"Reviews and syntheses: The mechanisms underlying carbon storage in soil" *by* Isabelle Basile-Doelsch et al.

Anonymous Referee #1

Received and published: 24 March 2020

Authors present an interesting review of mechanisms underlying carbon storage. I think it is a potentially interesing paper that however still requires considerable changes before I could recommend it for publication in Biogeosciences.

The main shortcomings that I currently see is that I miss appropriate referencing (detailed below)

→ We have provided additional references where needed (see below)

and I find the text somewhat inconsistent, e.g. in that some conclusions are not supported by sufficient parts of main text (more below)

→ We agree with this comment. Therefore, we have rephrased the conclusion

Some parts of text seem to apply only to cropland but from title/abstract/introduction it is not clear whether authors aim at all soils or only cropland or agricultural soil including grasslands.

→ Indeed, many examples refer to cropland soils because they are more documented in the literature. Moreover, most of the potential for a C stock increase is in arable soils because their initial soil C stocks are low. However, the mechanisms that control OM dynamics are largely the same for all soils, whatever the land-use. We believe that this review devoted to generic mechanisms applies to all soils. We thus feel that a title including "agricultural soils" would not be appropriate.

In general, manuscript could benefit from proofreading by a native speaker – I tried to suggest improvements myself but I am not a native speaker either.

→ We truly thank the refere#1 and took all the suggestions into account and had a native English-speaking scientific translator proofread it as well (added in the ackowledgments).

The overall structure is sometimes confusing, linking/aligning different parts of the text needs to be improved. I'd like to suggest that the structure of manuscript would maybe benefit from a section or a group of sections on "outputs" (following the logic of figure 2). this could include erosion as well as mineralization (where related terminology could be discussed maybe more briefly than now), followed by (de)stabilization mechanisms (which influence mineralization rate),

30 → We changed the structure and created an "ouputs" section as proposed (including erosion, DOC outputs and mineralization). However, to be consistent with fig. 2, stabilization mechanisms were not included at the end of the section as proposed by the referee.

this could again be referred to in the section about non-linear processes (Table 1) and factors (Table 2) influencing mineralization/mean residence time.

→ See below

35 In general, I like most Figures and Tables proposed by authors.

→ Thanks!

I struggle a bit with Figure 5 and 6. In Figure 6, I think the text nor the caption does not explain well enough how were these data obtained.

40 → The data come from the database available via the Balesdent et al. 2018 Nature paper : Jérôme Balesdent, Isabelle Basile-Doelsch, Joël Chadoeuf, Sophie Cornu, Delphine Derrien, Zuzana Fekiacova, Christine Hatté, Carbon transfer from atmosphere to deep soil layers over the last 50 years, Nature, 559 599-602, 2018. The paper is cited and all the data are available online.

The caption of figure 6 was rephrased to give more details. We added in the legend of the figure *"(Based on data from a meta-analyse of d13C studies Balesdent et al. (2018))."*

45 Also the figure is a bit overwhelming because it shows differences between grassland, forest and cropland but this aspect is not really leveraged in the main text so I suggest that authors think about what is the main message of this figure and either keep just one land use or discuss the differences more.

→ We agree that this may be confusing. In fact the main objective of this section is to consider soil C dynamics in deep soil layers. For clarification, we have changed the title of the sub-section, which is now:

50 *Renewal rates at the soil profile scale: deep C dynamics*

Authors offer some interesting conclusions but some of them are introduced for the first time in the Conclusions section and they are not well supported by the main text. E.g. in second sentence of Conclusions, authors mention that carbon inputs in croplands are often higher than in grasslands and forests, but main text (2.1.1) contains only discussion of a hypothetical example of C input calculation for a
55 crop of certain yield. Discussion of the range of yields (and inputs) observed in croplands as well as a comparison with C inputs estimated for grasslands and forests is missing. Therefore I would recommend authors to carefully review the whole conclusions section and see if the main text is supporting/explaining well all they are referring to.
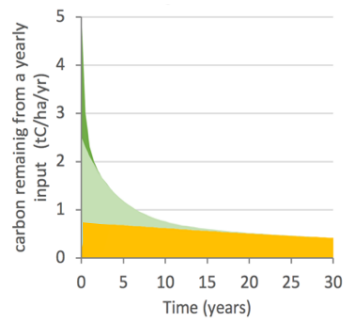
→ We agree with this comment. The conclusion was completely rephrased.

50 I struggle with Figure 5, especially the table part, was the last column calculated as "pool size after 30 years of input fluxes from first column with MRT in second column? Does this representation assume any fluxes between the pools? In the figure why does the slow pool first seem to be lower than 0.75 tC/ha/yr

→ Details have been added in the caption and the error on the graphic changed to 0.75

Figure 5: Left side: Simplified kinetic representation of the fate of plant organic inputs in soil (single
65 *input event, here 5 tC/ha/year). The kinetics is divided into three mineralization phases: fast, intermediate and slow. Organic matter can be divided into three corresponding pools, the size of which is represented in the figure by the colored areas. The sizes of the pools inherited from the inputs at year 0 decreases progressively with their own kinetics over 30 years. Right side: Pool sizes were calculated based on 30 years of yearly inputs (with fluxes between pools). The numerical values are typical of the*
70 *0-30 cm layer of temperate crops. Old carbon represents organic material inherited from a distant past.*

In Table 2, I miss effects of aggregation and erosion

→ In Table 2, we added:

	Water content (except pO$_2$)	↗ Microbial growth and mobility ↘ Sorption ↗ Diffusion and transfer ↗↘ Aggregation ↘↗ Erosion	↘ ↗↘ ↗↘	Yes, all mechanisms combined

75

↗	Mineralogy : - Short range order phases - Al, Fe, Ca complexes	↗ Coprecipitation ↗ Complexation	↗↗ ↗	No No

3

- 2:1 phyllosilicates	↗ Sorption		↗	No
	↘ Transfer		↗	No
	↗ Aggregation		↗	

In main text, I am missing also a part discussing the effect of nutrient availability/stoichiometry on SOM dynamics, maybe this could be discussed in section about chemical nature of OM

→ We agree with referee#1. However, instead of adding this information in the section devoted to the nature of OM, we added it in section 4 (Control of C turnover times in soil: biotic and abiotic factors):

The availability and abundance of N, P and S elements has various and complex effects. Organisms require specific ratios of C, N, S and P (i.e. stoichiometry) to survive and function optimally. For example, degradation of ligno-cellulosic debris (low nitrogen) is temporarily delayed in the absence of mineral nitrogen. Many other C, N and P stoichiometry effects are involved in priming, biotic interactions or carbon use efficiency (CUE) (Monzoni et al. 2012). C:N:P ratios ranging from 72:6:1 (topsoils) to 32:5:1 (pasture) have been reported. Soil vertical stratification C:N:P may, however, be important and impacts on the soil stoichiometry have also been reported following land-use shifts. Regarding the additional amount of nutrients required to store the quantity of carbon targeted by the 4/1000 initiative, it has been suggested N and P can be provided under current fertilization rates by reducing nutrient losses via improved management practices that include cover crops, fertilizer incorporation, etc (Bertrand et al., 2019).

In the introduction, I think authors should try to report on the on-going discussion of soil C sequestration potential in a more balanced way (since authors are not submitting an opinion paper but a review paper), see my suggestions below.

→ We agree with this suggestion. Some parts of the introduction have been rephrased (see below)

INTRODUCTION

→ Reviewer 2 has provided a very positive comment on the introduction ("*I liked the introduction very much and have no issues with it*"). However, reviewer 1 has provided valuable suggestions to improve it. Therefore, the introduction was changed as follows:

Page 1 L32 Add also references to replies from camp number 1: (Minasny et al., 2018; Loisel et al., 2019)

→ Done. We have also added new references (Rumpel et al. 2019; Baveye and White, 2020)

4

L33 please explain what you mean by "most of the criticism is focused on the political opportunity of the initiative" and at the minimum provide references to support this statement so that the author(s) of such criticism are clear

→ One key criticism is that the 4 per 1000 initiative may be misleading for policy makers if it encourages them to delay unpopular decisions needed to transition to renewable forms of energy. We have completed the sentence and added references to make it clearer:

Part of the criticism is focused on the political opportunity of the initiative as it may delay decision making on unpopular initiatives needed for the transition to renewable forms of energy (Baveye et al., 2018b; Baveye and White, 2020), as well as on the calculation itself, which is based on several assumptions, some of which are actually highly debatable (e.g. the soil depth to be considered).

L38-39 this sentence is rather vague and "recent findings are not always considered" and "misuse of the concepts" are strong statements, please support them by reference to paper(s) that expand further how Minasny et al. is guilty of either of those. Also please provide more details or reference to your example "e.g. confusion between soil C equilibrium and soil C saturation" this way it may not be clear what you mean.

→ We agree with this comment. As the second part of the sentence is not really addressed in the paper, we have deleted it. This section was rephrased as follows:

Other comments or questions have been more related to the processes underlying soil C storage: is there an upper limit to C storage in soils? What is the expected residence time of this carbon after its incorporation in soils? Is it possible to store more carbon without additional N and P inputs? Although substantial scientific knowledge exists on soil carbon dynamics, some uncertainty remains on these questions.

L40-L41 "Moreover, current soil C stocks are spatially highly variable, and factors that could ex- plain this variability are not fully understood, although it would be essential to clarify this aspect prior to any attempt to increase soil C stocks." This is a very strong opinion and it should be made clear that this is a point of view of authors or only part of the "critical" part of scientific community. Possibly authors should also voice the opposing "camp" who think that waiting until "we understand it fully" is definitely not required, because they think that the gathered evidence is significant enough to take action. I understand authors wanted to explain why their contribution is needed but the danger of writing introductions in reviews like this in the "we still know too little to take any action" man- ner is that the people outside science read this and interpret this as a consensus of a scientic community

→ We agree that this sentence may be misinterpreted. We have rephrased this section as follows:

Moreover, current soil C stocks are spatially highly variable, and factors that could explain this
35 *variability are not fully understood, although more knowledge in this area would be helpful to design*
soil C storage strategies more efficiently.

L42-43 "Apart from practices based on additional C inputs..." – are all these references related to reduced
tillage? If yes, provide a comparable number of references to first part of sentence about additional C
inputs and also consider to start the sentence in a more balanced way, e.g. "Although consensus exists on
40 practices based on additional C inputs, such as ... (refs), the outcome of other strategies, such as...., is more
unclear. What other strategies other than reduced tillage do you think there is no consensus on, please be
specific. What is described in 2.i (btw. Numbering of paragraphs should be double-checked) is true for
carbon fluxes in agricultural soils, this should be either emphasized in the beginning of the paragraph or
even the title of the paper or the content should be generalized to apply also to other ecosystems...

45 → We agree that the list of references put too much focus on reduced tillage. We have rephrased this
section according to the reviewer's suggestion:

Although there is consensus on practices that ensure additional C inputs in agricultural soils, such as
exogenous organic matter input, moderate intensification of extensive grasslands, limiting residue
exports, growing cover crops, promoting grass cover in vineyards, adopting agroforestry and growing
50 *hedges, etc., the outcomes of other strategies such as reduced tillage and liming are more unclear*
(Dignac et al., 2017).

The Numbering of paragraphs has been checked. The comment about the range of soil land use being
considered was answered above.

55 **PART "MAIN PROCESSES ..."**

58 Lower plants (algae, mosses, lichens), microbial and faunal necromass also contribute to C input

→ The sentence was changed as follows:

"Organic matter entering the soil system is mainly synthesized by higher plants"

59 please define here well what you mean by "restitution", e.g. "surface retention or incorporation through
60 tillage" because the term is later used a lot and is not a common one in biogeosciences

→ Restitution is used for "surface retention" (changed in the text when used). However, in this sentence,
this detail is not essential and we simplified the sentence as follows:

It reaches the soil through the roots (dead roots or root exudates) or in the form of shoot litter and via
unharvested aboveground plant parts.

6

65 60 this sentence is true only for cropland and ecosystems in which you assume constant standing plant biomass

→ We don't really understand this comment.

60 assuming you mean respiration of herbivores, is it better to say something like "losses by herbivory (production and respiration)" instead of "herbivore production and respiration" because this way it's not
70 that clear which respiration you mean

→ We agree. We suggest the following sentence, which also takes the comment of reviewer 2 into account:

The soil carbon input flux is the net primary production of the ecosystem minus the exported crop production, losses from herbivory (production and respiration) and dissolved and particulate organic matter outputs.

Page 3 65 explain what do you mean by "estimators of soil restitution fluxes" would "Soil carbon input can
75 be estimated based on" work too?

→ Yes, that works too and is even better, so we suggest changing the sentence to:

Estimators of soil restitution fluxes are often based on plant carbon allocation equations (allometric relationships) combined with carbon models.

66 the phrasing of the definition of harvest index (HI) is a bit unclear, would this work better? "(HI) is the
80 percentage of aboveground net primary production that is harvested"

→ Yes that works. We suggest changing the sentence to:

The harvest index (HI) is the harvested proportion of net primary production from shoots, while the rest is returned to the soil.

67 please provide reference for these values

85 → We have added a recent reference focusing on the harvest index (Fan et al., 2017 Harvest index-yield relationship for estimating crop residue in cold continental climates)

73 please provide reference for these values, missing bracket, also consider giving values as true ratios (0.1-0.3), in general please revise and be consistent about terms and corresponding values of ratios, proportion

90 → We have added some references (Bolinder et al., 1997 Estimating shoot to root ratios and annual carbon inputs in soils for cereal crops; Poeplau and Katterer, 2017 Is soil texture a major controlling factor of root:shoot ratio in cereals?). The missing bracket was added, and the ratio was expressed as true ratio.

7

76 exsudates should be "exudates", please check throughout the manuscript (also figures and tables)

→ OK corrected

95 92 what do you mean by OM mobilization, priming?

→ Yes. The sentence was rephrased to make it clearer

The latter probably have a greater impact on carbon dynamics through their effects on microorganisms and on organic matter (OM) mobilization by their priming effect than a structural OM source has (Keiluweit et al., 2015).

00 What do 78 please explain the term "net root production" and its relationship with rhizodeposition and belowground net primary production, this formulation implies that rhizodeposition is not part of net root production

→ The sentence was changed as follows:

It is estimated that the rhizodeposition flux represents 20 to 50% of the net root production

05 82 better "aboveground restitution" instead of "soil returns"

→ OK, corrected

83 specify in brackets which assumption you used for calculating the rhizodeposition (to comply with the structure of sentence

→ OK "(31% of root production)" added:

10 *For example, for a cereal producing 8.5 t dry matter (DM)/ha of grain, the aboveground restitution (stems, leaves) can be 7.5 t DM/ha (HI 53%) containing 450 mg/g of carbon, or 3.4 t C/ha. In addition, 1.3 t C/ha of roots (18% of aboveground production) and 0.4 t C/ha/year of rhizodeposition (31% of belowground production) are added.*

86 maybe better "Chemical nature of soil carbon inputs" or "Chemical nature of soil organic matter inputs"

15 → Yes, very good suggestion; "Chemical nature of soil organic matter inputs" preferred

Page 4 87 better "soil" than "ground"

→ OK changed

86-04 this whole section contains only one reference and that is after a sentence that needs the least support by reference

20 → We added the following references in the section : (Kogel-Knabner, 2017) (Guiboileau et al., 2010) (Kallenbach et al., 2016) (Senesi and Plaza, 2007; Larney and Angers, 2012) (Lehmann et al., 2011)

93 maybe better "reallocates"

→ OK changed

95 specify how green manure differs from other plant inputs in terms of chemistry

25 → OK , we propose the sentence:

Green manure derived from fresh cut living tissues differs from other plant inputs in this respect.

95 "same molecules" as what?

→ OK , we propose the sentence:

Microbial products are generally composed of the same molecules as plants products except for celluloses and
30 *lignins.*

99 give examples of non-industrial organic waste products

→ OK, added

 (e.g. poultry or cattle manure, pig slurry, etc.)

99-00 please rephrase, both these sentences carry the same information (that waste products are enriched
35 in microbial products compared to plant matter) but they are connected with contrasting conjunction "while"

→ OK , we propose the sentence:

Non-industrial organic waste products (e.g. poultry or cattle manure, pig slurry, etc.) are composed of
mixtures of plant or microbial molecules or their monomers, while compost and sewage sludge are enriched
40 *with microbial compounds (Senesi and Plaza, 2007; Larney and Angers, 2012).*

01 consider using "In addition to fresh/recently-derived organic matter described above, byproducts of incomplete combustion may also enter the soil, such as"

→ OK changed

01-02 double check phrasing and categorization, this way it seems that pyrolysis products belong to incomplete combustion byproducts, also it is not clear what you mean by mentioning coal mines? If you mean coal entering the soil (which is totally valid) that is not a product of pyrolysis .

→ In geology, OM transformation into coal during diagenesis is controlled by an increase in pressure and temperature. In sedimentary layers, this transformation is carried out in the absence of oxygen. We infer that coal mine wastes can therefore be described as a pyrolysis process. We thus propose the following sentence:

In addition to the fresh/recently-derived organic matter described above, byproducts of incomplete combustion (plant coal from fires, soot from regional or global fallout), biomass pyrolysis products (terra preta, biochar (Lehmann et al., 2011), charcoal production site and coal mine wastes), and plastics may also be present.

03 you may want to mention here the term "geogenic carbon", under this term coal and rock-derived C can be grouped

→ We agree that coal mine waste and black shale are both geogenic C. However, the impacted soil surfaces differ markedly: very local and circumscribed areas in the case of mining waste versus entire regions in the case of black shale. We feel it is important to illustrate both cases.

We propose to change the sentence to:

Moreover, soils may contain geogenic organic carbon, particularly when the parent rocks are organically rich, such as black shale which blackens the soil color.

08 specify whether you mean soil fauna or consider also microbiota associated with large herbi- vore

→ We propose to change the sentence to:

Biochemical reactions that occur during OM decomposition are mainly induced by microorganisms (fungi and bacteria), whether they are soilborne or associated with fauna microbiota (soil fauna and herbivores).

14 whose stability is altered?

→ We did not change the sentence, as it seems to us that it is clear

Digestion alters the chemical structure of OM: (i) by selective digestion of peptide compounds, which alters their stability

19 better "bacteria-feeding" instead of "bacterial"

→ OK changed

10

23 I recommend to use "belonging to" instead of "representing"

→ OK changed

24 I recommend switching the sentence structure of the part about fungi to match that about bacteria,.i.e. dozens of meters of filaments belonging to 1000 fungal species

→ OK changed. The new sentence is:

It is estimated that 1 g of soil can support up to 1 billion bacteria belonging to 1 million species (Gans et al., 2005), and dozens of meters of mycelial filaments belonging to 1000 fungal species (Bardgett et al., 2005; Buee et al., 2009).

