordeum vulgare*	C	[6], [70], [187], [190], [195]	13		16.3	
A		P	[46], [68], [166]	13	26	21.3	18.4
A	*Zea mays*	C	[56], [57], [91], [95], [114], [188]	15		18.8	
A		P	{65], [82], [168]	8	23	13.1	16.3
A	*Bromus madritensis*	P	[179]	8	8	13.1	5.7
A	*Brassica napus*	C	[195]	2		2.5	
A		P	[157]	1	3	1.6	2.1
A	*Lycopersicon esculente*	C	[191]	2	2	2.5	1.4
A	*Pisum sativum*	C	[191]	2	2	2.5	1.4
A	*Medicago truncatula*	C	[26]	1		1.3	
A		P	[26]	1	2	1.6	1.4
			Total continuous labeling experiments	80			
			Total pulse labeling experiments	61			
			Total	141			
P	*Lolium perenne*	P	[33], [107], [108], [109], [110], [134], [133], [142]	23		30.3	
P		C	[43], [61], [171], [195]	12	35	60.0	36.5
P	*Bromus erectus*	P	[179]	28	28	36.8	29.2
P	*Castanea sativa*	P	[147]	8	8	10.5	8.3
P	*Trifolium repens*	P	[169]	5	5	6.6	5.2
P	*Festuca arundinacea*	C	[43]	4	4	20.0	4.2
P	*Pinus taeda*	P	[144]	4	4	5.3	4.2
P	*Populus tremuloides*	P	[116]	4	4	5.3	4.2
P	*Festuca pratensis*	C	[69], [71]	3	3	15.0	3.1
P	*Cynodon dactylon*	P	[133]	2	2	2.6	2.1
P	*Lolium multiflorum*	P	[60]	2	2	2.6	2.1
P	*Bouteloua gracilis*	C	[34]	1	1	5.0	1.0
			Total pulse labeling experiments	76			
			Total continuous labeling experiments	20			
			Total	96			

* C = Continuous labeling, P = pulse labeling.

plants are greater than that of perennials, the contrary being observed for ROOT and RR coefficients. There are also differences between perennials and annuals for the belowground budget. Further investigations are needed to explore if these results are representative of a different strategy of assimilate partitioning to the soil between annual and perennial plants [179].

The SHOOT coefficient is significantly and negatively correlated to all of the belowground coefficients (ROOT, RR and RES) (Tab. VII). The correlations are stronger in pulse-chase experiments, which can be related to the greater temporal resolution of pulse labeling compared with continuous labeling. Whatever the kind of labeling, the ROOTBG coefficient is significantly and positively correlated to RRBG and to RESBG. This suggests a strong link between rhizodeposition and the metabolic activity of roots. This is consistent with the mechanisms involved in the release of C from roots. Indeed, a significant exportation of photoassimilates from the shoots to the

Table V. Age of plants and labeling characteristics in the tracer experiments reviewed.

		Continuous labeling experiments				Pulse labeling experiments			
	Annual (A) /Perennial (P)	N (*)	Mean	Median	CV of mean (**)	N (*)	Mean	Median	CV of mean (**)
Age (days)	A	80	31.7	24.0	51.2	60	97.5	82.5	68.2
	P	20	56.0	59.0	31.1	66	190.5	93.0	97.5
	Total	**100**	**36.6**	**28.0**	**52.1**	**126**	**146.2**	**86.5**	**101.9**
Chase (h)	A					60	230.6	92.0	96.5
	P					72	73.6	48.0	78.1
	Total					**132**	**145.0**	**48.0**	**120.0**
Length of labeling (h)	A					60	60.1	1.8	237.8
	P					72	148.2	76.0	105.8
	Total					**132**	**108.2**	**6.0**	**144.6**

*: Number of partitioning coefficient sets.
**: Coefficient of variation of the mean (%).

roots is expected to maintain the solute gradient between the root tissue and the soil solution, and so, to favor the passive diffusion of root exudates into the soil. Moreover, a rapid root growth should increase the number of border cells and mucilage deposited into the soil as the result of frictional forces experienced by the foraging root apices.

Data from continuous labeling experiments indicate that the RRBG and RESBG coefficients are significantly negatively correlated (r = –0.32). Hence, this might reflect the fact that according to the studies, a variable fraction of the rhizodeposits are mineralized by the microorganisms, which consequently symetrically alters the RESBG and RRBG coefficients. If this hypothesis is valid, this means that the rhizomicrobial respiration contributes significantly to the rhizosphere respiration. In pulse labeling experiments, no such correlation is observed, probably because of the variability of the length of the chase period.

