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Review paper

Sugars in soil and sweets for microorganisms: Review of origin, content, composition and fate

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ABSTRACT

Sugars are the most abundant organic compounds in the biosphere because they are monomers of all polysaccharides. We summarize the results of the last 40 years on the sources, content, composition and fate of sugars in soil and discuss their main functions. We especially focus on sugar uptake, utilization and recycling by microorganisms as this is by far the dominating process of sugar transformation in soil compared to sorption, leaching or plant uptake. Moreover, sugars are the most important carbon (C) and energy source for soil microorganisms.

Two databases have been created. The 1st database focused on the contents of cellulose, non-cellulose, hot-water and cold-water extractable sugars in soils (348 data, 32 studies). This enabled determining the primary (plant-derived) and secondary (microbially and soil organic matter (SOM) derived) sources of carbohydrates in soil based on the galactose + mannose/arabinose + xylose (GM/AX) ratio. The 2nd database focused on the fate of sugar C in soils (734 data pairs, 32 studies using ^{13}C or ^{14}C labeled sugars). ^{13}C and ^{14}C dynamics enabled calculating the: 1) initial rate of sugar mineralization, 2) mean residence time (MRT) of C of the applied sugars, and 3) MRT of sugar C incorporated into 3a) microbial biomass and 3b) SOM.

The content of hexoses was 3–4 times higher than pentoses, because hexoses originate from plants and microorganisms. The GM/AX ratio of non-cellulose sugars revealed a lower contribution of hexoses in cropland and grassland (ratio 0.7–1) compare to forest (ratio 1.5) soils.

^{13}C and ^{14}C studies showed very high initial rate of glucose mineralization (1.1% min^{-1}) and much higher rate of sugars uptake by microorganisms from the soil solution. Considering this rate along with the glucose input from plants and its content in soil solution, we estimate that only about 20% of all sugars in soil originate from the primary source – decomposition of plant litter and rhizodeposits. The remaining 80% originates from the secondary source – microorganisms and their residues. The estimated MRT of sugar C in microbial biomass was about 230 days, showing intense and efficient internal recycling within microorganisms. The assessed MRT of sugar C in SOM was about 360 days, reflecting the considerable accumulation of sugar C in microbial residues and its comparatively slow external recycling.

The very rapid uptake of sugars by microorganisms and intensive recycling clearly demonstrate the importance of sugars for microbes in soil. We speculate that the most important functions of sugars in soil are to maintain and stimulate microbial activities in the rhizosphere and detritusphere leading to mobilization of nutrients by accelerated SOM decomposition – priming effects. We conclude that the actual contribution of sugar C (not only whole sugar molecules, which are usually determined) to SOM is much higher than the 10 ± 5% commonly measured based on their content.

1. Introduction – why sugars?

Sugars are the most abundant organic compounds in the biosphere because they are the basic components of all polysaccharides: cellulose, hemicellulose (polyoses), starch, pectin,

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fructanes, and glucanes as well as of chitin (consists from amino sugars) (Kögel-Knabner, 2002). Considering the dominance of polysaccharides in plants (50–70% of dry mass), they are the most important primarily input of organic carbon (C) in soil. With a mean residence time (MRT) of few weeks to months (Martin et al., 1974), polysaccharides are decomposed by exoenzymes (cellulases, xylanases, glucosidases, hydrolases, chitinases) to oligo- and monosaccharides (termed sugars). Cellulose is the most abundant biopolymer and, consequently, glucose is the most abundant monomer released by its decomposition in soil. Sugars therefore dominate within low molecular weight organic substances (LMWOS) in all soils and affect various processes not only as a chemical compound group *per se*, but especially as C and an energy source for microorganisms.

All oligo- and monosaccharides are soluble, easily available for microorganisms, and are captured rapidly by microbes and used for maintenance (both respiration and anabolism), growth and C storage. Because sugars dominate LMWOS and cell metabolism, their role for microbial life in soil cannot be overestimated. For example, sugar concentration in soil solution stimulates the transition of microorganisms from dormant or potentially active to the active stages (Blagodatskaya and Kuzyakov, 2013). This activation contributes further to exoenzyme production, thus accelerating the decomposition of soil organic matter (SOM) and the release of stored nutrients, mainly N, P and S. This makes sugars the most common and no doubt very efficient substance group to induce priming effects (Kuzyakov, 2010).

Another important and frequently neglected relevance of carbohydrates is their contribution to aggregates formation – and thus to the formation of soils from parent materials. Poly-, oligo- and monosaccharides become sticky with increasing the concentrations and drying, and bind mineral and organic particles, resulting in microaggregates formation (Oades, 1984; Six et al., 1999). Even the role of particulate organic matter (POM) for aggregates formation is mainly connected with the release of polysaccharides and sugars due to POM decomposition.

Within the three most abundant classes of LMWOS in soil – sugars, carboxylic acids and amino acids – the concentration of sugars is about 2–3 times higher than both other classes. The fate and significance of other LMWOS in soil were intensively reviewed earlier: carboxylic acids (Jones, 1998) and amino acids (Jones et al., 2005), and we refer the readers to these excellent reviews for further information. No overview, however, focused on the composition, fate and relevance of sugars in soil. The sole detailed review about carbohydrates in soils was published about 40 years ago (Cheshire, 1979) and focused on the concentration and composition of sugars, but not on their fate and not on their relevance in soil. In the meantime, numerous studies have analyzed not only the composition of sugars, but also their fate in the soil. This includes the main processes in which they are involved, their residence time, microbial utilization, biochemical pathways, and contribution to SOM formation and C sequestration. Other work has described environmental factors and soil parameters, land use, etc. Therefore, our main objective is to provide a comprehensive overview about the fate of sugars in soil, including:

- analyzing the primary and secondary sources of carbohydrates in soil;
- re-evaluating the content and composition of cellulose and non-cellulose sugars in soils, including analysis of their dependence on soil parameters and origin;
- assessing the main fate of sugars in soil, including their sorption, migration through the soil profile, plant uptake and microbial uptake and utilization;
- estimating the rates of main microbial utilization processes;
- estimating annual sugar production and its microbial recycling in soil based on the cellulose and non-cellulose sugar content and their decomposition rates;
- evaluating the role of sugars for aggregates formation, SOM accumulation and priming effects; and
- providing an overall scheme of sugar transformation and recycling in soil.

It is beyond the scope of this review to provide methodological details of carbohydrate extraction, purification and analysis (Cheshire, 1979; Amelung et al., 1996).

2. Materials and methods

We use the term *carbohydrates* when we refer to monosaccharides, disaccharides, oligosaccharides and polysaccharides without their differentiation. In some literature, '*saccharides*' are used as a synonym of carbohydrates. For specification we use the respective terms (i.e. polysaccharides, monosaccharides, etc.). The term '*sugars*' is used for mono- and disaccharides.

For the review preparation, two sets of literature data were collected: 1) content and concentration of various groups of sugars in soils and soil solutions, respectively and 2) mineralization rates of sugars in soil and their participation in various fluxes including incorporation into microbial biomass (MB) and SOM.

2.1. Sugar content and composition

The first database is focused on sugar contents in soils and soil solutions and contains 348 data from 32 studies. Articles were searched in the Web of Knowledge and Scopus using the key words: "soil*" AND "carbohydrate*", "sugar content" AND "soil*". Information was collected on total sugars as well as content of individual sugars extracted by various procedures. Based on the extractants and pre-treatments (e.g. various hydrolysis procedures, temperature and soil:solution ratios), all sugars were divided into the following groups: 1) total, 2) non-cellulose, 3) hot-water extractable and 4) cold-water extractable. The specific soil parameters (C and N contents, pH, texture), land use, experiment conditions, depth of soil sampling and climate were included in the database. Only articles with total C in soil <6% of dry weight were included in order to consider mineral soils only. Soil texture was classified according to clay content as: clayey (>25% clay), loamy (15–25% clay) and sandy (10–15% clay). We found no carbohydrate studies for soils with <10% clay. All plant species or vegetation types were classified into three functional groups: forest, agricultural crops and grasslands. The original data on sugar contents (mg kg^{-1}, mg g^{-1}, mg 100 g^{-1}, μg g^{-1}, g kg^{-1} soil) were standardized to g sugar C kg^{-1} soil.

This database was used to analyze the primary (plant-derived) and secondary (microbially and SOM-derived) sources of sugars in soil and to evaluate the role of carbohydrates in aggregates formation, SOM dynamics and priming effects. The hexose/pentose ratio (galactose + mannose/arabinose + xylose) (GM/AX) for the non-cellulose sugars was calculated to analyze the origin of sugars in the soil (Oades, 1984). To estimate the possible contribution of plant sources to the origin of soil sugars, this ratio was also calculated for the plant tissues of the three plant functional groups: forest, agricultural crops and grasslands. The GM/AX ratio for microbial residues was taken >2.0 (Oades, 1984).