Page 5 32 better "produced by" instead of "due to the activity of"

→ OK changed

36 leave out "carried out by", because depolymerization is a type of degradation reaction

→ OK changed

38 better "represent" instead of "form"

→ OK changed

45 better "electron acceptors" instead of "oxidation-reduction reactions"

→ OK changed

46 better "can" instead of "could"

→ OK changed

48-49 revise the logical structure of sentence, unexpected usage of "while" maybe mention more reasons why are the costs higher (transport of enzymes through membrane, loss/dilution of both enzymes and degradation products outside the cell. . .)

→ OK changed. The new sentence is:

The extracellular nature of reactions has several consequences. On the one hand biodegradation has a high energy cost for organisms (e.g. transport of enzymes through cell membrane) and cells have to invest C, N, P and S. While on the other hand some compounds escape from the cells and are diluted in the soil solution or adsorb to other organic or mineral compounds.

11

51 add "with each other" before "to form"

→ OK changed.

Page 6 61 maybe better "taken up from" instead from "in"

→ OK changed.

66 maybe better "rate" than "performance"

→ OK changed.

60-67 can you provide some reference?

→ We added : Cotrufo et al. 2013, The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? Global Change Biology (2013) 19, 988–995, doi: 10.1111/gcb.12113

68 better "carbon use efficiency" than "efficiency of C use" to match the abbreviation

→ OK changed.

68 better just "is" instead of "can serve to estimate"

→ OK changed.

69 "material" "flux" can be left out, use "to be" instead of "at"

→ OK changed.

70 leave out "flux"

→ OK changed.

78-79 repetition of defining supramolecular structures (with line 51, page 5)

→ OK changed.

81 problematic usage of the word "source" (plants are the original source of the building blocks but these have to undergo microbial transformation), consider using "producers" instead

→ OK changed.

84 there is no section 1.4, check all similar references throughout the manuscript

→ OK changed. (appropriate section is 2.3)

85-89 provide reference(s)

→ The cited reference (Kleber et al. 2015) provides a comprehensive review in the section "1.4 Oxidation Enhances Solubility and Chemical Reactivity of Organic Compounds." We do not think that it is necessary to add more references.

Page 7 91 consider using "which contains" instead of "i.e."

→ OK changed.

In Figure 4, specify that you start off with 2-mm soil,

→ OK , <2 mm added in the legend.

also discuss

→ In the fig 4 caption, we added:

Organic matter makes up less than 10% of soil constituents. The stock of C in a soil is mainly made up of dead organic matter molecules mainly resulting from microorganisms activity.

93 say "fauna" instead of "microfauna" not to exclude mesofauna

→ OK changed.

94 reference to Figure 1 seems irrelevant

→ OK removed.

98 consider acknowledging that humification theory also worked with the contribution of decomposition products to OM pool (similar to progressive decomposition concept)

→ OK changed. The new sentence is:

This mechanism is at odds with the historical "humification" model, proposing the formation of "humic substances" by progressive condensation of plant molecules and their decomposition products into macromolecules.

04 consider leaving out "regarding some organic compounds"

13

→ OK removed.

08-09 2x "its" instead of "their" (OM)

→ OK changed.

09 leftover "Organic matter transfers"

→ OK removed.

11 did you mean "within" instead of "to".

→ OK changed.

Also consider adding a connecting sentence between sentence 1 and 2 to frame the whole section, saying that transfer occurs mainly via pedoturbation or water transport.

→ OK added.

13 consider replacing ". Otherwise bioturbation is" by "(bioturbation). Bioturbation occurs" to clarify that bioturbation is a subcategory of pedoturbation

→ OK changed.

17 the study by Jagercikova et al. 2017 does not support this statement

→ We made mistakes when citing the Jagercikova et al. papers. Appropriate Jagercikova et al. 2014 and 2015 papers are now cited.

19 better "mineral particles" than "minerals"

→ OK changed.

19 provide reference to statement "mix several dozen tonnes/ha/year"

→ We add the following reference: A review of earthworm impact on soil function and ecosystem services February 2013 https://doi-org.insu.bib.cnrs.fr/10.1111/ejss.12025

Page 8 24 "pore" instead of "poral"

→ OK changed

14

70 25 provide reference for the 2 μm cutoff and for this definition of leaching, I thought leaching is the transport of DOM (i.e. lixiviation in your definition which I am not familiar with at all)

→ These terms are used in different manners from one author to another and not that often used ("DOC/DOM fluxes" are more common!). To avoid any confusion, we changed "leaching" to "lessivage" (with a reference) and remove lixiviation.

75 26 I don't think OM co-precipitated with oxy-hydroxides counts as DOM (something is either dissolved or precipitated)

→ Coprecipitates can be smaller than 450 nm (see Tamrat et al. 2018 and 2019). So the C they contain is considered as dissolved OC when measured in a <0.45 μm fraction. But you are right, this is not true dissolved C! To avoid any misunderstanding we changed the sentence to:
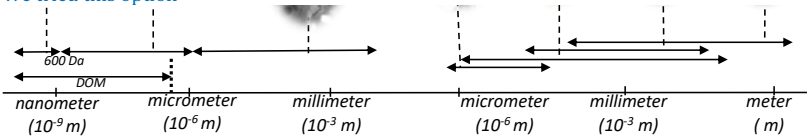
80 *OM of less than 0.45 μm is called "dissolved organic matter" (DOM). This OM is free, but may also include adsorbed on minerals and colloids smaller than 450 nm, co-precipitated with oxy-hydroxides smaller than 450 nm or complexed with metals.*

27-28 consider rephrasing this sentence to fit the whole paragraph better, I think translocation is movement of a particle or colloid or DOM within the soil profile, described is eluviation and is only one 85 type of translocation, again citing Jagercikova et al. here seems irrelevant

→ We removed that sentence which was inherited from a previous version and no longer really useful with regard to DOM

29 in Figure 4, I'd recommend to denote the DOM cutoff

→ We tried this option

600 Da					
DOM					
nanometer	micrometer	millimeter	micrometer	millimeter	meter
$(10^{-9} m)$	$(10^{-6} m)$	$(10^{-3} m)$	$(10^{-6} m)$	$(10^{-3} m)$	(m)

90

In doing so, one interpretation could be that any molecule <0.45 is dissolved in the soil solution. To avoid any confusion, we decided to not take advantage of this suggestion.

34 consider leaving out "depending on the site" and explain how did you obtain the value 0.7 Gt year-1

→ OK, changed. The new sentence (in the new section 2.5.2) is:

15

95 *When integrated on a global scale, C exports via DOC flux have been found to range from 0.002 to 0.05 t of C ha-1year-1 (Doetterl et al., 2016), i.e. 0.7 Gt year-1 (0.05 t of C ha-1year-1 times 15.109 ha).*

35 maybe better "OM transfer along the soil surface: erosion:"

→ OK changed

35 I'd recommend choosing a different intro sentence. Indeed enhanced erosion contributes to soil
00 degradation but this sentence implies that erosion is always a bad thing. This sentence can come later when you discuss that some level of erosion (which is balanced out by pedogenesis/weathering, actually some level of erosion promotes weathering and is a good thing which enables the mineralogy/nutrient availability of soil to be rejuvenated

→ We changed the sentence to:

05 *When no longer counterbalanced by pedogenesis, erosion is the major factor in soil degradation at the decade timescale*

43-45 this sentence feels clumsy, rephrase

→ The sentence was rephrased as follows:

Not considering the contribution of erosion to C flux budgets between soils and the atmosphere is a
10 *major source of error in the interpretation of soil C dynamics model outputs (Chappell et al., 2016).*

47 rephrase, it is not that clear what you mean by "results in C budgets that often generate debate regarding C sinks and sources"

→ The sentence was rephrased as follows:

C transferred laterally by erosion is lost at the pedon scale, but the integration of processes at the
15 *watershed scale (detachment, transport, sedimentation, burial in lowland areas) results in C budgets that often give rise to debate regarding C sinks and sources (Doetterl et al., 2016; Mulder et al., 2015).*

51 leftover "."

→ OK

Page 9 57 better "crystalline" than "crystallized", correct throughout manuscript

20 → OK, changed

16

62 what do you mean by "organic function"? Do you mean functional group?

→ Yes, changed

62 replace "on the" by "for a" and "the active" by "an active"

→ OK, changed

63 not sure what is mean by "localized", would "unevenly" work too?

→ Yes, changed

63 better "in patches" than "by patches"

→ OK, changed

65 better "is" than "leads to"

→ OK, changed

68 it doesn′t seem correct to include chelates in "mineral phases"

→ OK, changed. The new sentences are:

Allophanes, Fe and Al oxyhydroxides are the most commonly described mineral phases. They are often associated with chelates (organic ligands associated with a Fe or Al metal cation) in low pH soils (Rasmussen et al., 2018).

70 maybe better "dissolved" than "destructured"

→ OK, changed

71 better "can also play" instead of "also plays"

→ OK, changed

74 again, not clear what you mean by "organic function"

→ OK, changed

76 "bonds" or "associations" instead of "bounds"

17

→ OK, changed

77-81 given its great importance I think authors should expand this part on saturation concept. This comes out now as "saturation concept works only when we consider adsorption but now we know about other mechanisms so maybe saturation is not a real thing" but actually all organo-mineral associations require a mineral counterpart and the sources of mineral phases suitable for those associations is not infinite in soil so therefore saturation still should apply

→ We agree with the reviewer on the importance of the saturation concept–which is why we quoted it. However, our paper is a review, not an opinion paper. We just want to draw the reader's attention to the fact that this concept is very often used without the mechanisms behind it being clearly explained.

Page 10 3 explain why these models cannot be used at the plot level

→ The sentence was modified as follows:

They operate in short time steps and have been validated for simplified systems, but they cannot be used at the plot level because they require many parameters not available at this scale

8 Maybe better "Soil carbon pool" than "Soil carbon" to fit better with the following sentence

→ OK, changed

10 can you provide reference(s) for this equation

→ OK, Elzein and Balesdent (1995) added

14 here you define "carbon turnover time", then on page 13 section 3.4 you refer to "renewal rates", and on page 13, line 98 you define mean residence time, please unify the terminology/move all terms to when you mention turnover for the first time

→ We agree with this suggestion. Definitions have been detailed based on those provided by Sierra et al. (2016). The new text is:

The system is at equilibrium (as an annual average) if the input and output fluxes are equal. The system is at steady-state if these fluxes are constant (dC/dt = 0 and I = kC). The term "turnover time" (year) commonly refers to the ratio of total carbon stock to the input or output flux (Eriksson, 1971). In steady-state systems, turnover time, mean age, and mean transit time are synonymous terms. The term "residence time" (year) is used to describe the age of the C in the output flux, the age of the C stock or the turnover time. Hence the term is ambiguous. Sierra (2016) discouraged its use in carbon cycle research.

18

Renewal rate describes the quantity of new C that has been stored for a period of time. We added this definition in section 3.4.

Page 11 26 what is "hypercomplex functioning"?

→ We have replaced by "complex functioning" in the new version

27 delete "that"

→ OK, deleted

26-28 these two sentences seems to be duplicates of each other and

→ OK, changed:

Finally, dating methods have confirmed that organic materials can be inherited from a distant past of several decades (Mathieu et al., 2015).

33 I found the whole section a bit out of context here and somehow confusing, I'm not sure about its usefulness, I must say I haven't encountered the term mineralization (flux) too much, usually I think respiration is the prevailing term used, I'm also not sure about interpreting biological activity as "efficiency" and also using the term "efficient" decomposing organisms, with possible confusion with CUE. I agree biological activity is a vague term but I view it more as "how much microbes there are and how active (and growing) they are". How this translates into mineralization flux is a matter of CUE.

44 again, here you talk about k, but call it in several ways, but on page 10 you introduced it as mineralization rate, please unify

→ We agree with these comments and have removed the whole section.

Page 12 55 better just "Non-linear" processes ??

→ Yes, changed

59 here you repeat Equation 1 from section 3.1, can you somehow refer to it to frame it better

→ Ok, we referred to Eq 1

60 what do you mean by "change regimes"?

→ The sentence was changed for clarification

61-72 can you provide more references or is this all based on Vogel et al 2015?

19

→ We added: Nunan et al. 2020 The ecology of heterogeneity: soil bacterial communities and C dynamics

Also Table 1 does not contain any references

→ We added in the text a list of references where non-linear processes have been described (Liyanage et al., 2020; Montagnani et al., 2019; Banegas et al., 2015; McNicol and Silver, 2015; Chen et al., 2013; Wen et al., 2012; Bisigato et al., 2008; Keiluweit et al., 2015)

63 I don't understand how the first implies the second, would "driver" work better instead of "implication"?

→ OK, changed

68 better "help to gain" than "help gain"

→ OK, changed

70 what do you mean by "less determined and reversible changes"

→ This unclear sentence has been removed

73 better just "Priming effect"

→ OK, changed

75 this is confusing since priming studies typically use glucose as the source of labile C to induce priming effect (e,g, Bastida et al. 2019 Nat. Comm) please correct/explain, please also mention we distinguish positive and negative priming effect

→ This was a mistake. The text has been corrected.

Page 13 02 refer to the number of section rather than the name

→ The listed factors are not systematically linked to a section so we cannot refer to the number of section nor remove the name

03 explain how nature of incoming C affects organomineral interactions

→ We referred to section 2.2.3

05 better use "texture" or "particle size distribution"

→ OK, changed

8 better "caused by" than "in relation to"

→ OK, changed

25 8 better "drying-rewetting cycles"

→ OK, changed

Page 14 13 really there are no studies showing accelerated respiration after tillage?

→ We agree that the initial sentence was too affirmative. We moderated the text as follows:

Ploughing is often considered to accelerate biodegradation by aerating the soil, but tillage-induced CO_2
30 *release ends after a few days (Rochette and Angers, 1999)*

14-16 please provide references for all sentences

→ OK added

17 what do you mean by second sentence?

→ The sentence was changed as follows:

35 *Mineral phases interacting with SOM (particularly poorly crystalline minerals) are not always stable (Basile-Doelsch et al., 2015) and can be modified by land use, plants, pH and amendments (Collignon et al., 2011)*

24 refer to the section where you discuss Ca2+ bridges previously

→ OK done

40 24-25 provide references on each statement about Al and Na

→ We have added the following references: (Rasmussen et al., 2018; Heckman et al., 2018). (Qadir and Schubert, 2002).

26 section 2.5.2 doesn't exist

→ Yes, right. The correction was made.

45 26-31 please provide references

→ We have added the following references: Monzoni et al. (2012), Barrios et al. (2007), Daam et al. (2011)

32 mycorrhiza should be mention in this section (actually sentence in line 33 seems to be about mycorrhiza(?), but should also mention bacteria (who also participate in priming)

→ The sentence was changed as follows:

50 *Plants release exudates and feed fungi through symbiotic associations (mycorrhiza) and bacteria from the rhizosphere that biodegrade OM (Fontaine et al., 2011) or even destabilize organomineral associations (Keiluweit et al., 2015), while releasing nitrogen compounds or phosphorus.*

35 give examples of such interactions

→ The sentence was changed as follows:

55 *Many other plant-microorganism interaction mechanisms (e.g. mycorrhizal type or polyphenol concentration) can also exert control over soil C through N competition (Northup et al., 1995; Averill et al., 2014), which allows the ecosystem to maintain a substantial reserve of elements and therefore a high degree of resilience.*

41 maybe "limited" is better than "very confusing"

60 → Sorry, we think that confusing is more appropriate. We changed "very" to "rather"

Page 15 60-61 explain how? This should be expanded on in the main text

→ This has been removed from the conclusion

64 would this work better "predation and competition between fungi and bacteria"?

→ OK changed

65 70 delete "of"

→ OK deleted

74 maybe better "understood" instead of "explained"

→ OK changed

Page 30 65 "dashed" instead of "dotted"

22

Ref

Averill, C., Turner, B. L., and Finzi, A. C.: Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage, Nature, 505, 543-+, 10.1038/nature12901, 2014.

Balesdent, J., Basile-Doelsch, I., Chadoeuf, J., Cornu, S., Derrien, D., Fekiacova, Z., and Hatte, C.: Atmosphere-soil carbon transfer as a function of soil depth, Nature, 10.1038/s41586-018-0328-3, 2018.

Banegas, N., Albanesi, A. S., Pedraza, R. O., and Dos Santos, D. A.: Non-linear dynamics of litter decomposition under different grazing management regimes, Plant and Soil, 393, 47-56, 10.1007/s11104-015-2472-y, 2015.

Bardgett, R. D., Bowman, W. D., Kaufmann, R., and Schmidt, S. K.: A temporal approach to linking aboveground and belowground ecology, Trends in Ecology & Evolution, 20, 634-641, 10.1016/j.tree.2005.08.005, 2005.

Basile-Doelsch, I., Balesdent, J., and Rose, J.: Are Interactions between Organic Compounds and Nanoscale Weathering Minerals the Key Drivers of Carbon Storage in Soils?, Environ. Sci. Technol., 49, 3997-3998, 2015.

Baveye, P. C., Berthelin, J., Tessier, D., and Lemaire, G.: The "4 per 1000" initiative: A credibility issue for the soil science community?, Geoderma, 309, 118-123, https://doi.org/10.1016/j.geoderma.2017.05.005, 2018.

Baveye, P. C., and White, R. E.: The "4p1000" initiative: A new name should be adopted, Ambio, 49, 361-362, 10.1007/s13280-019-01188-9, 2020.

Bertrand, I., Viaud, V., Daufresne, T., Pellerin, S., and Recous, S.: Stoichiometry constraints challenge the potential of agroecological practices for the soil C storage. A review, Agronomy for Sustainable Development, 39, 10.1007/s13593-019-0599-6, 2019.

Bisigato, A. J., Laphitz, R. M. L., and Carrera, A. L.: Non-linear relationships between grazing pressure and conservation of soil resources in Patagonian Monte shrublands, Journal of Arid Environments, 72, 1464-1475, 10.1016/j.jaridenv.2008.02.016, 2008.

Buee, M., De Boer, W., Martin, F., van Overbeek, L., and Jurkevitch, E.: The rhizosphere zoo: An overview of plant-associated communities of microorganisms, including phages, bacteria, archaea, and fungi, and of some of their structuring factors, Plant and Soil, 321, 189-212, 10.1007/s11104-009-9991-3, 2009.

Chen, F. L., Zheng, H., Zhang, K., Ouyang, Z. Y., Wu, Y. F., Shi, Q., and Li, H. L.: Non-linear impacts of Eucalyptus plantation stand age on soil microbial metabolic diversity, Journal of Soils and Sediments, 13, 887-894, 10.1007/s11368-013-0669-3, 2013.