3.2. Factors that affect the partitioning of ^{14}C-assimilates to the soil: a quantitative approach

3.2.1. Methods for calculations

The following methods were applied to appreciate the effect of a factor on the partitioning of ^{14}C between plant-soil C pools. Given a factor F tested at n levels, the relative variation (RV) in a partitioning coefficient 'PC' was calculated as $RV = (PC_n - PC_{n-1})/PC_{n-1}$. The level 'n' of the factor F was always high relative to the level n–1. For example, if an article reports on the effect of N fertilization tested at N1 < N2 levels, the relative variation in partitioning of ^{14}C to shoots was calculated as follows: $RV_{SHOOT} = (SHOOT_{N2} - SHOOT_{N1})/SHOOT_{N1}$. The same calculations were performed for the other partitioning coefficients. Hence, a positive RV indicates that the factor increases the partitioning of assimilates to the compartment considered. If a second factor was studied such as the concentration of atmospheric CO_2, applied at two levels, L1 < L2, the effect of nitrogen was calculated at the two levels of CO_2: $(SHOOT_{N2L1} - SHOOT_{N1L1})/SHOOT_{N1L1}$ and $(SHOOT_{N2L2} - SHOOT_{N1L2})/SHOOT_{N1L2}$. If a factor was tested at more than two levels L1 < L2 < L3….< Ln, the effects were calculated relative to two subsequent levels: Ln vs. Ln–1, Ln–1 vs. Ln–2……..L2 vs. L1.

For each factor investigated, the relative variation coefficients' RVs were classified according to the labeling procedure (continuous or pulse). Then, the maximum, the minimum, the median, the mean and its coefficient of variation were calculated. The normality of the RVs' distributions were tested by the Shapiro-Wilk test. If normality was accepted (at alpha = 5%), the Student t test was used to test the null hypothesis: mean = 0, otherwise the non-parametric sign test was applied to test the null hypothesis: median = 0.

3.2.2. Plant age

The data from pulse-chase experiments summarized in Table VIII clearly demonstrate that plant age significantly influences C partitioning of photoassimilates between plant-soil compartments. As the plant gets older, less carbon is partitioned to belowground. As the data are non-normally distributed, the medians were examined. They are –43% to roots, –28% to rhizosphere respiration and –20% to soil residues (Tab. VIII). The variability is very important, as illustrated by the coefficients of variation. This is not surprising because the effect of age is more marked for young plants than for older ones, which is not taken into account in the calculations. No clear significant effect of age on C partitioning between belowground compartments can be observed. The medians of ROOTBG, RRBG and RESBG suggest that C allocated to belowground is less retained in roots when plant age increases. The partitioning coefficients from continuous labeling experiments do not evidence this pattern due to their low temporal resolution and due to the fact that very young plants were

Table VI. ^{14}C budget for tracer studies of C translocation into the soil. Results are expressed as percentages of the net ^{14}C fixed.