Our analysis was mainly focused on the total and non-cellulose sugars. We paid less attention to the sugar composition extracted by NaOH because alkali extracts also fulvic and humic acids, which were not in the scope of this review.

2.2. Fate of sugars

The second (2nd) database was developed to evaluate the fate of sugar C in soil. All polysaccharides pass through the sugar pool during their decomposition in soil. We therefore mainly focused on the fate of sugar C. Because its fate in soil cannot be investigated without isotopic labeling and tracing, only those papers using ^{13}C or ^{14}C labeled sugars were included. Articles were searched in Web of Knowledge and Scopus using the following key words: "sugar* decomposition in soil*", "glucose decomposition in soil*", "glucose ^{13}C soil*", "glucose ^{14}C soil*". This database contains 734 data pairs from 32 ^{13}C- and ^{14}C-labeling studies. The sugar C fate was analyzed based on ^{13}C or ^{14}C partitioning between the following pools: 1) mineralized to CO_2, 2) incorporated into soil MB and 3) incorporated into SOM.

All data about the fate were analyzed and presented in dynamics, i.e. depending on the time after sugar input into the soil. This enabled calculating: 1) maximal rate of glucose C decomposition, 2) MRT of C of the initially applied sugars, 3) MRT of C in 3a) MB and 3b) SOM pools.

Most studies on sugar fate in soil have been conducted using glucose due to its high abundance: glucose originates from cellulose decomposition and is also present in root exudates (Derrien et al., 2004). Even though the presented data on the fate of sugars in soil were mainly obtained based on glucose, the fate of other sugars is very similar (Derrien et al., 2007; Gunina et al., 2014).

All results from both databases are presented as means ± standard errors (SE).

2.3. Calculations and statistical analyses

Sugar C mineralization to CO_2 was estimated using the literature overview on glucose ^{14}C or ^{13}C decomposition within the first 24 h after its addition into soil based on 74 data collected from 16 studies. The maximal rate of glucose C decomposition was calculated as a tangent to its initial mineralization rate, using single exponential kinetics (Eq. (1)) (Parton et al., 1987; Kuzyakov, 2011). The MRT of the glucose C was calculated as 1/k.

$$^{Rate}CO_2(t) = k \cdot A \cdot \exp^{(-kT)} \quad (1)$$

where: $^{Rate}CO_2$ (t) is the rate of CO_2 efflux at time t (% min^{-1}), k is the decomposition rate of glucose (min^{-1}), and A is the size of the glucose pool at time 0 (%).

To calculate MRT of C originating from sugars and incorporated into MB and SOM, the parameters of double exponential kinetics (Eq. (2)) were fitted on all data from database II. Only the experiments with a duration <1 year were considered here.

$$C_x(t) = A \cdot \exp^{(-k_1 T)} + (90 - A) \cdot \exp^{(-k_2 T)} \quad (2)$$

where: $C_x(t)$ is the pool size of glucose C at time t (% of applied tracer), A is the size of the glucose C pool (%), 90 is a percentage of glucose C immediately after the incorporation of glucose into MB (% from applied tracer). 90% (not 100%) was taken as the pool of glucose C incorporated into MB because our database showed the direct decomposition of 10% of added glucose to CO_2, which does not participate in the further utilization within the MB pool. k_1 and k_2 are decomposition rates of glucose C (min^{-1}). The MRT of the glucose C incorporated into MB and SOM was calculated as 1/k.

Assuming that MB is a main sink of sugar C in soil (see below), the ^{14}C or ^{13}C from sugars in SOM presents the sum of the label in living MB and in microbial residues. Thus, the part of C from sugars in the composition of microbial residues was calculated by subtracting ^{14}C (or ^{13}C) in living MB from ^{14}C (or ^{13}C) in SOM.

Statistica 10.0 (StatSoft Inc.) was used to fit parameters for the single and double exponential kinetics described above.

3. Sources of sugars in soil

3.1. Primary sources of sugars

3.1.1. Plant sugars – input by decomposition of above- and belowground litter

Plant biomass, including above- and belowground litter, is the main primary source of carbohydrates in soil. Cellulose consists mainly of glucose, whereas hemicelluloses include the rests of various pentoses and hexoses: glucans, xylans, mannans, galactans, fructosanes, arabinogalactans, with abundant pentoses (arabinose and xylose) (Table 1). Some plant species contain significant amounts of galactose and mannose (Sariyildiz and Anderson, 2003; Schaedel et al., 2010).

The green leaves contain 15–35% cellulose and 20–40% hemicellulose of dry weight (Fig. 1). Cellulose is relatively enriched in forest litter (except coniferous trees), agricultural crops and grasses compared to green leaves (Fig. 1) (Salamanca et al., 2003; Sariyildiz and Anderson, 2005). Roots tissues contain 2–3 times more cellulose than green leaves (Fig. 1) (Zhang et al., 2014).

Cellulose decomposition in soil is estimated to range from 30% during 3 months (Blagodatskaya et al., 2014) to 50–86% during two years (Zech et al., 2012). The lowest MRT for intact cellulose ranges from 0.6 to 1.1 y^{-1}, depending on the type of litter (recalculated from Fioretto et al. (2005)). Decomposition of intact hemicellulose is faster than cellulose and amounted to 70% during 7 months (Cheshire, 1979). These rates show that most of the celluloses and hemicelluloses will be decomposed to their monomers – sugars – within a few months.

3.1.2. Sugars in root exudates

Plants release 15–40% of photosynthetically fixed C into the soil via rhizodeposition (Kuzyakov and Domanski, 2000; Warembourg and Estelrich, 2000; Hutsch et al., 2002). Among the numerous components exuded by roots, carbohydrates are the most abundant (Kraffczyk et al., 1984; Hutsch et al., 2002; Derrien et al., 2004). In root exudates, carbohydrates are present mainly in the form of monosaccharides, whereas in secretions mainly as polysaccharides, e.g. mucilage (Meharg, 1994). Sugars account for 46–52% in the exudates of wheat, alfalfa and pea plants, whereas they comprise only 15% in the exudates of oil radish and *Chenopodium album* (Hutsch et al., 2002). The dominant sugars in root exudates are glucose, fructose, galactose, arabinose, maltose, raffinose, rhamnose, sucrose and xylose (Grayston and Campbell, 1996). Glucose is common in root exudates of various trees species, whereas arabinose and ribose are absent (Grayston and Campbell, 1996). Glucose makes up the main part of root exudates ~40–50%, whereas fructose, saccharose and ribose presented 23, 23 and 8%, respectively (Hutsch et al., 2002).

C in root exudates is easily available for microorganisms and a major part of it (64–86%) is decomposed to CO_2 (Werth and Kuzyakov, 2008). About 2–5% of C released by roots to the soil is accumulated in the SOM (Helal and Sauerbeck, 1989; Hutsch et al., 2002).

3.2. Secondary sources of sugars

3.2.1. Sugars in soil organisms

Soil microorganisms are the secondary source of carbohydrates in soil, i.e. microorganisms synthesize their sugars from the sugar C

Table 1
Composition of sugars in plants (% from total sugars in the plant organs).

Plant type	Source of sugars	Glucose	Mannose	Galactose	Rhamnosa	Fucose	Fructose	Arabinose	Xylose
Deciduous trees	Leaves	3.0	3.2	25.7	7.0	2.2	n.a.	20.4	41.3
	Sapwood	4.0	3.0	4.0	3.0	1.0	n.a.	6.0	78.0
	Bark	3.0	2.0	13.0	3.0	2.0	n.a.	26.0	50.0
Coniferous trees	Niddles	16.3	31.5	19.2	2.4	1.4	3.5	23.4	13.1
	Roots	19.4	5.8	20.8	4.2	2.8	0.5	23.8	22.7
	Sapwood	5.0	17.0	25.0	2.0	1.0	n.a.	20.0	30.0
	Bark	4.0	10.0	15.0	4.0	2.0	n.a.	49.0	18.0
Grasses	Leaves	6.4	1.0	6.5	1.2	0.9	0.7	19.4	63.5
	Roots	6.8	3.0	11.3	2.0	1.4	0.6	18.7	55.3
Herbs	Leaves	5.0	3.0	25.0	3.0	3.0	n.a.	23.0	35.0
	Roots	14.0	2.0	13.0	2.0	2.0	n.a.	28.0	38.0

References: Sariyildiz and Anderson, 2003; Sariyildiz and Anderson, 2005; Schaedel et al., 2010; Nierop et al., 2001.