Collignon, C., Uroz, S., Turpault, M. P., and Frey-Klett, P.: Seasons differently impact the structure of mineral weathering bacterial communities in beech and spruce stands, Soil Biology & Biochemistry, 43, 2012-2022, 2011.

Dignac, M. F., Derrien, D., Barre, P., Barot, S., Cecillon, L., Chenu, C., Chevallier, T., Freschet, G. T., Garnier, P., Guenet, B., Hedde, M., Klumpp, K., Lashermes, G., Maron, P. A., Nunan, N., Roumet, C., and Basile-Doelsch, I.: Increasing soil carbon storage: mechanisms, effects of agricultural practices and proxies. A review, Agronomy for Sustainable Development, 37, 10.1007/s13593-017-0421-2, 2017.

Doetterl, S., Berhe, A. A., Nadeu, E., Wang, Z. G., Sommer, M., and Fiener, P.: Erosion, deposition and soil carbon: A review of process-level controls, experimental tools and models to address C cycling in dynamic landscapes, Earth-Science Reviews, 154, 102-122, 10.1016/j.earscirev.2015.12.005, 2016.

Eriksson, E.: Compartment Models and Reservoir Theory, Annual Review of Ecology and Systematics, 2, 67-84, 10.1146/annurev.es.02.110171.000435, 1971.

Fontaine, S., Henault, C., Aamor, A., Bdioui, N., Bloor, J. M. G., Maire, V., Mary, B., Revaillot, S., and Maron, P. A.: Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect, Soil Biology & Biochemistry, 43, 86-96, 10.1016/j.soilbio.2010.09.017, 2011.

Gans, J., Wolinsky, M., and Dunbar, J.: Computational improvements reveal great bacterial diversity and high metal toxicity in soil, Science, 309, 1387-1390, 10.1126/science.1112665, 2005.

Guiboileau, A., Sormani, R., Meyer, C., and Masclaux-Daubresse, C.: Senescence and death of plant organs: Nutrient recycling and developmental regulation, Comptes Rendus Biologies, 333, 382-391, 10.1016/j.crvi.2010.01.016, 2010.

Heckman, K., Lawrence, C. R., and Harden, J. W.: A sequential selective dissolution method to quantify storage and stability of organic carbon associated with Al and Fe hydroxide phases, Geoderma, 312, 24-35, 10.1016/j.geoderma.2017.09.043, 2018.

Kallenbach, C. M., Frey, S. D., and Grandy, A. S.: Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls, Nature Communications, 7, 10.1038/ncomms13630, 2016.

Keiluweit, M., Bougoure, J. J., Nico, P. S., Pett-Ridge, J., Weber, P. K., and Kleber, M.: Mineral protection of soil carbon counteracted by root exudates, Nature Clim. Change, 5, 588-595, 10.1038/nclimate2580
http://www.nature.com/nclimate/journal/v5/n6/abs/nclimate2580.html#supplementary-information, 2015.

Kogel-Knabner, I.: The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter: Fourteen years on, Soil Biology & Biochemistry, 105, A3-A8, 10.1016/j.soilbio.2016.08.011, 2017.

23

Larney, F. J., and Angers, D. A.: The role of organic amendments in soil reclamation: A review, Canadian Journal of Soil Science, 92, 19-38, 10.4141/CJSS2010-064, 2012.

Lehmann, J., Rillig, M. C., Thies, J., Masiello, C. A., Hockaday, W. C., and Crowley, D.: Biochar effects on soil biota - A review, Soil Biology & Biochemistry, 43, 1812-1836, 10.1016/j.soilbio.2011.04.022, 2011.

20   Liyanage, A., Grace, P. R., Scheer, C., de Rosa, D., Ranwala, S., and Rowlings, D. W.: Carbon limits non-linear response of nitrous oxide (N2O) to increasing N inputs in a highly-weathered tropical soil in Sri Lanka, Agriculture Ecosystems & Environment, 292, 10.1016/j.agee.2019.106808, 2020.

Mathieu, J., Hatté, C., Balesdent, J., and Parent, E.: Deep soil carbon dynamics are driven more by soil type than by climate: a worldwide meta-analysis of radiocarbon profiles, Global Change Biology, 21, 2015.

McNicol, G., and Silver, W. L.: Non-linear response of carbon dioxide and methane emissions to oxygen availability in a drained histosol, Biogeochemistry, 123, 299-306, 10.1007/s10533-015-0075-6, 2015.

25   Montagnani, L., Badraghi, A., Speak, A. F., Wellstein, C., Borruso, L., Zerbe, S., and Zanotelli, D.: Evidence for a non-linear carbon accumulation pattern along an Alpine glacier retreat chronosequence in Northern Italy, Peerj, 7, 10.7717/peerj.7703, 2019.

Mulder, V. L., Lacoste, M., Martin, M. P., Richer-de-Forges, A., and Arrouays, D.: Understanding large-extent controls of soil organic carbon storage in relation to soil depth and soil-landscape systems, Global Biogeochemical Cycles, 29, 1210-1229, 10.1002/2015GB005178, 2015.

Northup, R. R., Yu, Z. S., Dahlgren, R. A., and Vogt, K. A.: Polyphenol Control of Nitrogen Release from Pine Litter, Nature, 377, 227-229, 10.1038/377227a0, 1995.

30   Qadir, M., and Schubert, S.: Degradation processes and nutrient constraints in sodic soils, Land Degradation & Development, 13, 275-294, 10.1002/ldr.504, 2002.

Rasmussen, C., Heckman, K., Wieder, W. R., Keiluweit, M., Lawrence, C. R., Berhe, A. A., Blankinship, J. C., Crow, S. E., Druhan, J. L., Pries, C. E. H., Marin-Spiotta, E., Plante, A. F., Schadel, C., Schimel, J. P., Sierra, C. A., Thompson, A., and Wagai, R.: Beyond clay: towards an improved set of variables for predicting soil organic matter content, Biogeochemistry, 137, 297-306, 10.1007/s10533-018-0424-3, 2018.

Rochette, P., and Angers, D. A.: Soil surface carbon dioxide fluxes induced by spring, summer, and fall moldboard plowing in a sandy loam, Soil Science Society of America
35   Journal, 63, 621-628, 10.2136/sssaj1999.03615995006300030027x, 1999.

Senesi, N., and Plaza, C.: Role of humification processes in recycling organic wastes of various nature and sources as soil amendments, Clean-Soil Air Water, 35, 26-41, 10.1002/clen.200600018, 2007.

Wen, Y., Su, L. M., Qin, W. C., Fu, L., He, J., and Zhao, Y. H.: Linear and non-linear relationships between soil sorption and hydrophobicity: Model, validation and influencing factors, Chemosphere, 86, 634-640, 10.1016/j.chemosphere.2011.11.001, 2012.

40

24

Anonymous Referee #2

This manuscript is a review on the mechanisms of carbon storage in soils. The aim of the review was to provide a comprehensive, in-depth overview on the scientific knowledge on processes involved in soil C dynamics, how they develop over time and how they are controlled by different biotic and abiotic factors. The authors successfully present the state of the art in these fields. The main part of both the manuscript text and the Conclusions section centers around SOM transformation processes, less emphasis is given on the (long-term) dynamics and on potential implications for soil management.

On the level of headers, the manuscript is generally well organized and addresses all fields related to the stated aims. However, my impression is that in the sections, the flow is sometimes lost and a lot of details are discussed without properly putting them into the large context of the review. This is even true for the Conclusions section. As a result of that, the novelty and the synthesis character of the manuscript are not really obvious. As I think this manuscript can be revised to provide a timely, necessary and relevant review, I would like to ask the authors to highlight the novel insights with respect to the aims mentioned in the introduction more in their revision of the manuscript.

I also noted that the authors give relatively statements and quite detailed information without references at a number of places in the text. The authors thus should thoroughly check if additional referencing is needed.

→ We thank referee#2 for all these comments. We have endeavored to take them into account, adding references, removing unimportant details, highlighting the novel insights as much as possible (by adding *"It is important to highlight the recent insight… " "This leads to the following very important result…"),* as well as appropriate references. The structure has been slightly changed according to the suggestions of referee #1. The conclusion was completely rephrased.

Here are some more detailed comments:

Abstract: The abstracts needs an introductory sentence that should go beyond the statement that recent research improved our knowledge on SOM characteristics and turnover, and a concluding sentence which refers to the aims mentioned. Similar to the whole text, the novelty and synthesis character need to be

stressed more. A more formal issue is the list of bullet points, which I suggest to replace by running text, maybe with (1), (2) etc. to indicate the individual items.

→ According to the above-mentioned suggestions, the abstract has been modified as follows:

Soil organic matter (OM) represents a key C pool for climate regulation but also an essential component for soil functions and services. Scientific research in the 21st century has considerably improved our knowledge of soil organic matter and its dynamics, particularly under the pressure of the global disruption of the carbon cycle. This paper reviews the processes that control C dynamics in soil, the representation of these processes over time, and their dependence on variations in major biotic and abiotic factors. The most recent advanced knowledge gained on soil organic matter includes: (1) Most organic matter is composed of small molecules, derived from living organisms, without transformation via additional abiotic organic polymerization; (2) Microbial compounds are predominant in the long term; (3) Primary belowground production contributes more to organic matter than aboveground inputs; (4) The contribution of less biodegradable compounds to soil organic matter is low in the long term; (5) Two major factors determine the soil organic carbon production 'yield' from the initial substrates: the yield of carbon used by microorganisms and the association with minerals, particularly poorly crystalline minerals, which stabilize microbial compounds; (6) Interactions between plants and microorganisms also regulate carbon residence times, and therefore carbon stocks; (7) Among abiotic and biotic factors that regulate the carbon residence time, only a few are considered in current modelling approaches (i.e. temperature, soil water content, pH, grain size, sometimes C/N interactions); (8) Although most models of soil C dynamics assume that the processes involved are linear, there are now many indications of non-linear soil C dynamics processes linked to soil OM dynamics (e.g. priming). Farming practices therefore affect soil C stocks not only through carbon inputs but also via their effect on microbial and organomineral interactions, yet it has still not been possible to properly identify the main mechanisms involved in C loss (or gain). Greater insight into the mechanisms, their interdependencies, hierarchy and sensitivity to agricultural practices could provide future action levers for C sequestration in soil.

Introduction: I liked the introduction very much and have no issues with it.

→ We thank referee 2 for this comment. The Introduction has nevertheless been changed slightly according to some suggestions of referee#1, but the main structure is unchanged.

Main processes controlling the C stock and its dynamics in soils: This header needs rewording to better represent the content of the subsections which include information on fluxes and litter composition rather than on processes involved.

→ The header has been changed to:

Main processes controlling the C nature, stock and its dynamics in soils

- line 54: The TOC concentrations given here do not match the ones in Figure 1, to which this sentence refers. This is because the examples given in the text include organic layers on forest soils whereas the figure uses a grassland site as an example. I also suggest to use the same units in the text and the figures (either mg/g or g/kg). Although the numbers correctly represent the range of TOC concentrations expected in soil, the authors should include reference(s) for this information.

→ We specified "forest soil", used g/kg in the text and referred to Oades (1988) for TOC concentrations

- line 58: In addition to losses by mineralization to CO2, C might also be exported from soils by leaching as DOM or erosion of POM.

→ This sentence was changed as follows (also considering a suggestion from referee 1):

The soil carbon input flux is the net primary production of the ecosystem minus the exported crop production, losses from herbivory (production and respiration) and dissolved and particulate organic matter outputs.

- lines 64-66: The return of the harvested C in form of manure or sewage sludge is an interesting point. Is there any information or estimate available how much of the total input or of the total harvest this is?

→ Unfortunately we do not have this information

- lines 74-90: This section should be revised for a better structure with respect to total partial fluxes. Maybe simple separation into multiple paragraphs would already solve this problem. I also suggest to resolve some seeming contradictions, such as a higher contribution via roots (line 74) while shoot biomass dominates root biomass (line 77).

→ We separated the section into multiple paragraphs, and changed the first two sentences. The section now reads:

Above- and belowground input fluxes

Estimators of soil restitution fluxes are often based on plant carbon allocation equations (allometric relationships) combined with carbon models. The harvest index (HI) is the harvested proportion of net primary production from shoots, while the rest is returned to the soil. Note, for example, that HI values of 45–55% are commonly obtained for highly productive cereals (Fan et al., 2017). Genetic and agronomic optimization of yields generally increases the HI. It can therefore be said that, for a given crop production, carbon returns to soils increase with primary production, but the restitution/yield ratio decreases as the yield increases.

The belowground to aboveground biomass (root/shoot) proportion is an indicator that is closely dependent on environmental conditions while also being highly variable (0.1-0.3) (Bolinder et al., 1997; Poeplau and Katterer, 2017). However, a very important novel finding on SOM mechanisms is that

27

belowground input flux (much less documented than inputs from leaves and stems), are considered to
contribute more to soil organic matter through dead roots and rhizodeposition (Clemmensen et al.,
2013; Rasse et al., 2005; Katterer et al., 2011). Rhizodeposition represents the contribution of carbon
to the soil by living plants via roots. This may include root renewal, release of cells or tissues
(epidermis, root hairs, cap cells), macromolecules such as mucilage and extracellular enzymes, or small
molecules, i.e. exudates (Nguyen, 2003). Rhizodeposition is a series of processes generally related to
the acquisition of water and nutrients by plants (including P, N, K, Fe and Mg). Carbon transfer from
plants to symbiotic fungi is one of these processes. It is estimated that the rhizodeposition flux
represents 20 to 50% of the net root production (Nguyen, 2003; Jones et al., 2009; Balesdent et al.,
2011). Belowground inputs are still largely unknown, highly variable, and constitute a definite but still
relatively unexplored lever driving carbon storage in soil. The belowground proportion of primary
production is generally greater when the soil conditions are limiting (water, nitrogen, phosphorus,
iron).

For example, for a cereal producing 8.5 t dry matter (DM)/ha of grain, the aboveground restitution
(stems, leaves) can be 7.5 DM/ha (HI 53%) containing 450 mg/g of carbon, or 3.4 t C/ha. In addition,
1.3 t C/ha of roots (18% of aboveground production) and 0.4 t C/ha/year of rhizodeposition (31% of
belowground production) are added. The annual input into the soil is about 5.1 t C/ha/year in this
example. In grassland or fodder systems, a greater proportion of the aboveground parts are exported
or grazed, and belowground inputs account for the majority of the soil inputs.

- line 88: reword to read "The annual input to the soil adds up to 5.1 t C/ha/year in this example." I think it is important to keep in mind that these numbers do not apply to all soils, but that this is an example.

→ OK, "in this example" was added

- line 102: Another important component of microbial input is chitin from fungal cell walls.

→ OK added

- line 103: replace "amino-saccharides" by "amino sugars"

→ OK changed

- lines 105-106: I do not understand why there should be a contrast between "non- industrial organic waste products" and "compost and sewage slugde" which are certainly non-industrial organic waste products. I guess the term "non-industrial organic waste products" needs some explanation or definition.

→ We added examples and references; the new sentence is:

28

Non-industrial organic waste products (e.g. poultry or cattle manure, pig slurry, etc.) are composed of mixtures of plant or microbial molecules or their monomers, while compost and sewage sludge are enriched with microbial compounds (Senesi and Plaza, 2007; Larney and Angers, 2012).

- lines 109-111: This part has to be revised to remove a number of inconsistencies. For example, the list in the brackets "terra preta, biochar, coal mines and charcoal production sites" includes a soil type, organic material and sites. Out of these, only biochar would be a "biomass pyrolysis product". In addition, plastics do not really fit into a list about incomplete combustion products.

- line 110: replace "local organic carbon from rocks" by "organic carbon inherited from rocks"

→ We agree with this comment. Also in light of the comments of referee#1, the whole paragraph has been changed as follows:

In addition to the fresh/recently-derived organic matter described above, byproducts of incomplete combustion (plant coal from fires, soot from regional or global fallout), biomass pyrolysis products (terra preta, biochar (Lehmann et al., 2011), charcoal production site and coal mine wastes), and plastics may also be present. Moreover, soils may contain geogenic organic carbon, particularly when the parent rocks are organically rich, such as black shale which blackens the soil color.

- line 113: What exactly should be "physical and chemical biotransformation protagonists"? Both fauna and microflora are biological protagonists.

→ Yes they are both biological protagonists but do not have the same role in OM biotransformation

- lines 131-132: The partial sentence about the abundance of fungi and their hyphae length has to be reworded.

→ According to referee#1, the sentence was reworded as:

It is estimated that 1 g of soil can support up to 1 billion bacteria belonging to 1 million species (Gans et al., 2005), and dozens of meters of mycelial filaments belonging to 1000 fungal species (Bardgett et al., 2005; Buee et al., 2009).

- line 139: The lower microbial biomass in cultivated soils usually goes along with lower TOC concentrations.

→ OK added in the sentence

- line 150: How would growth (alone) affect substrate/enzyme contact?

→ For example, if a fungus hyphae is growing, it may reach organic compounds that were located too far away before growth and degrade them (via its enzymes).

29

- line 153: Please reword the phase about final electron acceptors and C oxidation, it combines reaction partners and processes in a strange way.

→ According to referee #1, the sentence has been changed to:

Oxidative degradation can occur with other electron acceptors, but with reaction rates that can be 10 times slower (Keiluweit et al., 2017; Klupfel et al., 2014).

- line 158: replace "microorganisms" by "microbial"

→ OK changed

- line 159: The production and release of extracellular enzymes does not only come with energy cost. The cells have to invest carbon and nitrogen (and sulfur), too. Also, as reactions take place outside the cells, extracellular enzyme activity is restricted to reactions which do not require energy input in form of ATP (or similar).

→ OK, we added "cells have to invest C, N and S"

- line 163: Uptake of almost all organic molecules into the cells is an active process. Please replace "adsorbed" by "transported"

→ OK changed

- line 180: This statement needs a reference.

→ According to referee#1, the whole paragraph on CUE has been moved to a new section devoted to outputs (including transfers (erosion and DOC) and mineralization). References have been added.

- line 195: "Many studies" requires a number of references.

→ The sentence has been simplified to:

Compounds of microbial origin (polysaccharides, proteins, etc.) have a longer lifespan in soil than structural compounds in plants (celluloses, lignins, etc.) (Amelung et al., 2008).

- line 199 and Fig. 2: Most depolymerization processes are hydrolytic processes

→ We added this information by changing the sentence:

Oxidative depolymerization reactions are mainly hydrolytic processes. They systematically lead to …

- lines 202-204: SOM carries a number of different functional groups in different chemical environments. Their pKa values cover a much wider range than pH 4-5.

→ Yes, of course. The COOH was just an example. We do not think that the sentence should be changed.

One example is the carboxyl group, which is mainly in the form of COOH at pH below 4 but of COO- at pH above 5.