	Labelling (*)	Annual (A) /Perennial (P)	N (**)	Mean	Max	Min	Median	CV of mean (***)	Pn (****)
S	C	A	80	56.6	78.9	34.8	55.2	16.8	
H	C	P	20	58.2	86.4	22.0	60.1	26.9	
O	C	All	100	57.0	86.4	22.0	55.6	19.2	0.302
O	P	P	76	56.5	99.1	18.8	56.8	33.9	
T	P	A	61	72.8	97.4	25.6	73.9	25.8	
	P	All	137	63.7	99.1	18.8	65.8	32.3	0.003
R	C	A	80	21.2	37.5	3.9	21.8	37.1	
O	C	P	20	27.1	40.4	9.1	28.9	33.8	
O	C	All	100	22.4	40.4	3.9	23.4	37.7	0.336
T	P	P	76	24.0	55.0	0.1	21.8	60.5	
	P	A	61	13.8	55.9	0.4	10.4	95.3	
	P	All	137	19.5	55.9	0.1	16.1	75.9	< 0.0001
R	C	A	80	14.5	26.1	0.1	15.3	44.5	
R	C	P	20	10.1	22.0	0.5	9.3	60.7	
	C	All	100	13.6	26.1	0.1	13.9	48.5	0.050
	P	P	76	14.3	57.0	0.5	14.2	66.6	
	P	A	61	8.9	35.7	0.9	6.2	81.2	
	P	All	137	11.9	57.0	0.5	10.9	75.3	< 0.0001
R	C	A	80	7.7	30.4	1.2	6.4	78.2	
E	C	P	20	4.5	23.0	1.9	3.6	100.1	
S	C	All	100	7.1	30.4	1.2	5.3	83.1	< 0.0001
	P	P	76	5.1	16.0	0.0	4.6	72.6	
	P	A	61	4.5	20.7	0.1	3.5	95.2	
	P	All	137	4.9	20.7	0.0	4.2	82.2	< 0.0001
R	C	A	80	48.4	76.8	10.0	51.2	28.2	
O	C	P	20	66.0	84.8	40.3	67.3	16.9	
O	C	All	100	52.0	84.8	10.0	55.2	28.7	0.181
T	P	P	76	53.9	90.8	1.6	57.9	40.6	
B	P	A	61	44.1	86.2	11.2	42.3	48.0	
G	P	All	137	49.6	90.8	1.6	52.1	44.5	0.006
R	C	A	80	34.0	79.3	0.2	36.2	41.9	
R	C	P	20	22.6	45.1	3.6	24.8	46.4	
B	C	All	100	31.7	79.3	0.2	33.4	45.0	0.024
G	P	P	76	34.2	86.4	1.2	29.2	64.4	
	P	A	61	35.6	63.8	7.0	37.6	41.0	
	P	All	137	34.9	86.4	1.2	33.1	54.7	0.015
R		A	80	17.6	69.4	2.4	15.3	68.0	
E	C								
S	C	P	20	10.9	29.5	4.3	8.8	57.6	
B	C	All	100	16.3	69.4	2.4	14.4	69.9	< 0.0001
G	P	P	76	11.8	35.6	0.1	11.9	61.1	
	P	A	61	20.2	69.9	1.1	19.6	77.1	
	P	All	137	15.6	69.9	0.1	13.9	79.5	< 0.0001

RR and RES are $\%^{14}C$ allocated to rhizosphere respiration and soil residues, respectively.
The suffix BG is used when partitioning coefficients are expressed as percentages of ^{14}C allocated to belowground.
* C = Continuous labelling, P = pulse labeling.
**: Number of partitioning coefficient sets.
***: Coefficient of variation of the mean (%).
****: Test for the normality of the distribution (Shapiro-Wilk test). Probability associated with the null hypothesis of normality of the distribution.

Table VII. Pearson correlation coefficients between partitioning coefficients in tracer studies. The value in italic is the probability associated with the null hypothesis Rho = 0.

Labelling (*)		SHOOT	ROOT	RR	RES
C	SHOOT	1			
C	ROOT	–0.675	1		
		< 0.0001			
C	RR	–0.433	–0.117	1	
		< 0.0001	0.2459		
C	RES	–0.417	–0.043	–0.141	1
		< 0.0001	0.6731	0.1614	
P	PA	1			
P	RAC	–0.857	1		
		< 0.0001			
P	RR	–0.648	0.217	1	
		< 0.0001	0.011		
P	RES	–0.515	0.257	0.341	1
		< 0.0001	0.0024	< 0.0001	

Belowground budget

		ROOTBG	RRBG	RESBG
C	ROOTBG	1		
C	RRBG	–0.696	1	
		< 0.0001		
C	RESBG	–0.452	–0.324	1
		< 0.0001	0.001	
P	ROOTBG	1		
P	RRBG	–0.782	1	
		< 0.0001		
P	RESBG	–0.535	–0.008	1
		< 0.0001	0.9239	

RR and RES are $\%^{14}C$ allocated to rhizosphere respiration and soil residues, respectively.
The suffix BG is used when partitioning coefficients are expressed as percentages of ^{14}C allocated to belowground.
* C = Continuous labeling, P = pulse labeling.

considered in these studies (37 days old on average, Tab. V). Thus, the decline in C inputs into the soil with plant age is related to the decrease in assimilate partitioning to roots, which is particularly marked for annual plants [81, 164, 166].

3.2.3. Microorganisms

Only eight experiments are reported here for continuous labeling experiments, and one in the case of pulse labeling studies (Tab. IX). This does not mean that the effects of microorganisms have not been investigated, but here, we only consider soil or sand culture experiments. In the literature, due to the difficulty of sterilizing soil microcosms efficiently, the great majority of work investigating the influence of microorganisms on rhizodeposition has been performed in nutrient solution, e.g. [90, 111].