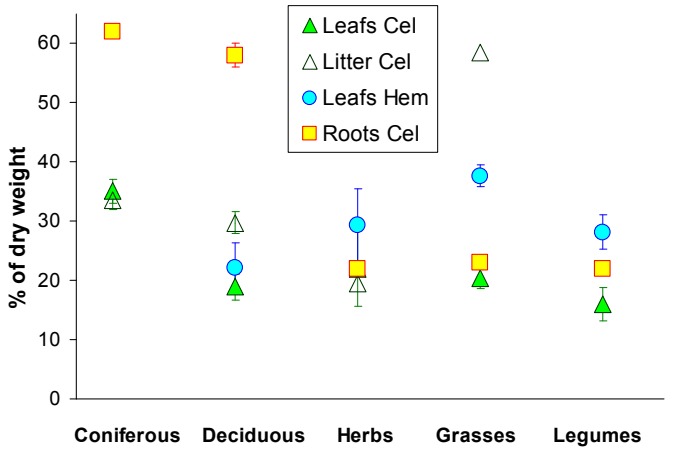

Fig. 1. Average content of cellulose (Cel) and hemicellulose (Hem) in green leafs, litters and roots of main plant groups (% of dry weight). Coniferous species (leafs cel n = 2; litter cel n = 5; roots cel n = 2); deciduous species (leafs cel n = 5; litter cel n = 6; leafs hem n = 5; roots cel n = 3); herbs (leafs cel n = 6; litter cel n = 1; leafs hem n = 4; roots cel n = 1); grasses (leafs cel n = 2; litter cel n = 1; leafs hem n = 2; roots cel n = 1); legumes (leafs cel n = 6; leafs hem n = 6; roots cel n = 1). (See references in Supplementary).

or other C-containing substances derived from plant litter. Earlier studies showed, that microbially derived polysaccharides predominantly consist of hexoses, mainly glucose, mannose and galactose (Oades, 1984). Later studies, however, demonstrated that soil bacteria, actinomyces and also pure cultures of bacteria or fungi contain considerable portions of pentoses, mainly ribose (Table 2).

Soil fauna can be an additional source of soil sugars. Earthworm cast and mucus are enriched with polysaccharides (Guggenberger et al., 1996; Zhang et al., 2009; Pan et al., 2010). Excretes of other insects (like plant louse), feeding on leafs, contain high sugar amounts. However, the contribution of this source to the total sugars input, compared to that of plants (primary source) and microorganisms (secondary source), is comparatively low.

3.2.2. Sugars in dissolved organic matter

Dissolved organic matter (DOM) is a small part of SOM, but DOM is an important source of carbohydrates, mainly mono- and oligosaccharides. Sugars in DOM are originated from the decomposition of plant litter (above- and belowground), root exudates and decomposition of SOM. They also contain sugars released by living microorganisms and from microbial residues. The monosaccharide concentration in DOM varies from 5 to 130 mg C kg^{-1} soil depending on ecosystem, which presents around 30% of C in DOM (Hishi et al., 2004; Fischer et al., 2007; Tian et al., 2010). The main component (30%) of sugars in DOM is glucose (Fischer et al., 2007).

4. Content, composition and source of sugars in soil

4.1. Extraction and analysis of soil sugars

Sugars identification in soil involves several steps: extraction, purification and analysis of composition and amounts. This review does not examine all methodological details of sugar extraction from soil, their purification and analysis. Here, we merely briefly provide the extraction approaches for clearly separating the groups of carbohydrates in soil.

Based on the extractions and pretreatments, the following groups of sugars can be distinguished (Table 3): cellulose, non-

Table 2
Composition of sugars in microorganisms (% from dry weight).

Microorganisms	Source of sugars	Glucose	Rhamnose	Mannose	Galactose	Arabinose + Fucose + Fructose	Ribose
Pure cultures							
Bacillus subtilis	Cell	45.9	4.3	8.9	26.2	n.a.	14.8
	EPS[a]	10.1	n.a.	89.9	n.a.	n.a.	n.a.
Pseudomonas fluorescens	Cell	42.0	37.0	4.6	n.a.	n.a.	16.3
	EPS	17.7	18.4	58.4	4.5	n.a.	1.0
Microbial groups extracted from soil[b]							
Bacteria	Cell	33.1	13.5	5.7	13.5	5.3	29.1
	EPS	6.5	0.2	96.6	1.2	0.6	0.3
Actinomyces	Cell	13.6	6.5	41.4	16.0	10.7	11.8
	EPS	1.3	n.a.	97.9	0.4	0.1	0.2
Fungi	Hyphae	97.1	n.a.	0.7	1.2	1.1	n.a.

References: Tanaka et al., 1990.
[a] EPS – extracellular polysaccharides, Cell – cell compounds, n.a. – data not available.
[b] Microbial groups have been selected from the andosols.

Table 3
Carbohydrate groups extracted from soil by various solutions. The groups are presented for single and not for sequential extractions.

Groups of carbohydrates (and average contribution to total carbohydrates)	Extraction solution	Uncertainties[a]	Reference
Monosaccharides (0.1% from total sugars in soil), oligosaccharides, and non- structural polysaccharides (1%)	Cold H_2O	Heterogenic mix of sugars from microorganisms, SOM and plants.	1, 2
Exocellular polysaccharides of microbial origin (10%)	Hot H_2O	Co-extraction of plant polysaccharides can occur	3, 4, 5
Microbial cellular polysaccharides; Potentially available of microorganisms	Inorganic salts or 0.5 M K_2SO_4	Co-extraction of non-microbial-derived sugars can occur after fumigation	6, 7, 8
Mix of sugars from humic and fulvic acids and plant residues	0.1 M NaOH	Heterogenic mix of sugars of unknown sources, Co-extraction of humic and fulvic acids	1, 4
Non-cellulose sugars	1) 0.5 M H_2SO_4 2) 2.5 M H_2SO_4 3) 1 M, 6 M HCl 4) 4 M TFA	Sugars from polysaccharides (hemicellulose, cellulose) and microorganisms	1, 9, 10
Total sugars (100%)	12 M H_2SO_4 + 1 M H_2SO_4	Sugars from hemicellulose and cellulose, also sugars from humic acids, $^1/_3$ of sugars is lost due to hydrolysis	11

References: 1: Tanaka et al., 1990; 2: Benzingpurdie 1980; 3: Oades 1984; 4: Ball et al., 1996; 5: Haynes and Francis, 1993; 6: Badalucco et al., 1992; 7: Joergensen et al., 1996; 8: Hofman and Dusek 2003; 9: Murata et al., 1999; 10: Amelung et al., 1996; 11: Cheshire and Mundie, 1966.
[a] Main uncertainties of the approaches are shortly described.

cellulose (Murata et al., 1999), NaOH-extractable, inorganic salt-extractable (Badalucco et al., 1992; Joergensen et al., 1996; Hofman and Dusek, 2003), hot- (Oades and Wagner, 1970) and cold-water extractable. Only independent extractions (not the sequential) are briefly described below.

Carbohydrates that are extracted by various water solutions – cold and hot water, salt and alkali (Table 3) – represent the easily available carbohydrate pool, consisting mainly of mono- and oligosaccharides. Monosaccharides can be released from these extracts by hydrolysis with 0.5 M H_2SO_4 (Tanaka et al., 1990).

Non-cellulose sugars can be extracted by diluted acids such as 2.5 M H_2SO_4 (Cheshire, 1979), 1 M HCl (Uzaki and Ishiwatari, 1983) or 4 M TFA (Amelung et al., 1996; Zhang et al., 2007) (Table 3).

Cellulosic sugars are extracted by two-step hydrolysis: 1) with cold 12 M H_2SO_4 (or 24 M H_2SO_4 (Cheshire and Mundie, 1966) and 2) high-temperature hydrolysis with 6–12 N H_2SO_4 to extract the maximum amount of sugars, including that in cellulose (Cheshire and Mundie, 1966; Amelung et al., 1996) (Table 3). Cold concentrated acids enable dissolving insoluble polysaccharides (in a cellulose composition) before hydrolysis.

To purify the extracts from the humic-like compounds, various sorbents (XAD-4, C-18, activated carbon) as well as a combination of XAD-7 with cation exchange resin are applied (Amelung et al., 1996). The obtained monosaccharides are derivatized for quantitative analysis by gas chromatography (GC) (reviewed in detail by Rodriguez-Sanchez et al. (2011)).

Finally, the extracted sugars can be identified and quantified spectrophotometrically (Doutre et al., 1978), by GC (Zhang et al., 2007), high-performance liquid chromatography (HPLC) (Tanaka et al., 1990) or ion chromatography (Martens and Loeffelmann, 2002). Spectrophotometric determinations with the phenol–sulfuric acid (Doutre et al., 1978; Martens and Frankenberger, 1990) or anthrone–sulfuric acid (Grandy et al., 2000) are used to estimate the total amount of sugars. The HPLC and GC allow further detailed quality and quantity identification of sugars (Basler and Dyckmans, 2013) to clarify their sources and fates in soil.