- line 209: Figure 1 does not inform about the contributions of the different types of plant material mentioned in line 208.

→ Yes, the reference to figure 1 was a mistake

- line 216: "elementary molecules": please reword

→ OK, changed to "smaller"

- line 226: Organo-mineral interactions are determined by both the availability of both the organic matter and the mineral to react with each other.

→ We agree. The sentence was changed (see section 2.3.1)

- line 226: Delete "Organic matter transfers"

→ Mistake, deleted

- sections "OM transfers within the soil profile" and "OM transfers on the soil surface: erosion": These sections seem to be a bit misplaced within the section about transformation processes. The whole section also fails to really link well to the processes of C cycling. I also suggest to replace "transfer" by "transport"

→ This is right. OM transfers within the soil profile section is now the title of section 2.3 (no longer in the biotransformation section). Erosion is now in section 2.5 (Soil carbon outputs) as recommended by referee #1

- line 228: The context suggests "transferred through" or "transferred within"

→ OK changed

- line 237: "10-30 mg/g/day of dry OM": The unit given here is confusing. First, "dry OM" obviously relates to the "g" and should be placed there. Secondly, is it per g plant organic matter or per g earthworm biomass (which would make more sense?)

→ Details have been added:

31

(plant residue or other organisms, equivalent to 10–30 mg of dry OM/g of fresh earthworm biomass/day)

55   - line 240: "hotspots of OM enriched in organic compounds" should be reworded to sound less repetitive.

→ OK changed to:

These biostructures represent hotspots of OM enriched in mucus that contribute to the stability of organomineral aggregates (Coq et al., 2007; Shan et al., 2010) and to C stabilization (Martin et al., 1990).

60   - lines 236-242: How do the different ecological groups of earthworms affect C redistribution?

→ We added a sentence at the end of the paragraph:

However, earthworms are placed into ecological groups, with each group occupying a specific ecological niche and influencing soil aggregation and C turnover differently (Frazão et al., 2019).

65   - line 243: "Water that circulates": Usually water movement in soil is vertical, not circular.

→ Changed to flows

- line 244: I never heard of the differentiation between "leaching" and "lixivation", which I found to simply be the French word for "leaching".

→ According referee #1, we simplified using only DOM

70   - line 246: If OM sorbed to minerals is < 0.45 μm to meet the definition of DOM, the minerals must be very small, rather colloids than particles.

→ Nanoparticles are nano-sized, yet they are still particles!

We added colloids

- lines 249-254: Additional references are required for this section.

75   → We added the Kleber et al. 2015 review in which there is a section devoted to DOM, entitled "Organic Matter in the Aqueous Phase is Small and Mobile"

- line 254: The DOC flux varies quite substantially. Is there more information about controlling factors?

→ We added the following sentence with a reference:

The DOM content thus depends on site-specific soil, climate, and land management conditions, but there is still a sparsity of experimental data on DOM mechanisms and processes in agricultural soils (Gmach et al., 2020)

- line 258: Erosion is just compensated for by pedogenesis only if the soil is in steady state. If this is not the case, soil is degraded or formed.

→ According to referee #1, The erosion section is now in the 2.5 Soil C outputs section.

We agree with referee #2: in the text, we say: *"In undisturbed natural systems, material loss through erosion is generally offset by pedogenesis (Doetterl et al., 2016), …".*

We don't really understand the referee's request here.

- line 263: depleted in what?

→ In C. Added

- lines 264-265: This sentence needs rewording. Also: The effect of neglecting erosion on the C balance depends on spatial scale and how much of the eroded soil ends up in surface waters.

→ According to referee #1, the sentence was reworded as:

Not considering the contribution of erosion to C flux budgets between soils and the atmosphere is a major source of error in the interpretation of soil C dynamics model outputs (Chappell et al., 2016).

- section "Stabilization and destabilization of soil organic matter": Although destabilization is an important aspect for SOM turnover, it is not discussed in this section.

→ This is right; destabilization has been removed from the header

- lines 272-281: The sorption capacity can be simply described by the density of sorption sites and the specific surface area of the minerals.

→ We do not totally agree: for a single mineral, the different sorption sites may have different adsorption coefficients.

33

- lines 275 and 278: "clays": The two definitions could also be reflected by using "clay particle size fraction" and "clay minerals"

→ The use of clay is often confusing because "particle size fraction" and "minerals" are often not specified. This is why we wanted to stress this possible double meaning by using other more rigorous terms which, when used, cannot lead to confusion (<2 μm and phyllosilicates). We added "clay particle size fraction" and "clay minerals":

The smallest minerals, mainly contained in the grain size class of less than 2 µm (clay particle size fraction, classified as "clays" by agronomists), (...)

These include phyllosilicates (clay minerals, classified as "clays" by mineralogists) (...)

- line 285: This statement is only true if sorption and degradation are in direct competition. As soil is a heterogeneous material, there sorption might be dominant in some microhabitats whereas degradation prevails in other places. In addition, spatial separation of enzymes/organisms and substrate may also limit degradation even if the substrate is not sorbed.

→ We agree with the reviewer. However, the idea was just to explain how adsorption leads to OM stabilization. Questions about colocation enzymes/substrate are discussed elsewhere (2.4.2)

- lines 292-293: As chelates are usually soluble, they cannot be considered a mineral phase.

→ We agree. The sentence was modified as follows:

Allophanes, Fe and Al oxyhydroxides are the most commonly described mineral phases. They are often associated with chelates (organic ligands associated with a Fe or Al metal cation) in low pH soils (Rasmussen et al., 2018).

- line 300: In acid soils, Fe and Al are effective complexing ions.

→ Added in the previous sentence

- line 308-309: A simple correlation does not prove causal relationship, and certainly is not appropriate to identify cause and effect.

→ We apologize but this comment is unclear for us and we are not sure of the changes that are being requested.

- lines 318-320: The term "microhabitats" should be introduced in this section. Soil heterogeneity also controls the accessibility of substrates.

34

→ OK, sentences modified to:

The action of decomposers on their organic substrates (see section 2.2.1) takes place in the soil pore network in microhabitats. Since the smallest bacteria are in the micron range, the soil structure and its heterogeneity controls accessibility and biodegradation at the micrometer spatial scale (Juarez et al.,
35 *2013)*

- line 331: Which information can be used for upscaling from the small scale to the plot scale?

→ This issue is the focus of ongoing research.

Time dependent processes: dynamic representations:

40 - line 337-340: In the description of the degradation equation (Equation 1), it should considered that it is not only k which is not fixed, but also inputs are not necessarily constant.

→ OK added.

- line 345: Isotope tracer approaches only rarely can address millennial scale processes.

→ This is true, but it does in some studies (Balesdent et al. 2018; Matthieu et al. 2015). We added
45 *these references at the end of the sentence.*

- Figure 5 is somehow misleading in this context as it only shows the fate of a single input event. It ignores repeated or continuous input and thus carbon accumulation over the years. It also remains unclear if fluxes between pools were considered, and how much of each carbon fraction is transferred between the pools.

50 *→ We agree with the referee that the figure is a simplified representation. We changed the legend to:*

Figure 5: Left side: Simplified kinetic representation of the fate of plant organic inputs in soil (single input event, here 5 tC/ha/year). The kinetics is divided into three mineralization phases: fast, intermediate and slow. Organic matter can be divided into three corresponding pools, the size of which is represented in the figure by the colored areas. The sizes of the pools inherited from the inputs at year
55 *0 decreases progressively with their own kinetics over 30 years. Right side: Pool sizes were calculated based on 30 years of yearly inputs (with fluxes between pools). The numerical values are typical of the 0-30 cm layer of temperate crops. Old carbon represents organic material inherited from a distant past.*

- line 354-356: rephrase to read "Finally, dating methods have shown that, in addition to OM several decades old, organic materials are partly inherited from a distant past (Mathieu et al., 2015)."

→ OK, the modified sentence is:

Finally, dating methods have confirmed that organic materials can be inherited from a distant past of several decades (Mathieu et al., 2015).

- line 366: I do not think that "mineralization" always implies "mineralization rate". It might also be used to describe cumulative mineralization over a given time or, in a slightly different field, the process of organic matter oxidation.

- line 368: replace "reserves" by "stock". One obvious reason for decoupling of miner- alization rate from C stock is the availability of OM for microorganisms as a substrate.

- line 379: Just slowing down plant debris biotransformation would result in accumula- tion of plant residues (e.g. in peat bogs) and slow down microbial C cycling and thus accumulation of microbial necromass. It would thus greatly affect the quality of SOM. The aim must be to optimize the delicate equilibrium between using SOM as a C and nutrient source and protecting SOM in order to remove CO_2 from the atmosphere and to improve soil properties.

- line 380: "equivalent" to what?

→ The four above comments refer to the previous section 3.2 (Ambiguous mineralization and biological activity paradoxes) which has been removed as suggested by referee #1.

- section "linear processes, non-linear processes": I had problems following this classification, in particular because first-order decay is classified as a linear process, while in fact it follows exponential decay kinetics. In addition, most soil C models assume a number of pools with different decay rate constants, and introduce "non-linearity" this way.

→ We do not fully agree with this comment. The definition of linear systems may be found, for example, at: https://en.wikipedia.org/wiki/Linear_system.

- line 393-394: "inputs, microorganisms and OM are not co-located": This statement needs to be rephrased as both inputs and microorganisms are part of OM. The message should be that the microorganisms might not be able to access a potential substrate because of spatial separation.

→ OK; the modified sentences are:

36

A major driver of non-linear behaviors is the fact that OM is not homogeneously distributed, and that plant inputs, microorganisms and dead OM are not co-located. Consequently, microorganisms might not be able to access a potential substrate because of spatial separation (Vogel et al., 2015) (Nunan et al, 2020).

- lines 396-400: This section remains rather general and would profit from some more information on potential mechanisms, feedbacks etc. Some additional references might also help.

- lines 409/410 and 412: There seems to be a contradiction between these two sentences: in lines 409/410, the authors state that the lower level of priming results in longer MRT in subsoil than in topsoil, whereas in line 412, they stress that priming is particularly important in deep soil horizons. This needs to be resolved. This also applies to Table 2, where an increase in decomposable carbon input flux is assigned a negative effect on C storage.

- line 412: I think that the "risk of destabilization of pre-existing OM by carbon inputs" in deep soils is overrated by the authors. Even if it is true that C input to these horizons might result in enhanced degradation of old SOM, the net effect would always be an increase in OM because the priming effect does not completely outweigh the C input.

→ We agree with the above three remarks and propose to modify and expand the section on the priming effect as follows:

A major non-linear effect is the so-called "priming effect" (Fontaine et al., 2007; Kuzyakov et al., 2000; Sallih and Bottner, 1988). In short, the supply of complex decomposable substrates provides competent microorganisms with the energy resources required to biodegrade stabilized OM. Typically, the soil OM residence time is thus shorter in soil zones that receive substantial inputs, such as on the surface, relative to deep horizons. Except in cases of the burial of exogenous OM (which is considered to represent a risk of destabilization of pre-existing OM especially in deep horizons), the rhizosphere is the main soil compartment concerned by priming. The rhizosphere priming effect (RPE) is defined as the stimulation (or suppression) of OM decomposition by live roots and associated rhizosphere organisms as compared to SOM decomposition from rootless soils under the same environmental conditions. Findings of studies conducted in plant growth chambers and glasshouses indicate that the magnitude of the RPE varies widely, ranging from 380% enhancement (positive RPE) to 50% reduction (negative RPE) as compared to basal respiration from root-free soils (Cheng et al. 2013). These RPE levels demonstrate that rhizosphere processes are major drivers of SOM mineralization. Yet the RPE does not necessarily result in an ultimate decline of total OM because the overall input of organic materials from the rhizosphere may compensate for the enhanced mineralization of accessible OM (Cheng et al. 2013). Priming mechanisms may also be linked to complex combined biotic–abiotic mechanisms whereby root exudates promote carbon loss by releasing organic compounds from protective associations with minerals (Keiluweit et al., 2015). Priming effect mechanisms are thus crucial in the dynamics of C, N and P elements and they highlight that carbon storage is not proportional to the inputs.

37

- line 423: As the authors want to stress how much of the C in deep soil horizons is young, I would suggest to reword to "more than 15% in permanent grasslands"

→ Yes. We changed this to "15-20%" to be more rigorous

- lines 424-426: Are the responsed of the subsoil as fast as in topsoil, or does it take some time until the signal arrives at larger depths?

→ In most cases, the subsoil response is posterior to the topsoil response. This is shown by the meta-analysis which calculated that, on average, "Renewal is 7-10 times slower in the 30-100 cm layer than in the 0-30 cm layer (Mathieu et al., 2015; Balesdent et al., 2017; Balesdent et al., 2018)"

Control of C residence times in soil: biotic and abiotic factors

- lines 438-439: Although temperature clearly increases mineralization, it is not clear yet how this is reflected in SOM concentrations, as net primary production and thus litter input to soil also increases with temperature.

→ Yes, this is right. However, we are focusing the discussion on factors controlling the turnover time, as stated in the introduction of this section: ..."*focusing on carbon turnover time variation factors (but variations in stocks also depend on incoming carbon fluxes that are not considered here*"

- line 441: 20-50% water content is rather moist. Assuming about 50% pore space, a 50% volumetric water content would correspond to saturated soil. At this water content I would already expect decreasing aerobic microbial activity.

→ These data come from Sierra (2015): See for example fig 8b and 8d.

- line 442: replace "desiccation-humectation" by "drying-rewetting"

→ OK changed

- line 444: Fermentation is energetically extremely unfavourable for microorganisms. In the absence of oxygen, they therefore tend to use alternative electron acceptors such as nitrate, ferric iron, sulfate rather than relying on fermentation.

→ OK, the sentence has been changed to:

The partial pressure of oxygen. In saturated environments, if the environment becomes anaerobic, microorganisms tend to use alternative electron acceptors such as nitrate, ferric iron and sulfate. The degradation of ligno-cellulosic debris is slowed or even stopped.

- line 448: Increased aeration is certainly one reason why ploughing accelerates biodegradation. Other factors such as making previously physically protected (en- trapped) substrates available also contribute.

→ This sentence has been changed to:

Ploughing is often considered to accelerate biodegradation by aerating the soil, but tillage-induced CO2 release ends after a few days (Rochette and Angers, 1999).

- line 449 - 452: This section needs substantial rewording. I also found the link between the very small scale (2 μm particles) and the national scale difficult to follow.

→ We propose to change this section to:

Grain size is quite closely correlated with carbon stocks. The <2 μm fraction content can lead to a 2-fold carbon stock variation. Fine granulometric fractions are often described as enriched with stable C, with turnover times longer than the average values in soil (Balesdent, 1998). Meta-analyses have shown that the <2 μm fraction contains between 0% and 50% of the C stocks in national soil C inventories (Hassink, 1997) (see section 2.4.1).

- lines 457-463: Microbial activity and community composition is clearly affected by soil pH. This should not be neglected.

→ We added:

The soil pH also seems to control the phylogenetic diversity of microbes (Shen et al., 2013).

- line 479: Most models use a number of pools with different degradation rate constants to describe C dynamics. This might not consider each and every mechanism, but has been found to sufficiently describe the dynamics over sufficiently long times. These models do not claim to identify factors and mechanisms, but to give quantitative estimates.

→ We added this last information and changed the sentence to:

In current operational models, only temperature, soil moisture, grain size and substrate C/N are taken into account. They give quantitative estimates but fail to properly model dynamics.

- lines 491-492: While it is true that crops are bread for maximized plant production, this refers to above ground biomass only, and in particular to grain yield. Belowground biomass might be smaller, but seems to be important as a C input to soil, in particular to subsoils.

→ The conclusion has been fully revised and this part was removed. New conclusion is:

80

Soil OM results from the biotransformation of inputs by plants (mainly underground inputs). In soil, decomposer food-webs and microorganisms are essential for the oxidative degradation and mineralization of organic molecules. The compounds that are not mineralized consists of microbe-derived (main contribution) and plant-derived small organic molecules and form the soil OM. In soil, transfer and association processes with minerals redistribute these organic molecules and/or more or less permanently shield them from the action of microorganisms though aggregation and organo-mineral interaction processes.

85

90

Long-term stabilization (this formulation is now preferred over the previous term 'humification') is therefore not driven by the same forces as short-term degradation rates. Plant and microbial biodiversity, mineralogy, water content, pO_2, soil solution chemistry and pH, N and P availability, as well as soil temperature, thus control the mineralization-stabilization balance. The interdependencies of these factors, their time dependence (short- versus long-term response), their relative importance with respect to the storage (or loss) of C, are often not explained in detail, thus making it difficult to link C stock changes to specific processes and/or factors.

95

C stock predictions are conventionally modelled by linear OM decay dynamics approaches, while only considering a few of these factors (temperature, water content, grain size, pH, sometimes C:N interactions). Very few models account for non-linear processes, such as priming, despite the increasing evidence of their key role in C dynamics.

00

Greater insight into the mechanisms, their interdependencies, hierarchy and sensitivity to agricultural practices could generate future action levers for C sequestration in soil. Due to the time-scale considered, the methods of choice should include retrospective studies or intercomparison of the findings of long-term experiments at specific sites.

05

- Table 2 needs some revision to fill missing information. In addition, this table is merely quantitative, it does not at all reflect shifts in SOM composition/quality. As peat bogs impressively demonstrate, accumulating large amounts of OM does not necessarily result in highly productive soils.

10

→ This table is not quantitative. Missing information has been added.

In our opinion, in terms of factors and mechanisms, this example of peat bogs refers to the line:

↘ O₂ (anaeroby)	↘ Microbial activity	↗	Yes

→ We have, however, added a few lines according the remarks of referee #1:

↗ _____	↗ Microbial growth and mobility		_____

Water content (except pO$_2$)	↘	Sorption	↘	Yes, all mechanisms combined
	↗	Diffusion and transfer		
	↗↘	Aggregation	↗↘	
	↘↗	Erosion	↗↘	

Mineralogy :				
		- Short range order phases		
	↗	Coprecipitation	↗↗	No
↗	- Al, Fe, Ca complexes	Complexation	↗	No
	↗	Sorption	↗	No
	- 2:1 phyllosilicates			
	↘	Transfer	↗	No
	↗	Aggregation	↗	

15 - Fig. 4: I really like this figure as it clearly shows the relative importance of different organic matter fractions and the contribution of different organisms.

→ Thank you!

- Fig. 5: This figure represents the fate of a single input event, this should be mentioned in the caption. It should also be noted that the numbers given in the table are only valid in case of steady state. It did also
20 not become clear to me if the pools are linked, i.e. if the C lost from the fast pool enters the intermediate and then the slow pool, or if each pool is only degraded. As the old C pool has a turnover time, it also needs some input to maintain steady state (0.002 tC/ha/yr).