The results indicate that microorganisms strongly increased the ^{14}C partitioned to the rhizosphere. On average, in non-sterile cultures, the RR and SOIL coefficients significantly increased by +249% and +37%, respectively (Tab. IX). The same effects are observed for the belowground budget. Belowground, less labeled C is partitioned to roots (–10%), whereas ^{14}C in rhizosphere respiration and in soil residues increased by +199% and +24%, respectively, but the variation of RESBG is not significant. Despite the small number of articles considered here, there is strong evidence that microorganisms greatly increase the partitioning of assimilates to the rhizosphere. There are several possible explanations. First, in non-sterile conditions, roots can establish symbiosis with mycorrhizal fungi. Mycorrhizae represent a significant sink for plant assimilates [89, 192] since up to 30% of the photoassimilates can be allocated to the symbiotic fungus [123]. Consequently, fungal respiration could explain the greater allocation of labeled C to rhizosphere respiration, whereas growth of extraradicular hyphae and the hyphal C exudation contribute to a large extent to the plant-derived carbon retrieved as soil residues [63, 72, 162]. On the other hand, non-symbiotic rhizosphere microorganisms take up and assimilate soluble low molecular weight compounds released passively from roots, and hence, they maintain the C gradient between the internal root tissues and the soil solution. Furthermore, rhizosphere microflora can synthesize enzymes or metabolites that can alter the integrity of root cells or the permeability of their membrane. Finally, root morphology can be modified directly by phytohormones produced by rhizosphere microorganisms, or indirectly by the changes in nutrient availability resulting from microbial processes. Consequently, any changes in the root branching pattern would be expected to have significant consequences on root exudation, which can be more important at the root apices, such as in maize, for instance [78]. Besides quantitative aspects of root exudation, both free and symbiotic microorganisms change the quality of root exudates. For example, Pinior et al. [139] demonstrated that exudates from non-mycorrhizal roots of cucumber stimulate hyphal growth of the mycorrhizal fungi *Gigaspora rosea* and *Gigaspora intraradices,* whereas exudates from roots colonized by *Gigaspora rosea* inhibited further root colonization by *Glomus mossae*. Therefore, the soil microflora strongly modify root exudation, which in turn alters both the size and the structure of microbial populations in the rhizosphere [18, 44].

3.2.4. Soil texture

Here, we report on experiments that compared plants grown on soils differing in their clay and loam contents. It is important to note that the range of the clay content reported here is low, from 2 to 15% (Tab. X) due to the difficulty of sampling roots in soils with high clay contents. An increase in the clay

Table VIII. Effect of plant age on labeled C partitioning between plant and belowground compartments. Effects are expressed as relative variations, see the text for explanations about the calculation of the effects.

Factor	Labeling (*)	References		N (**)	Relative variation (%)					Pn (***)	Pt (****)	Pm (*****)
					Mean	CV of mean	Max	Med	Min			
Age (days)												
	C		SHOOT	21	4	503	59	4	–33	0.376	0.373	
Min = 14	C		ROOT	21	4	1165	157	–8	–51	0.001		0.664
Max = 76	C	[91], [112], [113]	RR	21	15	266	111	5	–35	0.043		0.664
Mean = 39	C	[114], [95], [188],	RES	21	–11	–381	81	–19	–68	0.033		0.064
Median = 41	C	[191], [195]	ROOTBG	21	5	937	182	–2	–63	< 0.001		1.000
CV = 39	C		RRBG	21	16	211	132	2	–20	< 0.001		0.007
	C		RESBG	21	–9	–464	95	–21	–65	0.075	0.335	
	P		SHOOT	45	17	196	103	8	–57	0.013		0.000
Min = 28	P		ROOT	45	–26	–224	250	–43	–76	< 0.001		0.000
Max = 600	P	[46], [68], [81],	RR	45	–1	–10764	311	–28	–85	< 0.001		0.008
Mean = 151	P	[109], [132], [144],	RES	45	18	596	374	–20	–93	< 0.001		0.542
Median = 106	P	[147], [164], [166],[179]	ROOTBG	45	–6	–527	143	–14	–55	< 0.001		0.096
CV = 93	P		RRBG	45	26	288	293	10	–65	< 0.001		0.291
	P		RESBG	45	39	203	312	24	–77	< 0.001		0.096

RR and RES are $\%^{14}C$ allocated to rhizosphere respiration and soil residues, respectively.
The suffix BG is used when partitioning coefficients are expressed as percentages of ^{14}C allocated to belowground.
* C = Continuous labeling, P = pulse labeling.
**: Number of partitioning coefficient sets.
***: P associated with Shapiro-Wilk test for normality.
****: P associated with Student test for location Mu = 0 for data normally distributed.
*****: P associated with the non-parametric sign test for location Median = 0 for data not normally distributed.