4.2. Sugar amounts and composition in soil

4.2.1. Total sugars

According to the first database, sugar C content increases linearly with SOM content (Fig. 2, top). Previous reviews based on a much smaller database found linear or quadratic relationships between the sugar C and SOM contents in uncultivated soils (Folsom et al., 1974). The regression line (Fig. 2, top) clearly shows that sugars in their original structure (not the C metabolized by microorganisms to other substances) contribute 10 ± 5% to SOM. This portion is similar for all soils with a clay content exceeding 15%. Our large dataset, however, revealed that the portion of sugar C in sandy soils is less and accounts for only about 7% of SOM (Fig. 2, bottom left). Similar trends were obtained for the non-cellulose sugars (Fig. 1, supplementary).

Grassland and cropland soils have the same portions of total sugar C in SOM, namely 10 ± 5% (Fig. 2, bottom right). Forests soils have a 2.5 times higher contribution of sugar C to SOM ($R^2 = 0.99$). Nonetheless, the number of studies on total sugar content in forest soils is strongly limited and this high contribution should therefore be taken with caution.

Long-term cultivation (~40 years) decreases carbohydrate C content similarly to SOM content (Dalal and Henry, 1988; Dormaar, 1994; Bongiovanni and Lobartini, 2006). Twenty-five years of forest disturbance causes loss of carbohydrates from the organic horizon, whereas sugar stabilization was observed in the upper mineral horizons (Spielvogel et al., 2007).

Thus, the contribution of sugar C to SOM is very stable and amounts to about 10 ± 5%. Consequently, all land use changes and management practices affecting total SOM content have similar effects on the sugar content in soil.

4.2.2. Hexoses and pentoses in soil

Hexoses dominate over pentoses in soils (Fig. 3) because: 1) hexoses originate from microorganisms and partly from plants, 2) the synthesis of hexoses by microorganisms is much higher than pentoses. This already reflects the importance of microbial synthesis and recycling of sugars for their composition in soil (see below).

Even though plant litter components are rapidly decomposed, considerable amounts of pentoses are accumulated in SOM (Fig. 3, the inset). Pentose accumulation in soil occurs due to the selective decomposition of plant polymers (Cheshire et al., 1971).

Glucose is the dominant hexose overall and in the non-cellulose sugars (Fig. 4, top). The contents of galactose, mannose and rhamnose are similar, but 1.5–2 times lower than glucose. The fucose content is even 5 times lower than glucose. Arabinose and xylose are the dominant pentoses, with almost equal contents.

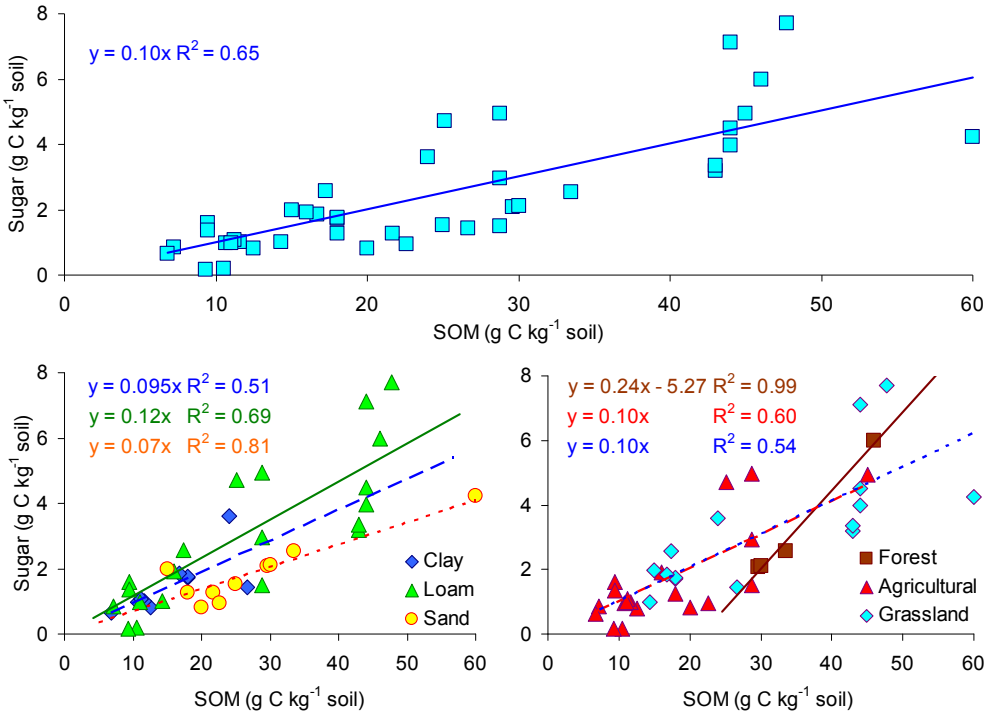

Fig. 2. Total sugar C content depending on: SOM (top), soil texture (bottom left), plant functional types (bottom right). Left and right bottom graphs are created with the same data, but left graph accounts only soil textures and right graph accounts only plant functional types. All regression lines are significant at least by $p < 0.05$. Because the intercepts in the most regression lines were not significantly different from 0, the intercept were fixed as 0 (except for forest). (See references in Supplementary).

1.5 times more glucose, rhamnose, ribose and fucose are obtained from the soil by total sugar extraction versus extraction of non-cellulose sugars (Fig. 4, top). In general, the amount of pentoses is comparable with the amount of all hexoses except glucose. The highest amount of glucose compared to other sugars is explained by its diverse origins: i) from the decomposed cellulose of plant residues, ii) released by living roots, and iii) synthesized by microorganisms. The same sugars are dominated in the hot-water extracts, but the content is 10–20 times lower than in total sugars. Cold-water extracts 10 times less sugars than hot water without any preference for distinct sugars (Fig. 4, bottom).

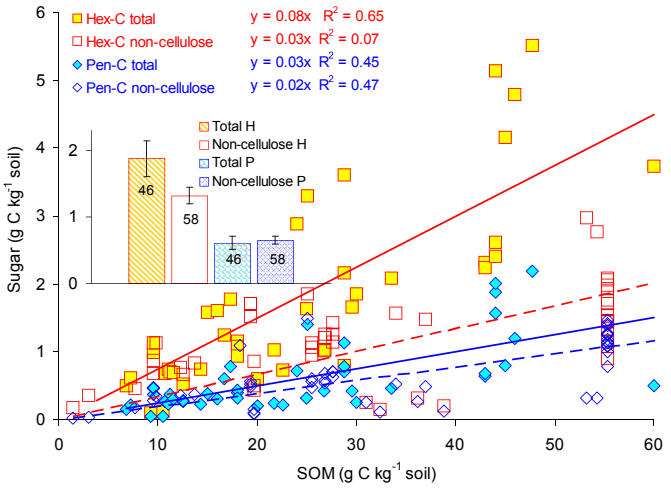

Fig. 3. Cellulose and non-cellulose hexoses (Hex) and pentoses (Pen) depending on SOM content. Solid lines reflect significant regressions ($p < 0.05$) (total hexoses and pentoses); dashed lines reflect non-significant trends (non-cellulose hexoses and pentoses). The insert shows the average content of total and non-cellulose hexoses (H) and pentoses (P) in soils. The numbers on the columns represent the number of individual values for the average. Hexoses were calculated as a sum of glucose, galactose, mannose, rhamnose and fucose. Pentoses were calculated as a sum ribose, arabinose and xylose (See references in Supplementary).

4.2.3. Plant and microbial origin of sugars in soil

The mixing of various sugar sources in soil makes it difficult to determine whether their origin is from plants or from microorganisms. Microorganisms synthesize mainly hexoses (glucose, mannose, galactose) (Oades, 1984). Pentoses, especially arabinose and xylose, are not synthesized by microorganisms in relevant amounts (except by the low-temperature yeasts) and are present mostly in plant residues (Cheshire et al., 1990). Therefore, the ratio GM/AX is used to identify the origin of carbohydrates in soil. The GM/AX ratio for non-cellulose sugars in soil varies from 0.5 to 2, whereas values <0.5 are common for plant polysaccharides, and >2 is typical for microbial polysaccharides (Oades, 1984). This ratio showed that hot-water extractable sugars mainly originate from microorganisms (Haynes and Francis, 1993), whereas NaOH-extractable sugars are from plant litter (Ball et al., 1996).