→ OK. We changed the legend to:

Figure 5: Left side: Simplified kinetic representation of the fate of plant organic inputs in soil (single input
25 *event, here 5 tC/ha/year). The kinetics is divided into three mineralization phases: fast, intermediate and slow. Organic matter can be divided into three corresponding pools, the size of which is represented in the figure by the colored areas. The sizes of the pools inherited from the inputs at year 0 decreases progressively with their own kinetics over 30 years. Right side: Pool sizes were calculated based on 30 years of yearly inputs (with fluxes between pools). The numerical values are typical of the 0-30 cm layer of temperate crops. Old*
30 *carbon represents organic material inherited from a distant past.*

- Fig. 6: Please include some information on the experiment presented here. These are data for a particular soil, they cannot be generalized.

→ These data come from a meta-analysis, and do not pertain to a particular soil. We changed the legend to clearly specify the data source:

35 *Figure 6: Vertical distribution of carbon incorporated by plant matter in the soil in 20 years under average temperate conditions. The data are from the quantification of a recent incorporation of atmosphere-derived*

carbon atoms into whole-soil profiles through a meta-analysis of changes in stable carbon isotope signatures at 112 grassland, forest and cropland sites, across different climatic zones, from 1965 to 2015. The quantity (in 10 cm increments) is expressed as a proportion of the total C incorporated in the first meter of soil. The value is a regression mean estimated from climate and land-use conditions. The error bars represent the 95% confidence interval of the estimate. (Based on data from Balesdent et al. (2018)).

40

45

Reviews and syntheses: The mechanisms underlying carbon storage in soil

Isabelle Basile-Doelsch[1], Jérôme Balesdent[1], Sylvain Pellerin[2]

50 [1] Aix Marseille Univ, CNRS, IRD, INRA, Coll France, CEREGE, Aix-en-Provence, France
[2] INRAE, Bordeaux Sciences Agro, Univ. Bordeaux, 33882, Villenave d'Ornon, France

Correspondence to: Isabelle Basile-Doelsch (basile@cerege.fr)

Abstract. Soil organic matter (OM) represents a key C pool for climate regulation but also an essential
component for soil functions and services. Scientific research in the 21st century has considerably
55 improved our knowledge of soil organic matter and its dynamics, particularly under the pressure of
the global disruption of the carbon cycle. This paper reviews the processes that control C dynamics in
soil, the representation of these processes over time, and their dependence on variations in major
biotic and abiotic factors. The most recent advanced knowledge gained on soil organic matter
includes: (1) Most organic matter is composed of small molecules, derived from living organisms,
60 without transformation via additional abiotic organic polymerization; (2) Microbial compounds are
predominant in the long term; (3) Primary belowground production contributes more to organic
matter than aboveground inputs; (4) The contribution of less biodegradable compounds to soil organic
matter is low in the long term; (5) Two major factors determine the soil organic carbon production
'yield' from the initial substrates: the yield of carbon used by microorganisms and the association with
65 minerals, particularly poorly crystalline minerals, which stabilize microbial compounds; (6) Interactions
between plants and microorganisms also regulate carbon residence times, and therefore carbon
stocks; (7) Among abiotic and biotic factors that regulate the carbon residence time, only a few are
considered in current modelling approaches (i.e. temperature, soil water content, pH, grain size,
sometimes C/N interactions); (8) Although most models of soil C dynamics assume that the processes
70 involved are linear, there are now many indications of non-linear soil C dynamics processes linked to
soil OM dynamics (e.g. priming). Farming practices therefore affect soil C stocks not only through
carbon inputs but also via their effect on microbial and organomineral interactions, yet it has still not
been possible to properly identify the main mechanisms involved in C loss (or gain). Greater insight
into the mechanisms, their interdependencies, hierarchy and sensitivity to agricultural practices could
75 provide future action levers for C sequestration in soil.

Supprimé: key
Supprimé: s in
Supprimé: knowledge are
Supprimé: C
Supprimé: ing
Supprimé: processes
Supprimé: the
Supprimé: without being able
Supprimé: identify
Supprimé: which of
Supprimé: is the main driver of the
Supprimé: of C
Supprimé: represents potential

1 Introduction

Increasing organic carbon stocks in agricultural soils has emerged as an effective means to improve soils and increase plant productivity, delay the rise of atmospheric carbon dioxide and the rate of climate change, while maintaining the quality of downstream ecosystems. The recent spotlight of the climate change issue has considerably renewed scientific interest on soil organic carbon, which is now seen as a main compartment of the global C cycle, thus providing opportunities for mitigation. In this context, the "4 per 1000 initiative: soils for food security and climate" was launched in 2015. Considering that the total amount of organic carbon in soils at the global scale is about 2400 Gt of C, and that anthropogenic CO_2 emissions are about 9.4 Gt C per year, a simple calculation suggests that an annual 4 per 1000 increase in the soil C stock could theoretically offset annual emissions (2400*0.04=9.6) (Minasny et al., 2017). Meanwhile, this initiative has given rise to a scientific controversy (Amundson and Biardeau, 2018, 2019; van Groenigen et al., 2017; de Vries, 2018; Baveye et al., 2018a; VandenBygaart, 2018; White et al., 2018; Minasny et al., 2018; Loisel et al., 2019; Rumpel et al., 2019; Baveye and White, 2020). Part of the criticism is focused on the political opportunity of the initiative as it may delay decision making on unpopular initiatives needed for the transition to renewable forms of energy (Baveye et al., 2018; Baveye and White, 2020), as well as on the calculation itself, which is based on several assumptions, some of which are actually highly debatable (e.g. the soil depth to be considered). Other comments or questions have been more related to the processes underlying soil C storage: is there an upper limit to C storage in soils? What is the expected residence time of this carbon after its incorporation in soils? Is it possible to store more carbon without additional N and P inputs? Although substantial scientific knowledge exists on soil carbon dynamics, some uncertainty remains on these questions. Moreover, current soil C stocks are spatially highly variable, and factors that could explain this variability are not fully understood, although more knowledge in this area would be helpful to design soil C storage strategies more efficiently. Last but not least, questions remain about farming practices which could potentially increase carbon stocks. Although there is consensus on practices that ensure additional C inputs in agricultural soils, such as exogenous organic matter input, moderate intensification of extensive grasslands, limiting residue exports, growing cover crops, promoting grass cover in vineyards, adopting agroforestry and growing hedges, etc., the outcomes of other strategies such as reduced tillage and liming are more unclear (Dignac et al, 2017). The gap between agronomic trials and scientific knowledge on soil C dynamics is partly responsible for this limited understanding of interactions underlying the effects of farming practices on soil C stocks. In order to foster progress in this area and facilitate proper interpretation of experimental results, this paper aims to provide a comprehensive and up-to-date review of processes that control soil C dynamics, a time-course representation of these processes, and their response to variations in major biotic and abiotic factors.

2   Main processes controlling the C nature, stock and dynamics in soils

Soil organic carbon (Figure 1) is distributed vertically with a strong concentration gradient decreasing from surface to depth: from 400 g/kg in organic "O" horizons at the surface of forest soils, nearly 100 g/kg in the first cm of the organomineral horizon, with concentrations averaging less than 5 g/kg at 1 m depth (Oades 1988). This element has a wide range of ages in soil, from a few days to several thousand years old (Figure 1) (Balesdent 2018). The soil carbon stock is the sum of what remains of each past annual input, so it depends on incoming carbon fluxes, biotransformations and the stabilization duration prior to the release of this element from the soil, mainly in the form of CO_2 produced by decomposers' respiration. The main processes that regulate organic matter (OM) dynamics in soils are summarized in Figure 2.

2.1   Carbon inputs into soil: nature and fluxes

Organic matter entering the soil system is mainly synthesized by higher plants. It reaches the soil through the roots (dead roots or root exudates) or in the form of shoot litter and via unharvested aboveground plant parts. The soil carbon input flux is the net primary production of the ecosystem minus the exported crop production, losses from herbivory (production and respiration) and dissolved and particulate organic matter outputs. The harvested primary production is transformed and some of it can subsequently be transferred to other soils as animal effluents (manure and slurry), or effluents and waste products from human activities (sewage sludge, compost from various sources, etc.).

2.1.1   Above- and belowground input fluxes

Estimators of soil restitution fluxes are often based on plant carbon allocation equations (allometric relationships) combined with carbon models. The harvest index (HI) is the harvested proportion of net primary production from shoots, while the rest is returned to the soil. Note, for example, that HI values of 45–55% are commonly obtained for highly productive cereals (Fan et al., 2017). Genetic and agronomic optimization of yields generally increases the HI. It can therefore be said that, for a given crop production, carbon returns to soils increase with primary production, but the restitution/yield ratio decreases as the yield increases.

The belowground to aboveground biomass (root/shoot) proportion is an indicator that is closely dependent on environmental conditions while also being highly variable (0.1-0.3) (Bolinder et al, 1997; Poeplau and Katterer, 2017). However, a very important novel finding on SOM mechanisms is that belowground input flux (much less documented than inputs from leaves and stems), are considered to contribute more to soil organic matter through dead roots and rhizodeposition (Clemmensen et al., 2013; Rasse et al., 2005). Rhizodeposition represents the contribution of carbon to the soil by living plants via roots. This may include root renewal, release of cells or tissues (epidermis, root hairs, cap cells), macromolecules such as mucilage and extracellular enzymes, or small molecules, i.e. exudates (Nguyen, 2003). Rhizodeposition is a series of processes generally related to the acquisition of water

and nutrients by plants (including P, N, K, Fe and Mg). Carbon transfer from plants to symbiotic fungi is one of these processes. It is estimated that the rhizodeposition flux represents 20 to 50% of the net root production (Nguyen, 2003; Jones et al., 2009; Balesdent et al., 2011). Belowground inputs are still largely unknown, highly variable, and constitute a definite but still relatively unexplored lever driving carbon storage in soil. The belowground proportion of primary production is generally greater when the soil conditions are limiting (water, nitrogen, phosphorus, iron).

For example, for a cereal producing 8.5 t dry matter (DM)/ha of grain, the aboveground restitution (stems, leaves) can be 7.5 DM/ha (HI 53%) containing 450 mg/g of carbon, or 3.4 t C/ha. In addition, 1.3 t C/ha of roots (18% of aboveground production) and 0.4 t C/ha/year of rhizodeposition (31% of root production) are added. The annual input into the soil is about 5.1 t C/ha/year in this example. In grassland or fodder systems, a greater proportion of the aboveground parts are exported or grazed, and belowground inputs account for the majority of the soil inputs.

2.1.2 Chemical nature of soil organic matter inputs

The main plant compounds that reach the soil are the plant structural constituents. These primarily include celluloses and hemicelluloses (neutral sugar polymers), then lignins (phenolic compound polymers), pectins (polymers containing charged sugars), proteins (structural or enzymes released by the roots), lipids from waxes, cuticles, bark and root cortexes. Plants also release secondary metabolites. They can be polyphenolic compounds, tannins and a multitude of small molecules constituting root exudates (complex sugars, organic acids) KogelKnaber 2017. The latter probably have a greater impact on carbon dynamics through their effects on microorganisms and on organic matter (OM) mobilization by their priming effect than a structural OM source has (Keiluweit 2015). Dead tissues that reach the soil do not have the same composition as living tissues because the plant reallocates many metabolites and mineral elements during senescence (particularly sugars and nitrogen compounds), while mainly leaving structural compounds Guiboileau et al. 2010. Green manure derived from fresh cut living tissues differs from other plant inputs in this respect. Microbial products are generally composed of the same molecules as plants products except for celluloses and lignins. Compared to plant OM, microbial products are comparatively enriched with other polysaccharides, lipids, proteins, amino-sugars, nucleic acids, chitin and a very diverse range of metabolites Kallenbach et al. 2016.

Soil organic matter is generated from all of these plant or microbial molecules or their monomers (Kelleher and Simpson, 2006). Non-industrial organic waste products (e.g. poultry or cattle manure, pig slurry, etc.) are composed of mixtures of plant or microbial molecules or their monomers, while compost and sewage sludge are enriched with microbial compounds (Senesi et al. 2007; Larney 2012). In addition to the fresh/recently-derived organic matter described above, byproducts of incomplete combustion (plant coal from fires, soot from regional or global fallout), biomass pyrolysis products (*terra preta*, biochar (Lehmann et al. 2011), charcoal production site and coal mine wastes), and plastics may also be present. Moreover, soils may contain geogenic organic carbon, particularly when the parent rocks are organically rich, such as black shale which blackens the soil color.

2.2 Organic matter transformation in soil

2.2.1 Physical and chemical biotransformation protagonists: fauna and microorganisms

Biochemical reactions that occur during OM decomposition are mainly induced by microorganisms (fungi and bacteria), whether they are soilborne or associated with fauna microbiota (soil fauna and herbivores). The essentially mechanical action of soil fauna is often distinguished from the predominant biochemical action of microorganisms. Recent studies have highlighted the close complementarity of all living organisms in the soil with regard to OM transformation.

Macrofauna (earthworms, termites, ants, etc.) act by fragmenting the litter, incorporating it into the soil profile and mixing the soil within the profile by bioturbation (Bohlen et al., 2004). Soil transit through the digestive tract of macrofauna (mainly earthworms) promotes contact between microbes and OM. Digestion alters the chemical structure of OM: (i) by selective digestion of peptide compounds, which alters their stability (Shan et al., 2010), (ii) by biochemical modifications due to alternating extreme pH or redox conditions, or (iii) by physical modification of particles (Brauman, 2000). Many soil fauna groups are thus recognized as stimulating microorganism activity and soil organic matter biodegradation (Vidal et al., 2016; Brown, 1995).

Micro- and meso-fauna (mites, springtails, collembola, tardigrades, protozoa, etc.) mainly form a food web that regulates decomposing microorganisms, e.g. protozoa and bacteria-feeding nematodes tend to decrease the microorganism density (Bonkowski, 2004; Trap et al., 2016).

Microorganisms (fungi and bacteria) are the main drivers of OM chemical biotransformation. They represent the most taxonomically and functionally diverse living component of soil (Torsvik and Ovreas, 2002; Curtis and Sloan, 2005; Hättenschwiler et al., 2018). It is estimated that 1 g of soil can support up to 1 billion bacteria belonging to 1 million species (Gans et al., 2005), and dozens of meters of mycelial filaments belonging to 1000 fungal species (Bardgett et al., 2005; Buee et al., 2009). Microbial biomass is the mass of living microorganisms in soil and generally amounts to a few hundred grams of dry matter per square meter of soil, but most of the microbes are dormant or barely active (Lennon and Jones, 2011). The rhizosphere (soil zone near the roots) concentrates a large proportion of the soil's microbial activity (Nguyen, 2003). A systematic inventory of bacterial biodiversity (species richness) throughout the French national territory yielded an average of 1300 different genera at each sampling site—the richness variance could be explained by pH, grassland, forest and agricultural land use, and the soil texture (Terrat et al., 2017). Microbial biomass is lowest in cultivated soil and goes along with lower C concentration in soil (Horrigue et al., 2016; Dequiedt et al., 2011).

Commenté [dm3]: suggest simply "throughout France"

Commenté [dm4]: this isn't clear, do you mean "and is accompanied by…"?

47

2.2.2 Biotransformation reactions

Biotransformation reactions in soil are chemical reactions catalyzed by enzymes produced by living soil organisms, in particular millions of microorganism species. These are both degradation and synthesis reactions, while uncatalyzed chemical biotransformations are very rare.

The degradation reactions of organic compounds (so-called catabolic reactions) are mainly hydrolytic or oxidative depolymerization (Lehmann and Kleber, 2015). The incoming plant compounds are mainly large molecules (Figure 3). These are cellulose, hemicelluloses, lignin, proteins, etc., all of which represent "substrates". Due to their large size, their depolymerization first takes place outside microbial cells (Burns et al., 2013). Co-location between substrates and microorganisms at the microbial habitat scale is essential for reactions to occur. Substrate/enzyme contact can take place by diffusion and advection of substrates and enzymes, or by microorganism growth and mobility. In addition, local environmental conditions (oxygenation, pH, water content, etc.) at the micrometer spatial scale must be favorable for microorganism activity (Chenu and Stotsky, 2002; Don et al., 2013; Pinheiro et al., 2015). In the particular case of fully or partially oxygen-depleted systems (so-called anaerobic conditions), oxygen cannot play its role as the final electron acceptor that accompanies C oxidation during degradation. Oxidative degradation can occur with other electron acceptors, but with reaction rates that can be 10 times slower (Keiluweit et al., 2017; Klupfel et al., 2014).

The action of extracellular enzymes continues until smaller reaction products (sugars, phenolic compounds, amino acids, lipids) can be transported through the microbial cell membranes. The extracellular nature of reactions has several consequences. On the one hand, biodegradation has a high energy cost for organisms (e.g. transport of enzymes through cell membrane) and cells have to invest C, N, P and S. While on the other hand some compounds escape from the cells and are diluted in the soil solution or adsorb to other organic or mineral compounds. Small molecules resulting from biodegradation can thus aggregate via weak bonds (hydrogen bonds or hydrophobic interactions) with each other to form supramolecular assemblies (Sutton and Sposito, 2005) or with minerals to form organomineral associations (Kleber et al., 2015; Kögel-Knabner et al., 2008).

Small molecular weight organic compounds (organic acids, sugars, amino acids) can be transported into the intracellular environment of microorganisms for further biotransformation. Oxidative degradation can continue until its ultimate stage when the elements are mineralized (CO_2, NH_4^+, H_2O, HPO_4^-, SO_4^{2-}). The entire biodegradation chain is shown in Figure 3.

Unlike oxidative degradation, synthesis of new organic molecules from small organic molecular weight compounds occurs in microorganism cells in so-called anabolic reactions. Inorganic ions taken up from the soil solution (orthophosphate, ammonium) are also involved in the synthesis of new molecules. These new molecules become cellular components or excreted metabolites (e.g. organic acids, polysaccharides, extracellular enzymes) and contribute to the soil OM pool. C incorporated by microorganisms and then re-incorporated into soil OM is repeatedly recycled. It is important to highlight the recent finding that when a molecule is quickly consumed by microorganisms this does not necessarily mean that its C will be rapidly mineralized into CO_2. The chemical stability or resistance to chemical attack of molecules reaching the soil is therefore not correlated with the soil's OM

formation rate. The most biodegradable compounds have high long-term soil organic matter
formation yields (Cortufo et al. 2013).