and loam content of soil greatly alters the partitioning of ^{14}C. Significantly more labeled C is retained aboveground and less is allocated to roots (mean variation = +15% and –25%, respectively, Tab. X). Both the global and the belowground ^{14}C budgets indicate that partitioning of ^{14}C to rhizosphere respiration and to soil residues are also increased, but these effects are not significant according to the work of Whipps and Lynch [190] that indicated surprisingly low values for RR in soil with a light texture. The increase in C loss from roots in soil with increasing clay and loam contents is not surprising because numerous soil properties, which favor microbial activity and nutrient cycling, are related to the clay content: water retention, organic matter stabilization and high cation exchange capacity, for example. Thus, the suggested stimulation of rhizodeposition in relation to the clay and loam contents of soil could be explained by some differences in fertility and in microbial activity. Besides, the effect of the soil texture on C fluxes to the rhizosphere can also be explained by the physical properties of the soil. Indeed, soil texture is interrelated with bulk density and porosity and the resulting mechanical impedance has been reported to increase rhizodeposition [13, 49]. From a theoretical point of view, the mechanical impedance in soils with a fine texture should promote the sloughing-off of root cap cells. Root exudation may also be favored by the small size of the soil pores, which increases the surface of the root that is covered by soil aggregates and which consequently facilitates mass flow diffusion of solutes. Hence, both experimental data and theoretical considerations support the relevancy of considering soil texture when investigating C fluxes to the rhizosphere.

3.2.5. Soil nitrogen

Soil nitrogen is a major factor that can severely limit plant growth, and therefore, the effect of N fertilization on C fluxes to the rhizosphere is a highly relevant question. We summarized 9 data sets for continuous labeling experiments and 19 for pulse-chase studies, the latter being mainly related to an experiment on *Bromus erectus* [179] (Tab. XI). All the data sets indicate that when plants are N fertilized, there is a highly significant decrease in labeled C partitioning to roots (–14% and –35% for continuous and pulse labeling, respectively) and conversely, an increase in ^{14}C retrieved in shoots (+11% and 36% for continuous and pulse labeling, respectively) (Tab. XI). The coefficients of variation are not excessive. The effect is more marked in pulse-chase experiments. This is consistent with the low root:shoot ratio of N-fertilized plants, which is commonly observed experimentally and which is well described by the functional equilibrium theory [36]. The global ^{14}C budget does not indicate a significant effect of nitrogen on C allocation to rhizosphere respiration and to soil residues, whatever the labeling procedure. However, the belowground budget is altered by N fertilization in pulse-chase experiments. Indeed, the percentages of ^{14}C in rhizosphere respiration and in the soil residues are both significantly increased by nitrogen fertilization (the means of

Table IX. Effect of soil microorganisms on labeled C partitioning between plant and belowground compartments. Effects are expressed as relative variations, see the text for explanations about the calculation of the effects.

Factor	Labeling (*)	References		N (**)	Relative variation (%)					Pn (***)	Pt (****)	Pm (*****)
					Mean	CV of mean	Max	Med	Min			
Microorganisms												
Non-sterile vs. sterile												
	C	[6], [96], [168]	SHOOT	8	–4	–316	21	–5	–24	0.841	0.400	
	C		ROOT	8	2	918	31	7	–22	0.524	0.767	
	C		RR	8	249	112	658	157	–15	0.086	0.040	
	C		RES	8	37	175	181	24	–16	0.017		0.727
	C		ROOTBG	8	–10	–110	7	–14	–21	0.246	0.037	
	C		RRBG	8	199	119	598	114	–18	0.097	0.049	
	C		RESBG	8	24	271	169	–7	–24	0.005		0.727
	P	[190]	SHOOT	1	–8		–8	–8	–8			
	P		ROOT	1	–26		–26	–26	–26			
	P		RR	1	37		37	37	37			
	P		RES	1	886		886	886	886			
	P		ROOTBG	1	–38		–38	–38	–38			
	P		RRBG	1	14		14	14	14			
	P		RESBG	1	723		723	723	723			

RR and RES are $\%^{14}C$ allocated to rhizosphere respiration and soil residues, respectively.
The suffix BG is used when partitioning coefficients are expressed as percentages of ^{14}C allocated to belowground.
* C = Continuous labeling, P = pulse labeling.
**: Number of partitioning coefficient sets.
***: P associated with Shapiro-Wilk test for normality.
****: P associated with Student test for location Mu = 0 for data normally distributed.
*****: P associated with the non-parametric sign test for location Median = 0 for data not normally distributed.

Table X. Effect of soil texture on labelled C partitioning between plant and belowground compartments. Effects are expressed as relative variations, see the text for explanations about the calculation of the effects.