Evaluation of the first database showed the lowest GM/AX ratio (calculated for non-cellulose sugars) in soils under grasses and the highest under trees (Fig. 5). This ratio for the green leaves of trees ranges from 0.5 to 1.4, and consist 0.09 and 0.5 for grasses and crops, respectively (Fig. 5). Thus, the high GM/AX ratio in forest soils is not due to a high contribution of sugars of microbial origin as supposed earlier, but reflects the high hexose content in the tree litter (mainly mannans). In contrast, the low ratio points to a higher input of microbial than plant residues to sugar accumulation in soils under crops and grasses. Nonetheless, a high portion of galactose in some crops and grasses (corn and bromegrass) have been reported (Angers and Mehuys, 1990). This can also lead to overestimation of the microbial sugars within the SOM. To overcome these uncertainties, the mannose/arabinose + xylose (Angers and Mehuys,

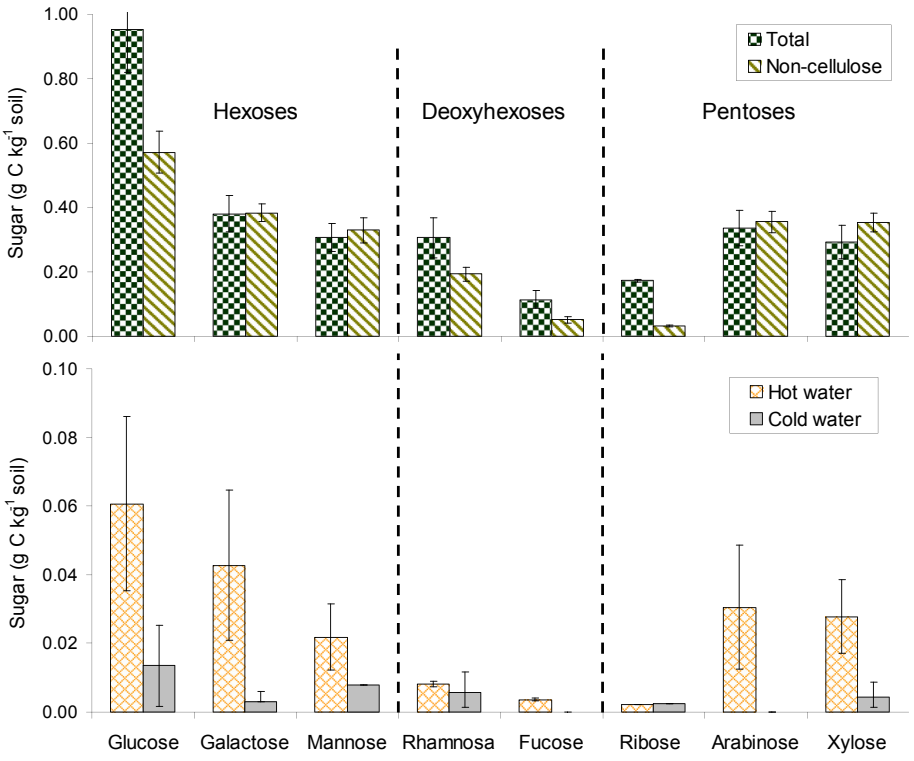

Fig. 4. Content of total and non-cellulose hexoses and pentoses in soils (top) and in hot and cold water extracts (bottom). Mean ± SE. (See references in Supplementary).

1990), mannose/xylose (Hu et al., 1995), glucose/mannose (Benzingpurdie, 1980), rhamnose + fucose/arabinose + xylose (Spielvogel et al., 2007) ratios have been used to estimate the origin of soil sugars. We conclude that there is no universal ratio allowing correct determination the origin of soil sugars. The highest uncertainties occur due to high amounts of hexoses in plant residues, potentially overestimating the contribution of microbial residues calculated based on the GM/AX ratio. On average, specific GM/AX ratios for various vegetation types vary between 0.09 and 1.4. Thus, drawing a correct conclusion about the contribution of plant and MB residues to the origin of soil sugars requires first determining the GM/AX ratio for residues of local plant species.

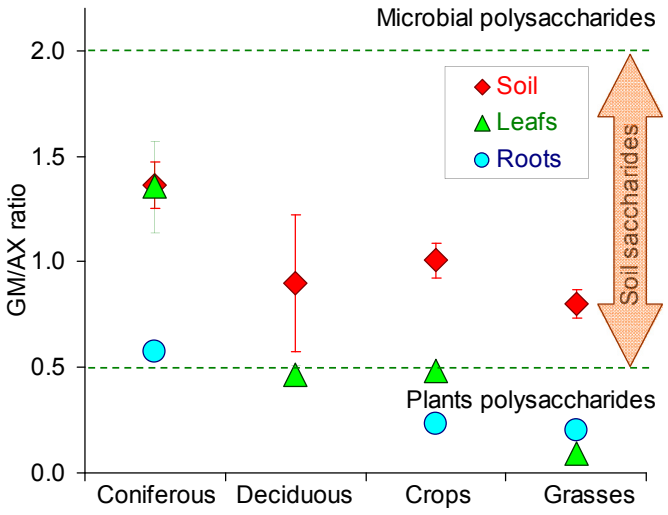

Fig. 5. The ratios of galactose + mannose/arabinose + xylose (GM/AX) in microbial and plant polysaccharides and in non-cellulose sugars in soils developed under coniferous and deciduous trees, crops and grasses. The GM/AX ratios of 0.5 for plant and 2.0 for microbial polysaccharides (dashed lines) were taken from Oades (1984) (See references in Supplementary).

5. Fate of sugars in soil

Similarly to all other substances, carbohydrates undergo various processes in soil (Fig. 6) including: 1) sorption by various soil components (organic matter, clay particles, sesquioxides), 2) leaching within DOM to deeper soil horizons, 3) uptake by plants, and 4) uptake and transformation by microorganisms including incorporation into metabolites and mineralization to CO_2. We begin by briefly describing the abiotic processes (1 + 2) and biotic processes (3 + 4).

5.1. Abiotic processes

5.1.1. Sorption of carbohydrates on mineral and organic surfaces

Firstly, the sorption of substances on mineral and organic particles is strongly connected with the surface charge or ability to form hydrophobic ligand interactions. Polysaccharides have neither surface charges nor hydrophobic groups and, therefore, their sorption is of minor importance. Similar to polysaccharides, monosaccharides have no charge and are neither zwitterions nor polar substances. Moreover, there are no significant functional groups by which sugars can be absorbed on the mineral surfaces. Only weak hydrogen bonds have been reported between glucose and goethite surface (Olsson et al., 2011).

Secondly, there is strong competition between sorption and microbial uptake (Fischer et al., 2010): the physicochemical sorption of glucose from the solution on the mineral soil surfaces reaches quasi-equilibrium within 400 min, with only about 7–10% in the sorbed form. In contrast, nearly 100% of the glucose is taken up within a few minutes by microorganisms (Fig. 3 in Fischer et al.

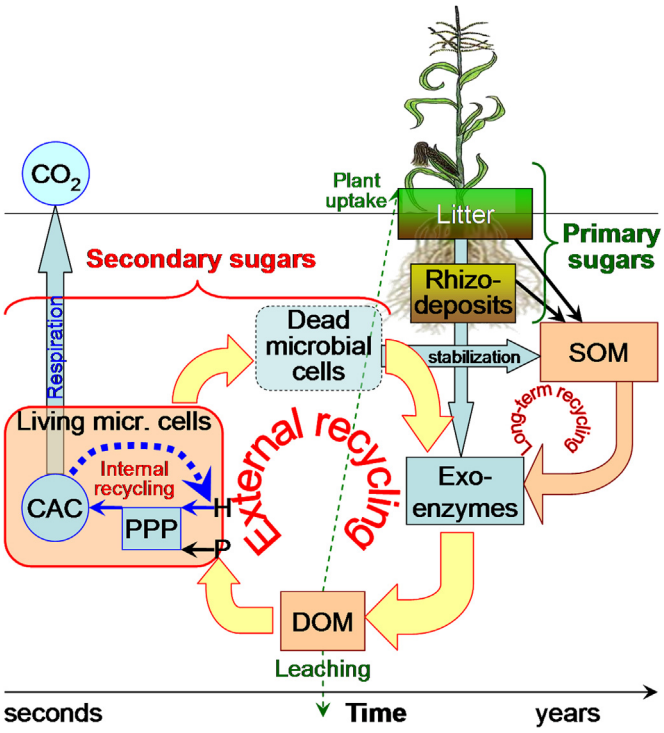

Fig. 6. Fate of sugars in soil. Primary (plant derived) and secondary (microbially derived) inputs of sugars are presented. The importance of three recycling cycles is underlined: internal recycling within microbial cells (in blue, the rates are within seconds to minutes), short-term external recycling (in red, the rates are within weeks to months) and long-term external recycling (in braun, the rates are within months to years and decades). SOM: soil organic matter, DOM: dissolved organic carbon, PPP: pentose phosphate pathway, CAC: citric acid cycle, H: hexoses, P: pentoses. Note that the size of the boxes does not correspond to the amount of sugar C in the pools. However, we tried to reflect the intensity of fluxes by the size of the arrows. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(2010)). We therefore conclude that carbohydrate sorption in soil is a minor of importance for their fate.

5.1.2. Leaching of carbohydrates from soil

Carbohydrates movement within and leaching from the soil profile is possible with DOM. DOM contains mono-, di- and oligosaccharides (Kaiser and Kalbitz, 2012) in total concentrations of 2–3 μM (Fischer et al., 2010). Considering a water flux below the root zone of about 200 mm per year, the carbohydrate losses by leaching amount to about 480 μmol m^{-2}, which is negligible compared to their total input and microbial uptake (see below).