2.2.3 Nature, properties and size classes of soil organic matter

Soil OM therefore consists of a continuum of organic compounds at different stages of the
biotransformation reactions described above, from particulate organic matter (POM) to the
elementary building blocks of living organisms (simple sugars, phenolic compounds, amino acids,
peptides, fatty acids, organic acids, lipids). The simplest molecules can form random assemblies into
supramolecular structures (Sutton and Sposito, 2005; Kelleher and Simpson, 2006) (Figure 3).
Compounds of microbial origin (polysaccharides, proteins, etc.) have a longer lifespan in soil than
structural compounds in plants (celluloses, lignins, etc.) (Amelung et al. 2008). This insight has led to
the following very important finding: ultimately, microorganisms are the main producers of long-term
stabilized organic compounds (relative to plants) (Derrien et al., 2006; Miltner et al., 2012; Kallenbach
et al., 2016) (see stabilization processes in Section 2.3).
Oxidative depolymerization reactions are mainly hydrolytic processes. They systematically lead to a
reduction in the size of molecules, but also to an increase in their aqueous solubility and in their
chemical reactivity. These properties are key to the behavior of soil solution compounds, particularly
with respect to their ability to form organomineral associations. Some organic compound functions
are also pH dependent. One example is the carboxyl group, which is mainly in the form of COOH at pH
below 4 but of COO- at pH above 5. The reactivity of soil OM is thus highly pH-dependent (Kleber et
al., 2015).
Finally, the average proportions of the different soil OM types and their size ranges are summarized in
Figure 4. From an operational standpoint, C analysis of soil samples is performed on "fine" soil, which
contains sieved to 2 mm, i.e. mainly C from simple and complex biopolymers (~75%), particulate
organic debris (including carbonized debris) (~20%), microorganisms (~2%), fauna (<1%) and the finest
roots (<2%). These proportions are approximate and vary greatly between soils and horizons.

2.2.4 The progressive decomposition model at odds with historical concepts

In the progressive decomposition conceptual model described above, soil OM consists of a range of
organic fragments and microbial products of all sizes at different decomposition stages (Figure 3). This
mechanism is at odds with the historical "humification" model, proposing the formation of "humic
substances" by progressive condensation of plant molecules and their decomposition products into
macromolecules. Moreover, the different classes of humic compounds identified in the past (humic
acids, fulvic acids, humins) do not correspond to molecules that exist *in situ*, but rather to
physicochemical rearrangements of smaller molecules during their extraction (Sutton and Sposito,
2005). These different concepts (humification, humic substances, humic and fuvic acids, humins),
which have been revealed as deficient by modern soil OM characterization methods, should no longer

49

be used by the soil science community (Lehmann and Kleber, 2015), nor showcased in teaching courses.

The selective preservation model has also been invalidated by dating techniques, demonstrating that
65 supposedly recalcitrant molecules are not specifically preserved in soil OM (Gleixner et al., 2001; Dignac et al., 2005; Amelung et al., 2008; Bol et al., 2009). Indeed, soil microbial communities, and implicitly the associated enzymatic repertoire, are able to degrade all types of substrate in almost any soil (Dungait et al., 2012). Soil OM preservation mechanisms are therefore not linked to its chemical recalcitrance but rather to other biological, physicochemical and structural factors (Schmidt et al.,
70 2011), particularly its ability to associate with minerals (see section 2.3.1).

2.3 OM transfers within the soil profile

Organic matter is transferred within the soil profile in particulate, colloidal or dissolved form. Transfer occurs mainly via pedoturbation or water transport.

Pedoturbation refers to the mixing of soil layers by physical processes in certain types of soil (frost,
75 clay swelling-removal and crack filling), but mainly by biological processes (bioturbation). Bioturbation occurs when particulate transport is linked to biological action, i.e. when soil fauna (e.g. earthworms, ants, termites, voles and moles) bury plant residue, gradually mix the soil, or move mineral material to the surface from deep horizons (Lavelle et al., 2016). The mixing process decreases exponentially with depth and becomes negligible below 50 cm over decades Jager 2015. Bioturbation is known to be
80 more prevalent in permanent grasslands and fields under conservation agriculture than in conventional cropfields (Jagercikova et al., 2017) A supprimer .Jagercikova 2014

Earthworms are essential actors in bioturbation as they ingest both organic matter (plant residue or other organisms, equivalent to 10–30 mg of dry OM/g of fresh earthworm biomass/day) and mineral particles (Curry and Schmidt, 2007) and mix several dozen t/ha/year of soil AJOUTER . Earthworms
85 bury these organomineral mixtures in the soil, excrete them along their galleries and, for some species, bring them to the surface as casts (Don et al., 2008). These biostructures represent hotspots of OM enriched in mucus that contribute to the stability of organomineral aggregates (Coq et al., 2007; Shan et al., 2010) and to C stabilization (Martin et al., 1990). It has been shown that the presence of earthworms can increase the C stock in soil by 30% (Zangerle et al., 2011). However,
90 earthworms are placed into ecological groups, with each group occupying a specific ecological niche and influencing soil aggregation and C turnover differently (Frazao et al., 2019).

Water that flows in the soil pore space is also a vector for vertical OM transport in the soil. By definition, this involves the transfer of particles less than 2 µm via leaching (Jagercikova 2014) and of organic matter less than 0.45 µm. OM of less than 0.45 µm is called "dissolved organic matter" (DOM).
95 This OM is free, but may also include adsorbed on minerals and colloids smaller than 450 nm, co-precipitated with oxy-hydroxides smaller than 450 nm or complexed with metals. DOM molecules are generally small (less than 100 kDa, Figure 4 molecules shown on the bottom left), thus facilitating their diffusion. Water draining the upper soil horizons (organic horizons and surface mineral horizons) can have a high DOM content, while water draining the soil at depth generally has a low DOM content.

50

DOM concentrations are also often correlated with the soil texture, with sandy soil solutions often having a higher DOM content than clay soils (under equivalent climatic conditions). There may also be marked seasonal variations in DOM (Kleber et al. 2015). The DOM content thus depends on site-specific soil, climate, and land management conditions, but there is still a sparsity of experimental data on DOM mechanisms and processes in agricultural soils (Gmach et al. 2020).

2.4 Soil organic matter stabilization

2.4.1 Organomineral interactions

Organomineral interactions have become recognized in the last 10 years as a key factor in stabilizing organic matter in soil (Schmidt et al., 2011; Lehmann and Kleber, 2015; Mathieu et al., 2015). Soil minerals account for over 90% of the solid constituents in soil (Figure 4). The smallest minerals, mainly contained in the grain size class of less than 2 µm (clay particle size fraction, classified as "clays" by agronomists), are highly effective in protecting OM. This particle size class includes a wide variety of minerals. Those with the greatest surface reactivity are the most involved in organomineral associations, and those with the highest specific surface area lead to greater quantities of stabilized OM. These include phyllosilicates (clay minerals, classified as "clays" by mineralogists), different forms of metal oxyhydroxides and poorly crystalline aluminosilicates (Basile-Doelsch et al., 2015; Kleber et al., 2015). Regardless of the nature of the minerals, the OM they stabilize is mostly made up of small molecules derived from microbial products (Miltner et al., 2012; Clemmensen et al., 2013; Cotrufo et al., 2015; Lavallee et al., 2018).

These minerals and poorly crystalline phases protect organic compounds from enzymatic degradation through two main mechanisms (Kleber et al., 2015):

(1) Adsorption on the surface of minerals is the first identified process (Kleber et al., 2007). When the adsorption affinity of an organic functional group for a mineral surface is greater than its affinity for an active enzyme site, oxidative degradation through enzymatic reactions cannot take place. Adsorption on mineral surfaces is unevenly. Organic compounds are adsorbed in patches but do not cover the entire surface of the particle (Vogel et al., 2014; Remusat et al., 2012).

(2) Co-precipitation is the formation of secondary mineral phases in the presence of OM. The size of these mineral phases ranges from one to a few dozen nanometers (Tamrat et al., 2018; Eusterhues et al., 2008; Levard et al., 2012; Rasmussen et al., 2018; Mikutta et al., 2006; Kleber et al., 2015; Torn et al., 1997; Tamrat et al., 2019). Allophanes, Fe and Al oxyhydroxides are the most commonly described mineral phases. They are often associated with chelates (organic ligands associated with a Fe or Al metal cation) in low pH soils (Rasmussen et al. 2018). A molecular structure of nano-sized coprecipitates of inorganic oligomers with organic compounds has also been recently proposed (Tamrat et al., 2019). Poorly crystalline mineral phases can also be dissolved by the action of organic ligands secreted by roots. Organic compounds then lose their mineral protection and can be used by microorganisms (Keiluweit et al., 2015).

51

Supprimé: are
Supprimé: too few
Supprimé: involving
Supprimé: tabilization of s
Supprimé: been
Supprimé: during
Supprimé: being
Supprimé: s
Supprimé:
Supprimé: are

A third process, i.e. cationic bridging by di- or trivalent ions, can also play an important role in OM stabilization in some soils. When this involves bridging between a mineral surface and an organic functional group —both negatively charged—it is referred to as "ternary complexation". In high pH and arid soils, cationic bridging with Ca^{2+} ions tends to override other organomineral bonds

60 (Rasmussen et al., 2018; Rowley et al., 2018).

A conceptual representation of carbon stabilization by adsorption alone (above-cited point (1)) on clay minerals has given rise to the saturation concept (Hassink, 1997) whereby mineral surfaces are assumed to accommodate a limited amount of carbon, thus limiting soil carbon storage. However, the concept has yet to be sufficiently validated to be operational (West and Six, 2007) and the mechanism

65 itself has been invalidated by certain observations (Vogel et al., 2014). In view of recent advances in knowledge of organomineral interactions, the saturation concept could now be revisited from a more mechanistic angle.

2.4.2 Soil structure and aggregation

Soil particle aggregation processes affect the OM mineralization rate (Rovira and Greacen, 1957). For

70 example, the residence time of C in microaggregates (< 50 μm) is greater than that in macroaggregates (> 50 μm) (Golchin et al., 1994; Besnard et al., 1996; Six et al., 1998; Balesdent et al., 2000; Six et al., 2002; Chevallier et al., 2004). However, the structural difference between micro- and macro-aggregates may not be the only factor underlying the difference in OM mineralization rate, because: (i) the nature of OM in these two entities may differ, and (ii) the lifespan of the macro- and micro-

75 aggregates, which regulate the OM trapping time, is not the same (Plante et al., 2006). Nevertheless, aggregates, and especially microaggregates, are often used as fractions indicating the "degree" of physical protection of carbon. Conceptual models describe the C dynamics in the different aggregates by considering the formation-destruction cycles of the aggregates, but their parameterization remains complex (Stamati et al., 2013).

80 The action of decomposers on their organic substrates (see section 2.2.1) takes place in the soil pore network in microhabitats. Since the smallest bacteria are in the micron range, the soil structure and its heterogeneity controls accessibility and biodegradation at the micrometer spatial scale (Juarez et al., 2013) and may be related to different microbial communities in these habitats. The rate of mineralization of simple substrates thus partly depends on the size of the pores in which they are

85 located (Killham et al., 1993; Ruamps et al., 2013). The geometry of the mineral particle associations creates microsites (micrometric to nanometric) in which OM is protected from enzymatic action. Within a microsite, regardless of whether or not organic compounds are directly bound to mineral surfaces, oxidative depolymerization (see section 2.2.2) is significantly slowed down by limiting enzyme access and O_2 diffusion (Zimmerman et al., 2004; Chevallier et al., 2010; Keiluweit et al.,

90 2017).

New models include an explicit 2D or 3D description of the pore network based on tomographic images (Monga et al., 2008; Monga et al., 2014; Blair et al., 2007; Falconer et al., 2015; Pajor et al., 2010; Resat et al., 2012; Vogel et al., 2015). They operate in short time steps and have been validated

Supprimé: the

for simplified systems, but they cannot be used at the plot level because they require many parameters which are not available at this scale. On the other hand, they should make it possible to prioritize the C dynamics control variables so as to be able to define soil structure descriptors other than those currently used in plot-scale models.

2.5   Soil carbon outputs

2.5.1   OM transfers out of the soil surface: erosion and DOC losses

When no longer counterbalanced by pedogenesis, erosion is the major factor in soil degradation at the decade timescale. It is mainly related to soil surface runoff and is therefore highly dependent on the climate, topography and land use conditions. Wind erosion can also be significant, especially in arid regions. In undisturbed natural systems, material loss through erosion is generally offset by pedogenesis (Doetterl et al., 2016), whereas agricultural use increases erosion rates by 100-fold by removing natural vegetation and reducing surface OM in litter (Montgomery, 2007). With agricultural expansion, conservation agriculture has been adopted in many parts of the world to reduce soil erosion. The high spatiotemporal variability in soil erosion is thus associated with the land use and management history. Surface horizons have been substantially depleted in C as a result of soil erosion (Lal, 2001). On a global scale, the quantity of soil C exported by lateral erosion is estimated at 0.3–1 Gt C/year. Not considering the contribution of erosion to C flux budgets between soils and the atmosphere is a major source of error in the interpretation of soil C dynamics model outputs (Chappell et al., 2016). C transferred laterally by erosion is lost at the pedon scale, but the integration of processes at the watershed scale (detachment, transport, sedimentation, burial in lowland areas) results in C budgets that often give rise to debate regarding C sinks and sources (Doetterl et al., 2016; Mulder et al., 2015). When integrated on a global scale, C exports via DOC flux have been found to range from 0.002 to 0.05 t of C ha^{-1}year^{-1} (Doetterl et al., 2016), i.e. 0.7 Gt year^{-1} (0.05 t of C ha^{-1}year^{-1} times 15. 10^9 ha).

2.5.2   OM mineralization

Mineralization is the result of the respiration and excretion of the inorganic compounds (CO_2, NH_4^+, H_2O, HPO_4^-, SO_4^{2-}) by organisms. Carbon mineralization is almost exclusively intracellular, despite the fact that extracellular catabolism of glucose has been observed (Kéraval et al., 2016). From a quantitative standpoint on a global scale, soils emit 10 times more CO_2 from autotrophic (roots) and heterotrophic (microorganisms and fauna) respiration than human activities (IPCC 2013). On a microscale, the carbon use efficiency by microorganisms (or CUE) is, for a given substrate, the quantity of microbial C formed in relation to the consumed C. The microbial production is estimated to be 0.3 to 0.4 times the plant material input into the soil (Sinsabaugh et al., 2014). This CUE varies according

Commenté [dm13]: this isn't clear? do you mean "beyond the soil surface", or "not at the soil surface"?

Supprimé: it is

Supprimé: on

Supprimé: of the decade

Supprimé: organic matter

Supprimé: introduced

Supprimé: history of

Supprimé: the

Supprimé: generate

Supprimé: l

Commenté [dm14]: do you mean "…times 15, i.e. 10^9 ha)."?

to: (i) the microbial species and their physiology, (ii) the availability of nutrient resources (N, P, S, etc.) required for microbial metabolism, (iii) interactions with the soil matrix and associated energy costs, and (iv) the physical soil conditions (temperature, pH, humidity, etc.) (Manzoni et al., 2012; Geyer et al., 2016; Lashermes et al., 2016; Mooshammer et al., 2014). It is also likely to change according to the climatic and atmospheric conditions (Schimel, 2013; Allison et al., 2010; Sistla et al., 2013).

3 Time-dependent processes: dynamic representations

3.1 Kinetics, characteristic times, turnover, balance and mathematical modeling

The soil carbon pool is subject to permanent renewal. It is mathematically represented as a "dynamic system". Changes in the organic carbon stock can be described by a general differential equation:

$$dC/dt = I - kC \quad \text{[Equation 1]},$$

where C is the carbon stock (tC/ha), t the time (year), I the input (tC/ha/year) and k the proportion of mineralized carbon (or lost by erosion, etc.) per unit of time (year^{-1}). I is not necessarily constant. k is not fixed and is dependent on the conditions, quantity and nature of the carbon stock. k is the mineralization rate and kC is the mineralization flux (respiration) (Elzein Balesdent, 1995). The system is at equilibrium (as an annual average) if the input and output fluxes are equal. The system is at steady-state if these fluxes are constant (dC/dt = 0 and I = kC). The term "turnover time" (year) commonly refers to the ratio of total carbon stock to the input or output flux (Eriksson, 1971). In steady-state systems, turnover time, mean age, and mean transit time are identical terms. The term "residence time" (year) is used to describe the age of the C in the output flux, the age of the C stock or the turnover time. It is thus difficult to unambiguously apply this term. Sierra (2016) discouraged its use in carbon cycle research.

Storage (dC/dt >0) is the result of increased I inputs or a reduced k mineralization rate. The increase in carbon stock over a year cannot be greater than I. Conversely, the system C stock decreases if dC/dt <0. However, the average k value masks the high heterogeneity in carbon residence times. Isotopic tracing and soil respiration monitoring have helped monitor the fate of plant compound inputs in the soil at day to millennium time steps (Balesdent et al. 2018; Matthieu et al. 2015). Most of these inputs are mineralized and transformed into microbial products in less than a year, or a few years for ligno-cellulosic compounds. The transformation products (10–20% of the carbon supply) are protected and mineralized very slowly over several decades. Figure 5 provides a numerical example of the fate of organic carbon reaching the soil.

The soil carbon stock is the sum of the remains of all of these past annual inputs. Several kinetic parameters can be calculated. In the example in Figure 5, the OM mineralization rate is 5/45 tC/ha/year (0.11 year^{-1}). The vast majority of the carbon (37.5/45 tC/ha/year) consists of long-standing C. The average age of the carbon is 42 years. These slow kinetic parameters cannot be explained by deterministic laws (e.g. enzymatic kinetics laws) but rather could be modelled by statistical

approaches integrating complex functioning. Finally, dating methods have confirmed that organic materials can be inherited from a distant past of several decades (Mathieu et al., 2015). Characteristic OM formation times are therefore long (several decades), OM currently present is inherited from past generations. Strictly speaking, kinetics representations should be based on continuous mathematical formalisms to predict time-course variations in carbon stocks. In practice, however, compartmentalization approaches are used in conventional models (Bosatta and Agren, 1995). While remaining fairly faithful to reality, they enable the simplification of mathematical formalisms via discretization kinetics.

3.2 Non-linear processes

3.2.1 Linear and non-linear processes

Conventional models (Hénin and Dupuis, 1945; Jenkinson and Rayner, 1977; Parton et al., 1987; Andriulo et al., 1999), consider that parameters of the OM fate are independent of the input flux and OM quantities. This results in first-order differential equations ($dC/dt = I - kC$ with k independent of C, equation 1) and exponential kinetics. These models are considered linear: dual inputs result in twofold increases in OM amounts and compartments fill or empty at their characteristic rate. However, there are now many indications of non-linear soil C dynamics processes linked to the soil OM dynamics (Liyanage 2020, Wangwang et al 2020, Montagnani 2019 Banegas McNicol Chen Wen Bisigato Keiluweit 2015) (Table 1).