Factor	Labeling (*)	References		N (**)	Relative variation (%)					Pn (***)	Pt (****)	Pm (*****)
					Mean	CV of mean	Max	Med	Min			
Soil texture (% of clay/loam)												
	C		SHOOT	11	15	130	42	11	–16	0.455	0.029	
Min = 2/10	C		ROOT	11	–25	–118	44	–22	–66	0.195	0.018	
Max = 15/71	C		RR	11	3479	181	19500	24	-44	< 0.001		1.000
Mean = 9/29	C	[43], [112], [113], [190]	RES	11	67	185	233	6	–72	0.025		1.000
Median = 13/12	C		ROOTBG	11	–19	–98	6	–12	–51	0.340	0.007	
CV = 71/83	C		RRBG	11	4789	184	27158	45	–38	< 0.001		0.549
	C		RESBG	11	77	169	320	24	–61	0.136	0.079	

RR and RES are $\%^{14}C$ allocated to rhizosphere respiration and soil residues, respectively.
The suffix BG is used when partitioning coefficients are expressed as percentages of ^{14}C allocated belowground.
* C = Continuous labeling, P = pulse labeling.
**: Number of partitioning coefficient sets.
***: P associated with Shapiro-Wilk test for normality.
****: P associated with Student test for location Mu = 0 for data normally distributed.
*****: P associated with the non-parametric sign test for location Median = 0 for data not normally distributed.

Table XI. Effect of soil nitrogen on labelled C partitioning between plant and belowground compartments. Effects are expressed as relative variations, see the text for explanations about the calculation of the effects.

Factor	Labeling (*)	References		N (**)	Relative Variation (%)					Pn (***)	Pt (****)	Pm (*****)
					Mean	CV of mean	Max	Med	Min			
Soil nitrogen (mg/kg)												
Soil content or applied as fertilization												
	C		SHOOT	9	11	78	27	9	0	0.470	0.005	
Min = 0	C		ROOT	9	–14	–79	0	–13	–32	0.712	0.005	
Max = 505	C		RR	9	–6	–186	12	–8	–21	0.795	0.145	
Mean = 152	C	[11], [69], [91], [114], [171]	RES	9	–15	–253	78	–28	–39	0.001		0.070
Median = 73	C		ROOTBG	9	–2	–380	10	–1	–24	0.059	0.453	
CV = 118	C		RRBG	9	7	127	18	9	–7	0.429	0.045	
	C		RESBG	9	–3	–1330	99	–20	–30	0.001		0.508
	P		SHOOT	19	36	96	109	23	–7	0.032		0.001
Min = 38.5	P		ROOT	19	–35	–84	38	–39	–84	0.006		0.001
Max = 970	P		RR	19	–4	–1028	96	–1	–64	0.210	0.677	
Mean = 694	P	[60], [116], [179]	RES	19	38	209	236	31	–69	0.292	0.052	
Median = 750	P		ROOTBG	19	–16	–167	67	–25	–42	< 0.001		0.001
CV = 32	P		RRBG	19	25	156	90	29	–49	0.717	0.012	
	P		RESBG	19	82	111	260	50	–51	0.262	0.001	

RR and RES are $\%^{14}C$ allocated to rhizosphere respiration and soil residues, respectively.
The suffix BG is used when partitioning coefficients are expressed as percentages of ^{14}C allocated to belowground.
* C = Continuous labeling, P = pulse labeling.
**: Number of partitioning coefficient sets.
***: P associated with Shapiro-Wilk test for normality.
****: P associated with Student test for location Mu = 0 for data normally distributed.
*****: P associated with the non-parametric sign test for location Median = 0 for data not normally distributed.

increase are +25% and +82%, respectively). This suggests that relative to C exported by shoots to belowground, N fertilization increases rhizodeposition. This hypothesis has some theoretical basis. Indeed, if rhizosphere microorganisms are in competition with plant roots for mineral N [80], a supply of nitrogen would be expected to stimulate microbial growth, and consequently, to increase the flux of passive exudation. Moreover, nitrogen deficiencies were reported to affect root morphology by reducing the branching [4], which may have significant consequences on the production of mucilage and the release of root cap cells, and on exudation. Thus, although there are clues indicating that N fertilization increases the percentage of belowground C that is released from roots, the overall effect of N fertilization on rhizodeposition is difficult to predict because in parallel, nitrogen stimulates the total plant growth and photosynthesis and reduces the percentage of photoassimilates that are allocated belowground.