5.2. Biotic processes of carbohydrate utilization

5.2.1. Sugars uptake by plants

Plants are not only the primary source of carbohydrates, but also can take them up (in the form of sugars) from soil solution. Sugar uptake occurs from decomposed litter, microbial residues and SOM as well as reuptake of sugars released by roots in the rhizosphere (Kuzyakov and Jones, 2006).

Up to 50% of the glucose ^{14}C may be taken up by plants from sterile hydroponics (Jones and Darrah, 1992). In contrast, studies under soil conditions showed that less than 1% of ^{14}C from glucose is taken up by roots (Kuzyakov and Jones, 2006; Biernath et al., 2008). Such strong differences between hydroponics and soil conditions reflect the absence of competition between microorganisms and roots for sugar uptake in hydroponics (Kuzyakov and Jones, 2006). In contrast, uptake by microorganisms under soil conditions is very fast and efficient. Accordingly, root uptake declines to a minimum (<1%) (Biernath et al., 2008), which is not relevant for the fate of sugars in soil.

5.2.2. Carbohydrate uptake and utilization by microorganisms

The most microbially available carbohydrates in soil are mono-, di- and oligosaccharides, which originate from polysaccharides after enzymatic hydrolysis (Cheshire, 1979; Blagodatskaya et al., 2014). Besides the intracellular utilization by microorganisms, exoenzymes can split and partly mineralize carbohydrates before the uptake. The hypothesis is that exoenzymes function in soil independently of the microorganisms (Maire et al., 2013). Nonetheless, the specific mechanisms of exoenzyme reactions and especially their persistence and relevance for sugars decomposition still need to be clarified.

The rates of monosaccharide uptake by microorganisms range from seconds to minutes (Jones and Murphy, 2007). This makes microbial uptake by far the dominating process among all other processes determining the fate of sugars in soils. Microbial utilization of sugars includes three stages: 1) uptake, decomposition of initial substance and mineralization the part of it to CO_2, 2) incorporation of C into anabolism products and recycling within the living MB, and 3) reuse of C from the components of microbial residues (Fig. 6). The most rapid stage is the first one (seconds to minutes) (Fig. 7), whereas the slowest is mineralization of microbial residues (from months to years, Fig. 8). Based on the 2nd database, we reviewed these three stages of sugar utilization and calculated MRT of sugar C for each stage. Most of the estimations below reflect process rates with glucose because only very few studies are available about other sugars.

Correct estimation of sugar decomposition rates requires the data on the sugar concentration remaining in soil solution (Coody et al., 1986). Most studies, however, analyzed the $^{14}CO_2$ or $^{13}CO_2$ efflux, but not the remaining sugar in solution. Sugars are taken up very fast by microorganisms (from seconds to minutes) and decomposed immediately. We therefore estimated their mineralization rates using the data on CO_2 emission for the very short time period after substance application. We used data on released $^{14}CO_2$ or $^{13}CO_2$ from added glucose only during the first 24 h (Fig. 7). Such a short period enabled calculating the initial sugar decomposition

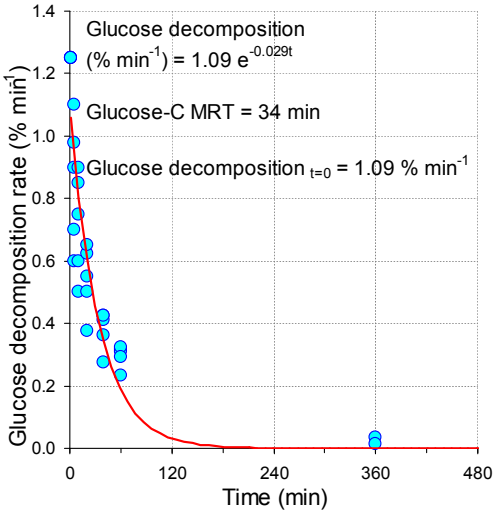

Fig. 7. Rates of glucose mineralization in soil estimated based on $^{14}CO_2$ or $^{13}CO_2$ emission. These rates reflect the original glucose before its incorporation into microbial products (See references in Supplementary).

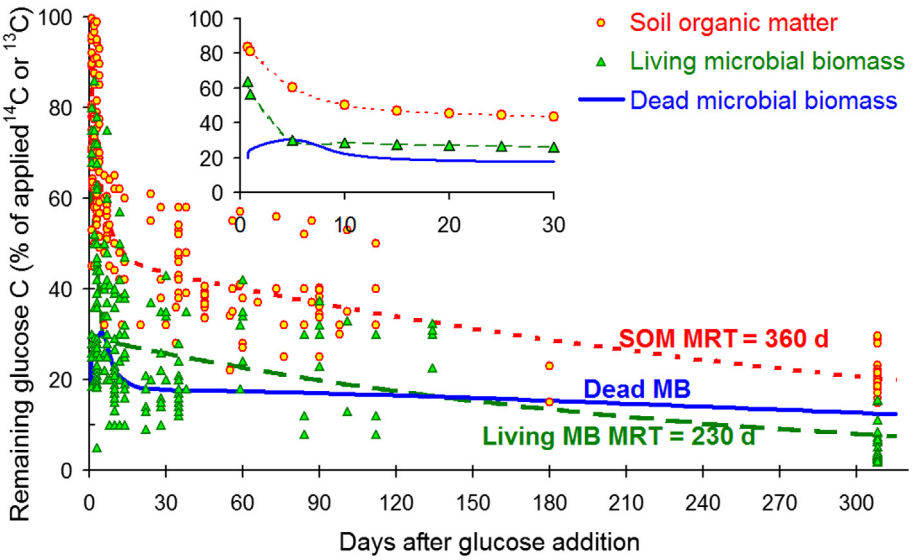

Fig. 8. Dynamics and partitioning of glucose-C for three pools: living microbial biomass, microbial residues and SOM. The experimental points (N = 451) are based on the 2nd database of 32 ^{14}C and ^{13}C labeling studies (See references in Supplementary).

rate and the MRT of sugar C before its incorporation into cell compounds. The estimated maximum glucose C decomposition rate to CO_2 was 1.1% min^{-1} (Fig. 7). At such high rates, half of the glucose C should be mineralized to CO_2 within the first hour. The values in the 2nd database showed that up to 80% of glucose C is still present in soil (not in soil solution) as metabolites after one day. This high percentage shows that the mineralization rate decreases dramatically after C incorporation into microbial cells. Based on Fig. 7 the estimated MRT of glucose C, before C is incorporated into microbial metabolites, is 34 min. This means that the time needed for glucose to pass through the biochemical cycles within the cells is around 30 min. As the glucose in the cell cycles is split into parts, the MRT time of glucose, as a whole molecule, during microbial metabolization is much shorter than 30 min.

5.3. External and internal recycling of sugar C

The assessment of sugar production (Fig. 1) and utilization by microorganisms (Fig. 7) clearly shows the importance of microbial recycling in soil. It is comparatively simple to calculate the primary input of sugars into soil: it corresponds to the total primary production of the ecosystem multiplied by carbohydrate contents in the most important pools (above- and belowground plant biomass, and root exudates). However, it is very challenging to estimate the recycling of sugars because it occurs i) externally (outside of living microbial cells), and ii) internally (within microbial cells) (Fig. 6) and because the recycling cannot be assessed solely by input and output.

The simplest way to assess the external recycling of sugars is to use i) their content in the DOM pool (because only dissolved organics can be taken up and utilized by microorganisms), ii) sugar decomposition rates, and iii) assume a steady state of sugars in the DOM pool over longer periods. For this approach, the DOM can be understood as a main sink for the products of external recycling (Fig. 6). In contrast, we cannot assess the intensity of recycling in microbial cells, but will briefly mention the biochemical pathways of sugars within microorganisms.

5.3.1. Fast external recycling of sugars and budgeting of input

Fast external recycling includes the decomposition of i) carbohydrates from microbial residues and ii) mono- and polysaccharides released by living MB (Fig. 6). Polysaccharides are decomposed by exoenzymes to oligo- and monomers and enter the DOM pool, where they can be further taken up by microorganisms or leached from the soil profile (small portion).

To estimate the total input of sugars into DOM, we assumed that their concentration in DOM is a nearly constant over a vegetation period (steady state conditions). Consequently, we calculated the amounts of annually decomposed sugars based on their content in the DOM pool and decomposition rates (calculated above according to 2nd database, Eq. (1)) using the following equation (Kuzyakov, 2011):

$$Pool_{t+1} = Pool_t + Input - Pool_t \cdot k_{Decomp} \quad (3)$$

where, *Pool* is the pool of sugar C in DOM (mg C kg^{-1} soil), *Input* is the input of sugar C into DOM (mg C kg^{-1} soil min^{-1}), and k_{Decomp} is the decomposition rate of sugar C in DOM (% min^{-1}), and *t* is time. According to the steady state, this decomposed amount corresponds to the input. *k* was taken from the calculated glucose C decomposition rates ($k = 0.03\%\ min^{-1}$, Fig. 7), and sugar content (on the example of glucose C in soil solution) was taken as 22 mg C kg^{-1} soil (Fig. 4).