A major driver of non-linear behaviors is the fact that OM is not homogeneously distributed, and that plant inputs, microorganisms and dead OM are not co-located. Consequently, microorganisms might not be able to access a potential substrate because of spatial separation (Vogel et al., 2015) (Nunan et al, 2020). Since they depend on local concentrations, non-linear process parameters are dependent on the observation scale, (i.e. the aggregate, horizon or profile scale), on root distances, etc. The dynamics are not the same *in situ* and in homogenized *in vitro* systems. *In vitro* they depend on the experimental design and duration. This could likely explain the high discrepancy in the literature with respect to the carbon dynamics processes and mechanisms involved, and their broad quantification range. Although *in vitro* experiments help to gain insight into the mechanisms involved, *in situ* experiments and observations at the square meter or plot scale, and at the decadal time scale, are obviously more relevant for addressing the carbon storage issue. Non-linear processes have yet to be incorporated into operational C dynamics models. The saturation concept (see 2.4.1), which typically takes the impact of the mineral/OM ratio on carbon stabilization into account, also leads to a non-linear behavior.

3.2.2 Priming effect

A major non-linear effect is the so-called "priming effect" (Fontaine et al., 2007; Kuzyakov et al., 2000; Sallih and Bottner, 1988). In short, the supply of complex decomposable substrates provides

55

competent microorganisms with the energy resources required to biodegrade stabilized OM. Typically, the soil OM residence time is thus shorter in soil zones that receive substantial inputs, such as on the surface, relative to deep horizons. Except in cases of the burial of exogenous OM (which is considered to represent a risk of destabilization of pre-existing OM especially in deep horizons), the rhizosphere is the main soil compartment concerned by priming. The rhizosphere priming effect (RPE) is defined as the stimulation (or suppression) of OM decomposition by live roots and associated rhizosphere organisms as compared to SOM decomposition from rootless soils under the same environmental conditions. Findings of studies conducted in plant growth chambers and glasshouses indicate that the magnitude of the RPE varies widely, ranging from 380% enhancement (positive RPE) to 50% reduction (negative RPE) as compared to basal respiration from root-free soils (Cheng et al. 2013). These RPE levels demonstrate that rhizosphere processes are major drivers of SOM mineralization. Yet the RPE does not necessarily result in an ultimate decline of total OM because the overall input of organic materials from the rhizosphere may compensate for the enhanced mineralization of accessible OM (Cheng et al. 2013). Priming mechanisms may also be linked to complex combined biotic–abiotic mechanisms whereby root exudates promote carbon loss by releasing organic compounds from protective associations with minerals (Keiluweit 2015). Priming effect mechanisms are thus crucial in the dynamics of C, N and P elements and they highlight that, rigorously, carbon storage is not proportional to the inputs.

3.3 Renewal rates at the soil profile scale: deep C dynamics

Historical studies on dynamic representations of C have mainly focused on the soil layer considered by agronomists, i.e. 0-30 cm depth. However, there is growing interest in understanding the subsoil mechanisms involved because half of the soil carbon is located below 30 cm depth (Mulder et al., 2016) (Jobbagy and Jackson, 2000; Hiederer and Köchy, 2011). Carbon-14 (^{14}C) dating and natural tracing by ^{13}C have shown that the median age of carbon at 1 m depth is beyond 1000 years (Figure 1). The renewal rate describes the quantity of new C that has been stored for a period of time. Renewal is 7-10 times slower in the 30-100 cm layer than in the 0-30 cm layer (Mathieu et al., 2015; Balesdent et al., 2017; Balesdent et al., 2018), but deep carbon is not inert. The above studies revealed that on average the 30-100 cm layer contains 25% of the "young" carbon stock (i.e. younger than 20 years) in the 0-100 cm layer in cultivated soils, and 15-20 % in permanent grassland and forest soils (Figure 6). Several studies have reported significant effects of land-use changes or agricultural practices on deep soil carbon, including a decrease in C through the cultivation of grasslands or forest areas (Guo and Gifford, 2002), an increase when forests are converted to pasture (Stahl et al., 2017).

4 Control of C turnover times in soil: biotic and abiotic factors

The mechanisms described above are expressed to different extents in soil as a function of a series of 10 main factors that control their intensity. These factors are comprehensively presented in

56

Wiesmeier et al. (2019). Here we propose a summary of the co-dependencies of these factors (Table 2) by focusing on carbon turnover time variation factors (but variations in stocks also depend on incoming carbon fluxes that are not considered here). In steady-state systems, the turnover time is equivalent to the mean age of C leaving the system (where age is the duration between the time when C enters the soil and the observation time), which is a more intuitive concept (Sierra 2017).

The nature of incoming C, particularly its biodegradability, has a counter-intuitive effect on carbon residence times (see "The progressive decomposition model" section). The nature of C affects turnover times through the microbial carbon use efficiency (CUE) and organomineral interactions.

Temperature is a major factor, among the best quantified, with mineralization rates rising by 2- to 3-fold at every 10°C increase, but this effect depends on the soil, in particular its particle size distribution.

As the soil **water content** increases, mineralization rates increase linearly with moisture to a maximum (reached at around 20-50% of the volumetric soil water content according to the models (Sierra et al., 2015)), followed by a plateau and a decrease caused by the oxygen deficit. The alternating drying-rewetting cycles accelerate mineralization.

The partial pressure of oxygen. In saturated environments, if the environment becomes anaerobic, microorganisms tend to use alternative electron acceptors such as nitrate, ferric iron and sulfate. The degradation of ligno-cellulosic debris is slowed or even stopped. However, there is no evidence of temporary anaerobic effects on carbon storage. Anaerobic environments are also unfavorable for roots, wildlife or microorganism activity. Ploughing is often considered to accelerate biodegradation by aerating the soil, but tillage-induced CO_2 release ends after a few days (Rochette and Angers, 1999).

Grain size is quite closely correlated with carbon stocks. The <2 μm fraction content can lead to a 2-fold carbon stock variation. Fine granulometric fractions are often described as enriched with stable C, with turnover times longer than the average values in soil (Balesdent 1998). Meta-analyses have shown that the <2 μm fraction contains between 0% and 50% of the C stocks in national soil C inventories (Hassink 1997) (see section 2.4.1).

Mineralogy is a major determinant of OM stabilization but is still poorly quantified and is combined with the nature of the ions available in solution (Rasmussen et al., 2018). Mineral phases interacting with SOM (particularly poorly crystalline minerals) are not always stable (Basile-Doelsch et al., 2015) and can be modified by land use, plants, pH and amendments (Collignon 2011).

Soil pH and ions in the soil solution. The soil pH determined by conventional measurements is an average value that does not reflect the spatial heterogeneity of pH at the micro- to nano-scale. The pH has a greater effect on the soil physicochemistry than on the microbial physiology. The presence of calcium or magnesium ions in solution (dominant at pH > 5) and of active limestone tends to insolubilize OM and adsorb it by electrostatic interactions, via Ca^{2+} bridges (section 2.4.1), thus reducing its biodegradation (Rowley et al., 2018). Aluminium has an equivalent role, but in acidic (< 4.5) and aluminous soil (Rasmussen 2018 Heckman 2018). Conversely, biodegradation rates are high in salty soil where Na^+ predominates in the exchange complex (Qadir 2002). The action of K^+ has not

30 been assessed. The soil pH also seems to control the phylogenetic diversity of microbes (Shen et al. 2013).

The availability and abundance of N, P and S elements has various and complex effects. Organisms require specific ratios of C, N, S and P (i.e. stoichiometry) to survive and function optimally. For example, degradation of ligno-cellulosic debris (low nitrogen) is temporarily delayed in the absence of
35 mineral nitrogen. Many other C, N and P stoichiometry effects are involved in priming, biotic interactions or carbon use efficiency (CUE) (Monzoni 2012). C:N:P ratios ranging from 72:6:1 (topsoils) to 32:5:1 (pasture) have been reported. Soil vertical stratification C:N:P may, however, be important and impacts on the soil stoichiometry have also been reported following land-use shifts. Regarding the additional amount of nutrients required to store the quantity of carbon targeted by the 4/1000
40 initiative, it has been suggested N and P can be provided under current fertilization rates by reducing nutrient losses via improved management practices that include cover crops, fertilizer incorporation, etc. (Bertrand et al. 2019).

Biodiversity. Since bacteria are major actors in OM mineralization as well as in the production of stabilized compounds, the effects of nematode and protist predation of bacteria, as well as bacterial
45 regulation by fungi, is uncertain (Barrios 2007). The impact of pesticides on protists, nematodes and soil fungi could affect these regulations (Daam 2011).

Biotic/abiotic interactions. The priming effect mechanism is involved in plant nutrient (N, P, K) acquisition strategies. Plants release exudates and feed fungi through symbiotic associations (mycorrhiza) and bacteria from the rhizosphere that biodegrade OM (Fontaine et al., 2011) or even
50 destabilize organomineral associations (Keiluweit et al., 2015), while releasing nitrogen compounds or phosphorus. Many other plant-microorganism interaction mechanisms (e.g. mycorrhizal type or polyphenol concentration) can also exert control over soil C through N competition (Northup et al., 1995; Averill et al., 2014), which allows the ecosystem to maintain a substantial reserve of elements and therefore a high degree of resilience.
55 Quantification of the effects of individually considered factors and mechanisms is still very incomplete, and perhaps inappropriate, because: (i) a single law controlling the turnover time of the different C pools is not expected when several mechanisms are involved (Table 2); and (ii) several factors interact (Cotrufo et al., 2015). Quantification procedures described in the scientific literature are rather confusing: many research groups estimate the weight of a factor by varying it and measuring
60 mineralization flows, often in the short-term, despite the fact that these flows are not correlated with long-term carbon turnover times. For example, the effect of temperature has given rise to a number of divergent results (Davidson and Janssens, 2006; Sierra et al., 2015). Responses are also highly dependent on the soil type (von Luetzow et al., 2008).

In current operational models, only temperature, soil moisture, grain size and substrate C/N are taken
65 into account. They give quantitative estimates but fail to properly model dynamics. However, there are other overriding factors and priming effect modeling is emerging.

Supprimé: S
Supprimé: seems
Supprimé: s
Supprimé: amount
Supprimé: thanks to
Supprimé: like
Supprimé: strategies for
Supprimé: s
Supprimé: s
Supprimé: s
Supprimé: for example
Supprimé: a
Supprimé: the
Supprimé: . P

5   Conclusion

Soils have a decreasing C concentration gradient from the surface (a few percent by mass) to about 1 m deep (less than 1%). The 0-30 cm horizon has mainly been studied, but it was recently shown that deep horizons (> 30 cm) contribute up to 20% to the sequestration of new C over 20 years. OM observed in a soil at a given date thus results from a complex inheritance history linked to the functioning (and possible use) of a soil over several hundreds (or even thousands) of years.

Soil OM results from the biotransformation of inputs by plants (mainly underground inputs). In soil, decomposer food-webs and microorganisms are essential for the oxidative degradation and mineralization of organic molecules. The compounds that are not mineralized consists of microbe-derived (main contribution) and plant-derived small organic molecules and form the soil OM. In soil, transfer and association processes with minerals redistribute these organic molecules and/or more or less permanently shield them from the action of microorganisms though aggregation and organo-mineral interaction processes.

Long-term stabilization (this formulation is now preferred over the previous term 'humification') is therefore not driven by the same forces as short-term degradation rates. Plant and microbial biodiversity, mineralogy, water content, pO_2, soil solution chemistry and pH, N and P availability, as well as soil temperature, thus control the mineralization-stabilization balance. The interdependencies of these factors, their time dependence (short-, versus long-term response), their relative importance with respect to the storage (or loss) of C, are often not explained in detail, thus making it difficult to link C stock changes to specific processes and/or factors.

C stock predictions are conventionally modelled by linear OM decay dynamics approaches, while only considering a few of these factors (temperature, water content, grain size, pH, sometimes C:N interactions). Very few models account for non-linear processes, such as priming, despite the increasing evidence of their key role in C dynamics.

Greater insight into the mechanisms, their interdependencies, hierarchy and sensitivity to agricultural practices could generate future action levers for C sequestration in soil. Due to the time-scale considered, the methods of choice should include retrospective studies or intercomparison of the findings of long-term experiments at specific sites.

6   Acknowledgements

59

Supprimé: gradient in

Supprimé: been

Supprimé: has been

Supprimé: deeper than

Supprimé: The organic matter

Supprimé:)

Supprimé: organic matter

Supprimé: the

Supprimé: s

Supprimé: in

Supprimé: organic matter

Supprimé: the

Commenté [dm25]: "mineral transfer and association   … [1]

Supprimé: eliminate

Supprimé: -

Supprimé: The l

Supprimé: term

Supprimé: to

Supprimé: old

Commenté [dm26]: PO₂ ?

Supprimé: s

Supprimé: time response

Supprimé: time

Supprimé: and

Supprimé: e

Supprimé: the

Supprimé: s

Supprimé: Prediction of

Supprimé: s

Supprimé: modelling of OM decay dynamics

Supprimé: only

Supprimé: knowledge emphasizin

Supprimé: g

Supprimé: represents

Supprimé: potential

Commenté [dm27]: OK?

Supprimé: sites

Supprimé: would be methods of choice

Houot, S., Klumpp, K., Letort, E., Litrico I., Martin, M., Menasseri, S., Meziere, D., Morvan, T., Mosnier, C., Roger-Estrade, J., Saint-André, L., Sierra J., Therond, O., Viaud, V., Grateau R., Le Perchec S., Savini I., Rechauchère, O. (2019). *Stocker du carbone dans les sols français ; quel potentiel au regard de l'objectif 4 pour 1000 et à quel coût ?* Research report summary, INRA (France), 114 p. We thank Claire Chenu, Bertrand Guenet and Denis Angers for their proofreading of the first French version.

7 Author contributions

Isabelle Basile-Doelsch and Jerome Balesdent contributed equally to the French chapter "Les mécanismes à l'origine du stockage/déstockage de C dans les sols" of the above-cited INRA report. Isabelle Basile-Doelsch drafted the English version. Sylvain Pellerin commented the manuscript and led the INRA report.

8 Competing interests

The authors declare no competing interests.

9 References

Allison, S. D., Wallenstein, M. D., and Bradford, M. A.: Soil-carbon response to warming dependent on microbial physiology, Nat. Geosci., 3, 336-340, 10.1038/NGEO846, 2010.

Amelung, W., Brodowski, S., Sandhage-Hofmann, A., and Bol, R.: Combining Biomarker with Stable Isotope Analyses for Assessing the Transformation and Turnover of Soil Organic Matter, Advances in Agronomy, Vol 100, 100, 155-250, 2008.

Amundson, R., and Biardeau, L.: Soil carbon sequestration is an elusive climate mitigation tool, Proceedings of the National Academy of Sciences of the United States of America, 115, 11652-11656, 10.1073/pnas.1815901115, 2018.

Amundson, R., and Biardeau, L.: Opinion: Soil carbon sequestration is an elusive climate mitigation tool (vol 115, pg 11652, 2018), Proceedings of the National Academy of Sciences of the United States of America, 116, 13143-13143, 10.1073/pnas.1908917116, 2019.

Andriulo, A., Mary, B., and Guerif, J.: Modelling soil carbon dynamics with various cropping sequences on the rolling pampas, Agronomie, 19, 365-377, 10.1051/agro:19990504, 1999.

Averill, C., Turner, B. L., and Finzi, A. C.: Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage, Nature, 505, 543-+, 10.1038/nature12901, 2014.

Balesdent, J.: Les isotopes du carbone et la dynamique des matières organiques des sols, Cahiers agriculture, 7, 201-206, 1998.

Balesdent, J., Chenu, C., and Balabane, M.: Relationship of soil organic matter dynamics to physical protection and tillage, Soil & Tillage Research, 53, 215-230, 2000.

Balesdent, J., Derrien, D., Fontaine, S., Kirman, S., Klumpp, K., Loiseau, P., Marol, C., Nguyen, C., Péan, M., Personi, E., and Robin, C.: Contribution de la rhizodéposition aux matières organiques du sol, quelques implications pour la modélisation de la dynamique du carbone, Etude et Gestion des Sols, 18, 201-216, 2011.

Balesdent, J., Basile-Doelsch, I., Chadoeuf, J., Cornu, S., Fekiacova, Z., Fontaine, S., Guenet, B., and Hatte, C.: Turnover of deep organic carbon in cultivated soils: an estimate from a review of isotope data, Biotechnologie Agronomie Societe Et Environnement, 21, 181-190, 2017.

Balesdent, J., Basile-Doelsch, I., Chadoeuf, J., Cornu, S., Derrien, D., Fekiacova, Z., and Hatte, C.: Atmosphere-soil carbon transfer as a function of soil depth, Nature, 10.1038/s41586-018-0328-3, 2018.

Banegas, N., Albanesi, A. S., Pedraza, R. O., and Dos Santos, D. A.: Non-linear dynamics of litter decomposition under different grazing management regimes, Plant and Soil, 393, 47-56, 10.1007/s11104-015-2472-y, 2015.

Bardgett, R. D., Bowman, W. D., Kaufmann, R., and Schmidt, S. K.: A temporal approach to linking aboveground and belowground ecology, Trends in Ecology & Evolution, 20, 634-641, 10.1016/j.tree.2005.08.005, 2005.

Basile-Doelsch, I., Balesdent, J., and Rose, J.: Are Interactions between Organic Compounds and Nanoscale Weathering Minerals the Key Drivers of Carbon Storage in Soils?, Environ. Sci. Technol., 49, 3997-3998, 2015.

Baveye, P. C., Berthelin, J., Tessier, D., and Lemaire, G.: The "4 per 1000" initiative: A credibility issue for the soil science community?, Geoderma, 309, 118-123, 10.1016/j.geoderma.2017.05.005, 2018a.

Baveye, P. C., Berthelin, J., Tessier, D., and Lemaire, G.: The "4 per 1000" initiative: A credibility issue for the soil science community?, Geoderma, 309, 118-123, https://doi.org/10.1016/j.geoderma.2017.05.005, 2018b.

Baveye, P. C., and White, R. E.: The "4p1000" initiative: A new name should be adopted, Ambio, 49, 361-362, 10.1007/s13280-019-01188-9, 2020.

Bertrand, I., Viaud, V., Daufresne, T., Pellerin, S., and Recous, S.: Stoichiometry constraints challenge the potential of agroecological practices for the soil C storage. A review, Agronomy for Sustainable Development, 39, 10.1007/s13593-019-0599-6, 2019.

Besnard, E., Chenu, C., Balesdent, J., Puget, P., and Arrouays, D.: Fate of particulate organic matter in soil aggregates during cultivation, Eur. J. Soil Sci., 47, 495-503, 10.1111/j.1365-2389.1996.tb01849.x, 1996.