3.2.6. Atmospheric CO_2 concentration

The elevation in atmospheric CO_2 concentration consecutive to the use of fossil C has raised the question as to whether C fluxes to the rhizosphere would be modified. This is of particular importance for understanding nutrient cycling and C sequestration in soil under elevated atmospheric CO_2. We report here on 24 data sets related to ^{14}C distribution within the plant and to the soil under elevated CO_2 (Tab. XII). Pulse and continuous labelings are equally represented. Studies concerned both herbaceous plants (ryegrass, wheat and maize) and trees (aspen and chestnut, data not shown). There is no clear effect of elevated CO_2 on the partitioning of assimilates to shoots and roots. However, in continuous labeling experiments, the ^{14}C retrieved in the rhizosphere respiration is significantly increased under elevated CO_2 (+36%). This is consistent with the data reviewed by Zak et al. [196], which evidence an increase in soil and microbe respiration under elevated CO_2. Apart from that, the data do not indicate a clear effect of elevated CO_2 on C partitioning to the rhizosphere. This is not surprising because atmospheric CO_2 is not a factor directly connected to the rhizosphere. Any effect of atmospheric CO_2 enrichment on rhizodeposition is through plant growth, in contrast to factors such as the soil texture or the presence of microorganisms, that act more directly on the release of C from roots. Soil nitrogen can be considered as intermediate because it stimulates both the growth of plants and the growth of microorganisms. Hence, elevated CO_2 can alter the partitioning of assimilates to the rhizosphere through several mechanisms such as a change in plant structure, itself depending on the plant species [141], a modification of the

Table XII. Effect of atmospheric CO_2 on labeled C partitioning between plant and belowground compartments. Effects are expressed as relative variations, see the text for explanations about the calculation of the effects.

Factor	Labelling (*)	References		N (**)	Relative variation (%)					Pn (***)	Pt (****)	Pm (*****)
					Mean	CV of mean	Max	Med	Min			
Atmospheric CO_2 (ppm)												
	C		SHOOT	12	–6	–158	13	–10	–18	0.460	0.051	
Min = 350	C		ROOT	12	21	201	113	5	–23	0.032		0.774
Max = 800	C		RR	12	36	132	107	40	–61	0.734	0.024	
Mean = 633	C	[11], [43], [171], [188]	RES	12	–2	–2459	126	–11	–50	0.005		0.388
Median = 700	C		ROOTBG	12	5	461	54	–2	–22	0.022		0.146
CV = 24	C		RRBG	12	24	201	113	16	–69	0.996	0.112	
	C		RESBG	12	–13	–280	90	–20	–45	0.003		0.039
	P		SHOOT	12	–3	–505	25	–4	–28	0.490	0.507	
Min = 350	P		ROOT	12	10	315	87	7	–28	0.041		0.774
Max = 720	P	[134], [133], [142], [147], [116]	RR	12	2	2656	115	–5	–87	0.304	0.899	
Mean = 477	P		RES	12	43	169	215	19	–23	0.024		0.388
Median = 450	P		ROOTBG	12	–3	–307	15	–3	–22	0.811	0.284	
CV = 32	P		RRBG	12	–4	–1269	129	–9	–86	0.053	0.790	
	P		RESBG	12	21	166	99	8	–17	0.087	0.061	

RR and RES are $\%^{14}C$ allocated to rhizosphere respiration and soil residues, respectively.
The suffix BG is used when partitioning coefficients are expressed as percentages of ^{14}C allocated to belowground.
*: C = Continuous labeling, P = pulse labeling.
**: Number of partitioning coefficient sets.
***: P associated with Shapiro-Wilk test for normality.
****: P associated with Student test for location Mu = 0 for data normally distributed.
*****: P associated with the non-parametric sign test for location Median = 0 for data not normally distributed.

root to shoot ratio [145], an alteration in root morphology, nutrient stress due to the stimulation of plant growth, etc.

4. OUTLOOKS

Tracer experiments are very useful tools for investigating C fluxes from plant roots to the soil because they allow the separation of root-derived C from the C of the native soil organic matter. With such techniques, investigations on rhizodeposition can be performed on plants growing in soil, including the microflora, which is more realistic than experiments in nutrient solution. However, in soil, it is difficult to estimate the fraction of rhizodeposits that is mineralized by microorganisms and consequently, the amount of C released from roots cannot be determined in a reliable manner. The partitioning of rhizosphere respiration between roots and microbial contributions is of particular importance if rhizodeposition is investigated to understand processes that are mediated by microbes. In that case, it is essential to evaluate how much energy is available to microorganisms to predict microbial growth in the vicinity of roots. Several attempts have been made to evaluate the rhizomicrobial contribution to rhizosphere CO_2 [22, 58, 69, 87, 168, 176] but at the present time, none of them is fully satisfactory because all these studies rely on strong assumptions that are difficult to test. As an alternative, metabolic activity (growth and maintenance) of rhizosphere microbes can be determined or compared between different treatments to investigate its relationships with root activity [129, 159]. However, quantification of root-derived C fluxes in non-sterile soil is undoubtedly a key point that needs further investigation and methodological developments to aim at engineering the rhizosphere to manage nutrient and pollutant cycling or to control soil-borne pathogens.