The total (primary and secondary) input of sugar C into DOM estimated by this approach was 0.0065 mg C kg^{-1} soil min^{-1}. The input for a half year (corresponding to a vegetation period) was 1.7 g kg^{-1} soil (262,800 (min in half of a year) *0.0065)/1000). Sugar C input on 1 ha soil was 5.1 Mg C half $year^{-1}$ ($3*10^6$ (kg soil in 1 ha) *1.7). This input includes sugar C from the primary source (plant biomass) and from the secondary source (microbially recycled sugars).

For the estimation we calculated the possible input of sugar C from deciduous forests (Table 4) (Basilevich, 1993). We calculated the possible input of sugar C from plant biomass (primary source) into the soil considering 1) the annual plant biomass production, 2) the known percentage of cellulose, and 3) assuming that the most sugar C enters the soil as cellulose. To calculate the cellulose portion in the above- and belowground plant biomass, we used the mean values from Fig. 1. The amount of root exudates has been calculated as $^1/_3$ of the root biomass (Kuzyakov and Domanski, 2000); the proportion of sugars in the composition of root exudates has been taken as 50% (Hutsch et al., 2002). Total input of glucose C from

Table 4
Estimated glucose-C input from plants on the example of deciduous forest.

Mg ha^{-1} y^{-1}	Above ground biomass	Below ground biomass	Root exudates
Net primary production[a]	6.1	1.4	0.5
Cellulose	1.8	0.8	n.a.
Glucose-C	0.7	0.3	0.1
Total input of glucose-C from plants (Mg C ha^{-1} y^{-1})			1.1

n.a. – not applicable.
[a] Data were taken from Basilevich (1993).

plant biomass has been calculated as the sum of aboveground and belowground plant biomass and root exudates. The comparison of sugar C input from plants (about 1.1 Mg C ha^{-1} year^{-1}) with the calculated theoretical total input into DOM (~5.1 Mg C) leads us to conclude that $^4/_5$ of sugars in DOM are sugars from the secondary source – living microorganisms and microbial residues. The remaining 20% originate from plant biomass. We expect that portion of secondary sugar C will be even higher in ecosystems with higher temperatures because primary productivity increases with temperature slower than microbial turnover.

The very high portion (~80%) of the secondary sugars in soil strongly contradicts with the classical view on carbon use efficiency (CUE) (Payne, 1970; Lettau and Kuzyakov, 1999). Even if only one step of microbial recycling for sugar C is assumed, the CUE should be about 0.8, but this is nearly two fold higher than CUE values frequently reported for soil (Sinsabaugh et al., 2013). Assuming, that sugar C is recycled in soil more than once (Basler et al., 2015a, 2015b), the CUE should be close to 1.0. The discordance between very high efficiency of C recycling by soil microorganisms (not only of sugars (Hobbie and Hobbie, 2013)) and the frequently reported low CUE values should be clarified in theoretical concepts and justified in experiments.

5.3.2. Internal recycling and biochemical pathways of sugars within microorganisms

Despite the high microbial demand for sugars, C from them is not mineralized to CO_2 completely. Rather, part of the C undergoes intensive internal recycling. Therefore, sugar C is 'stabilized' or actually stored in living MB. To estimate MRT of sugar C within MB, we applied the double exponential model to the data on ^{13}C or ^{14}C glucose incorporation into MB (Eq. (2)). The first exponent was responsible for the fast-utilized C, mainly allocated in the cytoplasm. The MTR of sugar C in MB calculated by *k1* (see Eq. (2)) was 1.25 d. The rate of the second exponent reflects the C incorporated into the stable cell components such as cell walls. MRT of C in that pool calculated by *k2* was 230 d (Fig. 8). Calculated glucose C MRT in MB is in accordance with estimated turnover times of bacterial (120–180 d) and fungal biomass (270 d) in soil (Moore et al., 2005; Rousk and Baath, 2007).

The main pathways of the glucose utilization by soil microorganisms are the pentose phosphate cycle and glycolysis (Embden–Meyerhof–Parnas). The latter is part of the Krebs cycle. These pathways of sugars within the cells are described in detail in microbial biochemistry (Lengeler et al., 1999) and will not be reviewed here. As a result of internal recycling, sugar C can be included into various metabolic products such as other sugars, carboxylic acids or amino acids and can be used to construct cell structural components including cell membranes and cell walls (Gunina et al., 2014; Apostel et al., 2015), or cell polymers like DNA or RNA.

For internal recycling it is important that mainly glucose (hexoses, H in Fig. 6) will be produced within the gluconeogenesis (Apostel et al., 2015). Pentoses will be produced within internal recycling only to a very minor extent. This explains why microbially produced sugars consist nearly entirely of hexoses, and the pentoses (pentoses, P in Fig. 6) originate mainly from plant residues.

5.3.3. Sugar C stabilization in SOM and long-term external recycling

Together with decomposition, sugar C can be stabilized in the SOM pool and further participate in long-term external recycling (Fig. 6). There are two ways to stabilize sugar C in SOM: 1) stabilization within the composition of recalcitrant plant polymers such as cellulose means stabilization of the primary source, and 2) stabilization within the microbial residues means stabilization of the secondary source. Cellulose as well as microbial residues are quite recalcitrant and, thus, C in these sources is preserved in the soil for long periods.

To estimate sugar C stabilization within the composition of recalcitrant plant polymers, we calculated the cellulose decomposition rates in the soil. We used the annual input of glucose with plant cellulose (approximately 1 Mg C ha^{-1} = 300 mg C kg^{-1} soil, see Table 4) and the content of cellulose-derived glucose C in SOM composition (400 mg kg^{-1}, Fig. 4) to calculate the rate of cellulose decomposition in soil. We assumed that the content of cellulose-derived glucose C in SOM (Fig. 4) is nearly constant over a vegetation period. The first-order kinetics was used:

$$Pool_{t+1} = Pool_t + Input - Pool_t \cdot k_{Decompos} \quad (4)$$

where: *Pool* is the pool of cellulose sugar C (mg kg^{-1}) in SOM at time *t* or *t*+1, *Input* is an input of cellulose (mg C kg^{-1} soil) with plant biomass and $k_{Decompos}$ is the decomposition rate of cellulose (day^{-1}).

The calculated decomposition rate of cellulose was 0.002 day^{-1}, and MRT of cellulose was 1.4 y^{-1}. The latter value is in the range of cellulose MRT reported in the literature (Zech et al., 2012; Blagodatskaya et al., 2014).

To estimate the portion of sugar C stabilized in microbial residues (stabilization in secondary source), we subtracted the percentage of sugar ^{13}C or ^{14}C incorporated into living MB from the percentage of sugar ^{13}C or ^{14}C remaining in SOM (Fig. 8). Here, we assumed that sugar C remaining in SOM consists of the sum of that in living MB plus in the composition of microbial residues (because other processes are negligible, see above). The sugar C in microbial residues already peaked on day 5 after glucose addition. It decreased rapidly up to day 15 and the further decrease was very slow (Fig. 8). The initial fast increase of sugar C in microbial residues involves the release of metabolic products from microbial cells into the soil (Cheshire, 1979). The fast depletion of one third of the dead microbial pool reflects further microbial decomposition of metabolites to CO_2 and is ~500 times slower than the initial sugar utilization. The slow decrease of sugar C in the pool of microbial residues reflects the dying MB and thus the slow degradation of sugar C incorporated into cell polymers (long-term external recycling).

Thus, sugar C incorporated into the microbial residues starts to dominate in SOM and determines the long-term MRT of sugar C in soil (Fig. 8). This corroborates the results of long-term experiments that applied ^{14}C-labeled glucose into the soil: three years after glucose addition, 15–20% of ^{14}C were still present in SOM (Cheshire, 1979).

6. Relevance of carbohydrates for soil processes

Carbohydrates play multiple roles in soil. The key ones are: strong contribution to aggregates formation, C sequestration, and maintenance and stimulation of microbial activities and functions.

6.1. Aggregates formation

Carbohydrates are natural glue. They agglutinate mineral and organic particles well and thus promote the formation of water-stable aggregates. The capacity to affect aggregates formation depends on the composition of the carbohydrates: monomers are mainly responsible for the short-term (hours – days) aggregates stabilization, whereas polysaccharides can glue particles together for much longer periods (Jastrow, 1996; Abiven et al., 2009). Plant litter, enriched by carbohydrates, is mainly responsible for macro-aggregates formations, whereas root mucilages also contribute to the formation of microaggregates in the rhizosphere (Oades, 1984; Puget et al., 1999; Carminati and Vetterlein, 2012).