Rhizodeposits cover a wide range of compounds that have very different characteristics in terms of interactions with the soil matrix, availability to microbial assimilation, chemical properties, etc. Moreover, the release of root C into the root environment originates from various mechanisms (i.e. passive diffusion of solutes to the soil solution, active secretion of molecules and senescence of root tissues), the distribution and intensity of which are not homogenously distributed along the root. This complexity is well illustrated by the great difficulty of proposing a nomenclature for the rhizodeposits. Consequently, the composition of C released from roots is extremely variable. Indeed, the composition of rhizodeposits depends on the relative proportion of each category (exudates, secretion and senescing tissues) as well as on the intrinsic composition

of each of these categories. For example, nutrient or toxicity stress is know to significantly increase the concentration of organic acids in root exudates [73]. It is thus crucial to investigate in more detail the mechanisms by which root C is released into the soil. For example, the production of root cap cells and mucilage has been extensively studied in vitro, under experimental conditions that probably increase the phenomena. Very little is known about environmental control of rhizodeposition by root apices in soil conditions. If the mucilage sticks to the root cap even at soil water potentials close to 0.01 MPa, the continuous production of slime and the release of root cap cells might not be as significant as suggested by laboratory investigations. There is also great debate about whether the plant does have a control over the amount of C that passively diffuses to the soil solution. The ATPase transporters, which can actively reabsorb solutes in vitro, provide a mechanism by which the root can virtually modulate exudation. However, does the plant regulate the flux of exudates by controlling the number of these transporters and their activity? Research aimed at understanding the regulation of these proteins is particularly relevant. Indeed, these transporters would offer the opportunity to manipulate the flow of exudation both in terms of quantity by over-expressing or inhibiting the transporters' synthesis, and in terms of quality by acting specifically on target transporters and thus on changing the exudation flux of a particular compound.

The spatial heterogeneity of rhizodeposition along a root segment outlines the need to link investigations on rhizodeposition to the root. From a theoretical point of view, the branching pattern, which determines the number of apices, would be expected to have a significant effect on the number of sloughoff root cap cells as well as on mucilage production and on the release of exudates if their diffusion is more significant at the root tips, as was observed in maize. Moreover, the exudation, the release of border cells and the senescence of the epidermis is proportional to the root radius. Hence, it is necessary to determine if in soil root morphology does indeed have significant effects on rhizodeposition.

The "rhizosphere effect" observed experimentally for numerous soil processes mediated by the microflora is frequently related to the greater microbial abundance at the soil-root interface compared to bulk soil. Therefore, a major goal for investigations on rhizodeposition is to predict microbial growth in the root environment [12, 30, 31, 127, 167]. In the last decade, the development of techniques to establish microbial fingerprints evidenced that the structure of rhizosphere communities was both physiologically and genetically different from that of bulk soil and different between plant species. The relationships between the size of the microflora, structure of microbial communities and the functions performed by them is far from being elucidated and there is a relevant need to investigate the factors that determine the structure of microbial communities in the rhizosphere. Among them, rhizodeposits have been demonstrated to be relevant [10, 48]. Since growth of soil microbes is generally limited by availability of C, it can reasonably be assumed that the dynamics of microbial community structure might derive from the competitive ability of rhizosphere microorganisms with respect to the amount of available C. On the other hand, plant roots are "chemical factories" that synthesize a wide variety of secondary metabolites [3], which are biologically active and which might orient the dynamics of microbial communities. Root-microbe interactions might not only be governed by trophic competition between microorganisms for rhizodeposits and by sophisticated signalling involved in the symbiosis process. Allelopathy, which can play a significant role in the dynamics of the plant community structure, might also contribute to determining the structure of rhizosphere microbial communities. The chemical diversity of secondary metabolites released into the rhizosphere is probably large, and rhizodeposition of such compounds offers an exciting area of investigation and additional outlook to the use of the plant for engineering the rhizosphere.

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