The carbohydrates from plant debris and root mucilages stimulate intensive microbial growth and, as a consequence, accumulation of bacterial and especially fungal mucilages in the rhizosphere and detritusphere; these mucilages serve as additional binding agents. Unlike plant carbohydrates, however, microbially derived polysaccharides bind mainly clay particles and promote the formation of microaggregates <50 μm (Puget et al., 1999). Additionally, the gluing role of glucoproteins (e.g. glomalin-related proteins) released by hyphens and spores of arbuscular mycorrhiza should be underlined (Wright and Upadhyaya, 1996; Wright et al., 1996; Rillig, 2004). Beside proteins, glucoproteins contain up to 85% of sugars, mainly glucose, which are very slowly decomposed in soil (years to decades). These glucoproteins therefore bind the mineral and organic particles to soil aggregates for long periods.

Thus, independent of origin (roots, hyphens, bacteria), carbohydrates affect aggregates formation and are the main structure-forming agents in soils. This is crucial for aeration, water permeability and holding capacity, bulk density, rooting ability, C sequestration, microbial activities, plant nutrition and ultimately soil fertility. As chemical agents, carbohydrates strongly affect the physical and biological properties of soils (Majumder and Kuzyakov, 2010).

6.2. SOM formation

Plant carbohydrates are rapidly decomposed in soil and therefore, do not contribute directly to long-term C stabilization because they are not recalcitrant. Even plant residues encapsulated in fine aggregates (Sollins et al., 1996; von Luetzow et al., 2006) are released fast, due to aggregates turnover (destruction and rebuilding) during few weeks to months (Plante and McGill, 2002), Thus, as shown above, most of the carbohydrates within SOM are of microbial origin.

Carbohydrate C, determined by total hydrolysis, presents on average 10 ± 5% of SOM (Fig. 2) and is a mixture of plant litter, microbial residues and microbial recycling products. Nonetheless, these 10% show only the direct contribution of sugars themselves to SOM. Indirect contribution involves the substances originating from sugar C during microbial metabolism and stabilized later by microbial residues in SOM. Such an indirect contribution of sugar C to SOM is no doubt much higher than the direct one because sugars are used to produce nearly all microbial compounds (Lengeler et al., 1999; Gunina et al., 2014). The other main compound classes such as carboxylic acids, proteins and lipids are much less involved in the synthesis of cell compounds. Consequently, the total contribution of sugar C to SOM is much higher than its directly measures portion.

6.3. Sugars: the main triggers of priming effects in rhizosphere

About 10–30% of assimilated C is released by roots in the rhizosphere. About 50% of this C consists of sugars, and the remaining part is comprised by carboxylic acids, amino acids and phenolic compounds. The ecological relevance of the last three groups is well known: carboxylic acids decrease pH in the rhizosphere as well as complex and chelate metals; amino acids help mobilize Fe, Zn and certain other micronutrients and may play a role as signaling substances; phenolic compounds are important allelopathic agents (Blum, 1998) and signaling compounds. Nonetheless, the role of sugars (comprising about twice the amount of all other compounds released together in the rhizosphere) remains unknown. Clearly, sugars are not merely useless C losses in the rhizosphere. Such inefficient plants would not be competitive during evolution compared to others plants that avoid C losses. None of the identified functions, such as signaling agents or mucilage on root tips – can explain the huge amounts of sugars released by roots.

Sugars are labile organic compounds that are not absorbed by the soil mineral matrix or by SOM after release from roots. Rather, they are taken up by microorganisms within minutes and used very efficiently for both energy and cell compound production. We therefore hypothesize that the main role of sugars released by roots is to maintain interactions with rhizosphere microorganisms and to stimulate their activity. The much higher number and activity of microorganisms in the rhizosphere compared to the root-free soil accelerate SOM decomposition with mineralization of stored nutrients, mainly N, P, S (Spohn and Kuzyakov, 2013). If the ability of roots to solubilize nutrients by carboxylic acids is based solely on chemical processes, then the released sugars contribute to nutrient mobilization by biotic mechanisms: stimulate microbial activity and promote the release of exoenzymes and mineralization of SOM – the phenomenon known as priming effects (Kuzyakov, 2010).

The few studies that compared the priming effects between sugars, amino acids, carboxylic acids and phenols concluded the highest stimulation by amino acids (Hamer and Marschner, 2005). Importantly, however, the amino acid concentrations in the soil and in the rhizosphere are usually one order of magnitude lower than sugars (Kraffczyk et al., 1984; Fischer et al., 2007). Amino acids may also be absorbed by organic and mineral soil compounds. Consequently, sugars should play a greater role in the unspecific stimulation of microorganisms. Therefore, we hypothesize that the main ecological function of the root-released sugars is to maintain high microbial activity in the rhizosphere and to trigger the priming effects (Pausch et al., 2013). The subsequent SOM mineralization provides nutrients not only for microorganisms but also for plants, boosting their development and competitive strength compared to other plants that lack such interactions in the rhizosphere. These hypothesized functions of sugars in soil should be proven in further studies.

From various components of global change, the increasing atmospheric CO_2 concentration and N deposition promote net primary productivity (Johnson and Pregitzer, 2007) and so, increase the carbohydrate input into soil. Additionally, elevated CO_2 increases carbohydrates percentage in plant tissues (Liu et al., 2005). These increase of carbohydrate inputs as well as raising C/N ratios of the plant litter, will decrease its decomposition rates and consequently, prolong the MRT of sugar C in soil. However, raising N deposition may at least partly compensate the effects of elevated CO_2 on MRT of sugar C.

7. Conclusions and relevance

With this review, we close several gaps in our knowledge on the content, composition and fate of carbohydrates in soil. This review compiled and analyzed two databases: the first focused on the content of total, non-cellulose, hot-water and cold-water extractable sugars in soils, as well as on the origin of sugars in soil. The

second database summarized the dynamics of ^{13}C and ^{14}C sugar (mainly glucose) utilization in three pools: mineralized (CO_2), incorporated into living MB and stabilized within the microbial residues. We also estimated primary (from plants) and secondary (from microorganisms) sources of glucose C in soil and calculated their MRT.

Glucose dominated within the cellulose and non-cellulose sugars in soil due to its diverse origins: plant and microbial residues as well as root and microbial excretions. The ratio of hexoses to pentoses of non-cellulose sugars (applied to estimate the origin of sugars) revealed the highest values for forest soil (1.5), whereas for grasses and crops it was 0.7 and 1.0, respectively. The high ratio for forest soils was due to the presence of high amounts of hexoses in forest litter, especially in conifers, and not due to high input of microbial residues. Thus, applying the hexose to pentose ratio to identify sugar origin requires analyzing the chemical composition of plant litter.

Based on the amount of cellulose-derived glucose in soil and the assessed input of cellulose from plant biomass (using deciduous forest as an example), the MRT of cellulose was calculated as 1.4 y^{-1}. Slow decomposition of plant polysaccharides continuously delivers sugars for microorganisms to maintain their metabolism and functions. The maximal initial decomposition rate of glucose, taken up from soil solution, was 1.1% min^{-1}, whereas the MRT of glucose in MB was 34 min^{-1}. Such rapid decomposition of glucose together with fast uptake from soil solution must be compensated by high sugars input. Based on the sugar content in DOM and initial glucose C decomposition rate, the possible input of sugar C into soil solution was calculated as 5 Mg ha^{-1}. The assessed input of total glucose C from plants (example: deciduous forest) was 1 Mg ha^{-1}. Thus, only 1/5 of all available sugars in soil solution is from plant biomass and 4/5 is from recycling processes.

Despite the high microbial demand for sugars, C from sugars is not mineralized to CO_2 completely, but part of it undergoes intensive internal recycling. The calculated MRT of sugar C in living MB was 230 d. This comparatively long MRT of C in MB can be related to i) the intensive recycling of glucose C within the MB pool and ii) its incorporation into cell polymers.

Based on the dynamics of labeled glucose C in SOM and in MB, we assessed the sugar C portion in microbial residues. The distribution of sugar C in microbial residues showed a nearly constant value (18% of applied tracer) during a 300 d period. This reflects the use of sugar C to produce polymer cell compounds that can be stabilized within the SOM. Thus, we conclude that the contribution of sugar C to the soil sugar C pool is higher than the traditionally estimated 10 ± 5% and that its importance for SOM formation is much higher than the actual amount of sugar C in the soil.

Of all processes involving sugars in soil (Fig. 6), microbial uptake and utilization dominate by far, strongly exceeding sorption, leaching and plant uptake. This, combined with the higher input of carbohydrates versus other organic compounds into soil, makes sugars especially important for maintaining soil microorganisms and their activities. Further studies should focus not only on the decomposition of sugars in soil (as done in most previous experiments), but especially on their importance for microbial activities and plant–microbial interactions, where, we hypothesize, sugars play the most significant role compared to other organics released by roots.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2015.07.021.

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