Bisigato, A. J., Laphitz, R. M. L., and Carrera, A. L.: Non-linear relationships between grazing pressure and conservation of soil resources in Patagonian Monte shrublands, Journal of Arid Environments, 72, 1464-1475, 10.1016/j.jaridenv.2008.02.016, 2008.

Blair, J. M., Falconer, R. E., Milne, A. C., Young, I. M., and Crawford, J. W.: ModelingThree-dimensional microstructure in heterogeneous media, Soil Science Society of America Journal, 71, 1807-1812, 10.2136/ssaj2006.0113, 2007.

Bohlen, P. J., Pelletier, D. M., Groffman, P. M., Fahey, T. J., and Fisk, M. C.: Influence of earthworm invasion on redistribution and retention of soil carbon and nitrogen in northern temperate forests, Ecosystems, 7, 13-27, 10.1007/s10021-003-0127-y, 2004.

Bol, R., Poirier, N., Balesdent, J., and Gleixner, G.: Molecular turnover time of soil organic matter in particle-size fractions of an arable soil, Rapid Communications in Mass Spectrometry, 23, 2551-2558, 2009.

Bolinder, M. A., Angers, D. A., and Dubuc, J. P.: Estimating shoot to root ratios and annual carbon inputs in soils for cereal crops, Agriculture Ecosystems & Environment, 63, 61-66, 10.1016/S0167-8809(96)01121-8, 1997.

Bonkowski, M.: Protozoa and plant growth: the microbial loop in soil revisited, New Phytologist, 162, 617-631, 10.1111/j.1469-8137.2004.01066.x, 2004.

Bonneville, S., Morgan, D. J., Schmalenberger, A., Bray, A., Brown, A., Banwart, S. A., and Benning, L. G.: Tree-mycorrhiza symbiosis accelerate mineral weathering: Evidences from nanometer-scale elemental fluxes at the hypha-mineral interface, Geochimica Et Cosmochimica Acta, 75, 6988-7005, 2011.

Bosatta, E., and Agren, G. I.: The Power and Reactive Continuum Models as Particular Cases of the Q-Theory of Organic-Matter Dynamics, Geochimica Et Cosmochimica Acta, 59, 3833-3835, 10.1016/0016-7037(95)00287-A, 1995.

Brauman, A.: Effect of gut transit and mound deposit on soil organic matter transformations in the soil feeding termite: A review, European Journal of Soil Biology, 36, 117-125, 10.1016/S1164-5563(00)01058-X, 2000.

Brown, G. G.: How Do Earthworms Affect Microfloral and Faunal Community Diversity, Plant and Soil, 170, 209-231, 10.1007/BF02183068, 1995.

Buee, M., De Boer, W., Martin, F., van Overbeek, L., and Jurkevitch, E.: The rhizosphere zoo: An overview of plant-associated communities of microorganisms, including phages, bacteria, archaea, and fungi, and of some of their structuring factors, Plant and Soil, 321, 189-212, 10.1007/s11104-009-9991-3, 2009.

35 Burns, R. G., DeForest, J. L., Marxsen, J., Sinsabaugh, R. L., Stromberger, M. E., Wallenstein, M. D., Weintraub, M. N., and Zoppini, A.: Soil enzymes in a changing environment: Current knowledge and future directions, Soil Biology and Biochemistry, 58, 216-234, https://doi.org/10.1016/j.soilbio.2012.11.009, 2013.

Calvet, R., Chenu, H., and Houot, S.: Les matières organiques des sols : rôles agronomiques et environnementaux, edited by: Agriproduction, Editions France Agricole, 347 pp., 2011.

40 Chen, F. L., Zheng, H., Zhang, K., Ouyang, Z. Y., Wu, Y. F., Shi, Q., and Li, H. L.: Non-linear impacts of Eucalyptus plantation stand age on soil microbial metabolic diversity, Journal of Soils and Sediments, 13, 887-894, 10.1007/s11368-013-0669-3, 2013.

Chenu, C., and Stotsky, G.: Interactions between microorganisms and soil partilces : an overview, in: Interactions between soil partilces and microorganisms edited by: Huang, P. M., Bollag, J. M., and Senesi, N., Wiley & Sons, 2002.

45 Chevallier, T., Blanchart, E., Albrecht, A., and Feller, C.: The physical protection of soil organic carbon in aggregates: a mechanism of carbon storage in a Vertisol under pasture and market gardening (Martinique, West Indies), Agriculture Ecosystems & Environment, 103, 375-387, 10.1016/j.agee.2003.12.009, 2004.

Chevallier, T., Woignier, T., Toucet, J., and Blanchart, E.: Organic carbon stabilization in the fractal pore structure of Andosols, Geoderma, 159, 182-188, 10.1016/j.geoderma.2010.07.010, 2010.

50 Clemmensen, K. E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R. D., Wardle, D. A., and Lindahl, B. D.: Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest, Science, 339, 1615-1618, 10.1126/science.1231923, 2013.

Collignon, C., Uroz, S., Turpault, M. P., and Frey-Klett, P.: Seasons differently impact the structure of mineral weathering bacterial communities in beech and spruce stands, Soil Biology & Biochemistry, 43, 2012-2022, 2011.

55 Coq, S., Barthes, B. G., Oliver, R., Rabary, B., and Blanchart, E.: Earthworm activity affects soil aggregation and organic matter dynamics according to the quality and localization of crop residues - An experimental study (Madagascar), Soil Biology & Biochemistry, 39, 2119-2128, 10.1016/j.soilbio.2007.03.019, 2007.

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M. L., Wall, D. H., and Parton, A. J.: Formation of soil organic matter via biochemical and physical pathways of litter mass loss, Nat. Geosci., 8, 776-+, 10.1038/NGEO2520, 2015.

50 Curry, J. P., and Schmidt, O.: The feeding ecology of earthworms - A review, Pedobiologia, 50, 463-477, 10.1016/j.pedobi.2006.09.001, 2007.

Curtis, T. P., and Sloan, W. T.: Exploring microbial diversity - A vast below, Science, 309, 1331-1333, 10.1126/science.1118176, 2005.

Davidson, E. A., and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, Nature, 440, 165-173, 10.1038/nature04514, 2006.

55 de Vries, W.: Soil carbon 4 per mille: a good initiative but let's manage not only the soil but also the expectations, Geoderma, 309, 111-112, 10.1016/j.geoderma.2017.05.023, 2018.

Dequiedt, S., Saby, N. P. A., Lelievre, M., Jolivet, C., Thioulouse, J., Toutain, B., Arrouays, D., Bispo, A., Lemanceau, P., and Ranjard, L.: Biogeographical patterns of soil molecular microbial biomass as influenced by soil characteristics and

70 management, Global Ecology and Biogeography, 20, 641-652, 10.1111/j.1466-8238.2010.00628.x, 2011.

Derrien, D., Marol, C., Balabane, M., and Balesdent, J.: The turnover of carbohydrate carbon in a cultivated soil estimated by 13C natural abundances, Eur. J. Soil Sci., 57, 547-557, doi:10.1111/j.1365-2389.2006.00811.x, 2006.

Dignac, M.-F., Bahri, H., Rumpel, C., Rasse, D. P., Bardoux, G., Balesdent, J., Girardin, C., Chenu, C., and Mariotti, A.: Carbon-13 natural abundance as a tool to study the dynamics of lignin monomers in soil: an appraisal at the Closeaux

75 experimental field (France), Geoderma, 128, 3-17, 2005.

Dignac, M. F., Derrien, D., Barre, P., Barot, S., Cecillon, L., Chenu, C., Chevallier, T., Freschet, G. T., Garnier, P., Guenet, B., Hedde, M., Klumpp, K., Lashermes, G., Maron, P. A., Nunan, N., Roumet, C., and Basile-Doelsch, I.: Increasing soil carbon

storage: mechanisms, effects of agricultural practices and proxies. A review, Agronomy for Sustainable Development, 37, 10.1007/s13593-017-0421-2, 2017.

Doetterl, S., Berhe, A. A., Nadeu, E., Wang, Z. G., Sommer, M., and Fiener, P.: Erosion, deposition and soil carbon: A review of process-level controls, experimental tools and models to address C cycling in dynamic landscapes, Earth-Science Reviews, 154, 102-122, 10.1016/j.earscirev.2015.12.005, 2016.

Don, A., Steinberg, B., Schoening, I., Pritsch, K., Joschko, M., Gleixner, G., and Schulze, E. D.: Organic carbon sequestration in earthworm burrows, Soil Biology & Biochemistry, 40, 1803-1812, 10.1016/j.soilbio.2008.03.003, 2008.

Don, A., Roedenbeck, C., and Gleixner, G.: Unexpected control of soil carbon turnover by soil carbon concentration, Environmental Chemistry Letters, 11, 407-413, 10.1007/s10311-013-0433-3, 2013.

Dungait, J. A. J., Hopkins, D. W., Gregory, A. S., and Whitmore, A. P.: Soil organic matter turnover is governed by accessibility not recalcitrance, Global Change Biology, 18, 1781-1796, 10.1111/j.1365-2486.2012.02665.x, 2012.

Eriksson, E.: Compartment Models and Reservoir Theory, Annual Review of Ecology and Systematics, 2, 67-84, 10.1146/annurev.es.02.110171.000435, 1971.

Eusterhues, K., Wagner, F. E., Hausler, W., Hanzlik, M., Knicker, H., Totsche, K. U., Kogel-Knabner, I., and Schwertmann, U.: Characterization of Ferrihydrite-Soil Organic Matter Coprecipitates by X-ray Diffraction and Mossbauer Spectroscopy, Environ. Sci. Technol., 42, 7891-7897, 10.1021/es800881w, 2008.

Falconer, R. E., Battaia, G., Schmidt, S., Baveye, P., Chenu, C., and Otten, W.: Microscale Heterogeneity Explains Experimental Variability and Non-Linearity in Soil Organic Matter Mineralisation, Plos One, 10, 10.1371/journal.pone.0123774, 2015.

Fan, J. L., McConkey, B., Janzen, H., Townley-Smith, L., and Wang, H.: Harvest index-yield relationship for estimating crop residue in cold continental climates, Field Crops Research, 204, 153-157, 10.1016/j.fcr.2017.01.014, 2017.

Fontaine, S., Barot, S., Barre, P., Bdioui, N., Mary, B., and Rumpel, C.: Stability of organic carbon in deep soil layers controlled by fresh carbon supply, Nature, 450, 277-U210, 10.1038/nature06275, 2007.

Fontaine, S., Henault, C., Aamor, A., Bdioui, N., Bloor, J. M. G., Maire, V., Mary, B., Revaillot, S., and Maron, P. A.: Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect, Soil Biology & Biochemistry, 43, 86-96, 10.1016/j.soilbio.2010.09.017, 2011.

Frazão, J., de Goede, R. G. M., Capowiez, Y., and Pulleman, M. M.: Soil structure formation and organic matter distribution as affected by earthworm species interactions and crop residue placement, Geoderma, - 338, 453- 463, 2019.

Gans, J., Wolinsky, M., and Dunbar, J.: Computational improvements reveal great bacterial diversity and high metal toxicity in soil, Science, 309, 1387-1390, 10.1126/science.1112665, 2005.

Geyer, K. M., Kyker-Snowman, E., Grandy, A. S., and Frey, S. D.: Microbial carbon use efficiency: accounting for population, community, and ecosystem-scale controls over the fate of metabolized organic matter, Biogeochemistry, 127, 173-188, 10.1007/s10533-016-0191-y, 2016.

Gleixner, G., Czimczik, C. J., Kramer, C., Luehker, B., and Schmidt, M. W. I.: Plant compounds and their turnover and stabilization as soil organic matter, in: Global biogeochemical cycles in the climate system, edited by: Schulze, E. D., Heimann, M., Harrison, S., Holland, E. A., Llyod, J., Prentice, I. C., and Schimel, D. S., Academic Press, San Diego, 201-215, 2001.

Gmach, M. R., Cherubin, M. R., Kaiser, K., and Cerri, C. E. P.: Processes that influence dissolved organic matter in the soil: a review, Scientia Agricola, 77, 10.1590/1678-992X-2018-0164, 2020.

Golchin, A., Oades, J. M., Skjemstad, J. O., and Clarke, P.: Study of free and occluded particulate organic matter in soils by solid-state C-13 CP/MAS NMR-spectroscopy and scanning electron microscopy, Australian Journal of Soil research, 32, 285-309, 1994.

Guiboileau, A., Sormani, R., Meyer, C., and Masclaux-Daubresse, C.: Senescence and death of plant organs: Nutrient recycling and developmental regulation, Comptes Rendus Biologies, 333, 382-391, 10.1016/j.crvi.2010.01.016, 2010.

Guo, L. B., and Gifford, R. M.: Soil carbon stocks and land use change : a meta analysis, Global Change Biology, 8, 345-360, 2002.

Hassink, J.: The capacity of soils to preserve organic C and N by their association with clay and silt particles, Plant and Soil, 191, 77-87, 10.1023/A:1004213929699, 1997.

Hättenschwiler, S., Barantal, S., Ganault, P., Gillespie, L., and Coq, S.: Quels enjeux sont associés à la biodiversité des sols ? , Innovations Agronomiques, 69, 1-14, 2018.

Heckman, K., Lawrence, C. R., and Harden, J. W.: A sequential selective dissolution method to quantify storage and stability of organic carbon associated with Al and Fe hydroxide phases, Geoderma, 312, 24-35, 10.1016/j.geoderma.2017.09.043, 2018.

Hénin, S., and Dupuis, M.: Essai de bilan de la matière organique du sol,, Ann. Agron. , 11, 17-29, 1945.

Hiederer, R., and Köchy, M.: Global Soil Organic Carbon Estimates and the Harmonized World Soil Database, 79, 2011.

Horrigue, W., Dequiedt, S., Prevost-Boure, N. C., Jolivet, C., Saby, N. P. A., Arrouays, D., Bispo, A., Maron, P. A., and Ranjard, L.: Predictive model of soil molecular microbial biomass, Ecol. Indic., 64, 203-211, 10.1016/j.ecolind.2015.12.004, 2016.

IPCC 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, , Cambridge, United Kingdom and New York, NY, USA,, 1535 pp.,

Jagercikova, M., Cornu, S., Bourles, D., Evrard, O., Hatte, C., and Balesdent, J.: Quantification of vertical solid matter transfers in soils during pedogenesis by a multi-tracer approach, Journal of Soils and Sediments, 17, 408-422, 10.1007/s11368-016-1560-9, 2017.

Jenkinson, D. S., and Rayner, J. H.: The turnover of soil organic matter in some of the Rothamsted classical experiments, Soil Science, 123, 298-305, 1977.

Jobbagy, E. G., and Jackson, R. B.: The Vertical Distribution of Soil Organic Carbon and Its Relation to Climate and Vegetation, Ecological Applications, 10, 423-436, 10.2307/2641104, 2000.

Jones, D. L., Nguyen, C., and Finlay, R. D.: Carbon flow in the rhizosphere: carbon trading at the soil-root interface, Plant and Soil, 321, 5-33, 10.1007/s11104-009-9925-0, 2009.

Juarez, S., Nunan, N., Duday, A.-C., Pouteau, V., Schmidt, S., Hapca, S., Falconer, R., Otten, W., and Chenu, C.: Effects of different soil structures on the decomposition of native and added organic carbon, European Journal of Soil Biology, 58, 81-90, 10.1016/j.ejsobi.2013.06.005, 2013.

Kallenbach, C. M., Frey, S. D., and Grandy, A. S.: Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls, Nature Communications, 7, 10.1038/ncomms13630, 2016.

Katterer, T., Bolinder, M. A., Andren, O., Kirchmann, H., and Menichetti, L.: Roots contribute more to refractory soil organic matter than above-ground crop residues, as revealed by a long-term field experiment, Agriculture Ecosystems & Environment, 141, 184-192, 10.1016/j.agee.2011.02.029, 2011.

Keiluweit, M., Bougoure, J. J., Nico, P. S., Pett-Ridge, J., Weber, P. K., and Kleber, M.: Mineral protection of soil carbon counteracted by root exudates, Nature Clim. Change, 5, 588-595, 10.1038/nclimate2580

http://www.nature.com/nclimate/journal/v5/n6/abs/nclimate2580.html#supplementary-information, 2015.

Keiluweit, M., Wanzek, T., Kleber, M., Nico, P., and Fendorf, S.: Anaerobic microsites have an unaccounted role in soil carbon stabilization, Nature Communications, 8, 10.1038/s41467-017-01406-6, 2017.

Kelleher, B. P., and Simpson, A. J.: Humic substances in soils: Are they really chemically distinct?, Environ. Sci. Technol., 40, 4605-4611, 10.1021/es0608085, 2006.

Kéraval, B., Lehours, A. C., Colombet, J., Amblard, C., Alvarez, G., and Fontaine, S.: Soil carbon dioxide emissions controlled by an extracellular oxidative metabolism identifiable by its isotope signature, Biogeosciences, 13, 6353-6362, 10.5194/bg-13-6353-2016, 2016.

Killham, K., Amato, M., and Ladd, J. N.: Effect of Substrate Location in Soil and Soil Pore-Water Regime on Carbon Turnover, Soil Biology & Biochemistry, 25, 57-62, 10.1016/0038-0717(93)90241-3, 1993.

Kleber, M., Sollins, P., and Sutton, R.: A conceptual model of organo-mineral interactions in soils: self-assembly of organic molecular fragments into zonal structures on mineral surfaces, Biogeochemistry, 85, 9-24, 10.1007/s10533-007-9103-5, 2007.

Kleber, M., Eusterhues, K., Keiluweit, M., Mikutta, C., Mikutta, R., and Nico, P. S.: Chapter One - Mineral–Organic Associations: Formation, Properties, and Relevance in Soil Environments, in: Advances in Agronomy, edited by: Donald, L. S., Academic Press, 1-140, 2015.

Klupfel, L., Piepenbrock, A., Kappler, A., and Sander, M.: Humic substances as fully regenerable electron acceptors in recurrently anoxic environments, Nat. Geosci., 7, 195-200, 10.1038/NGEO2084, 2014.

Kogel-Knabner, I.: The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter: Fourteen years on, Soil Biology & Biochemistry, 105, A3-A8, 10.1016/j.soilbio.2016.08.011, 2017.

Kögel-Knabner, I., Guggenberger, G., Kleber, M., Kandeler, E., Kalbitz, K., Scheu, S., Eusterhues, K., and Leinweber, P.: Organo-mineral associations in temperate soils: Integrating biology, mineralogy, and organic matter chemistry, Journal of Plant Nutrition and Soil Science, 171, 61-82, 10.1002/jpln.200700048, 2008.

Kuzyakov, Y., Friedel, J. K., and Stahr, K.: Review of mechanisms and quantification of priming effects, Soil Biology & Biochemistry, 32, 1485-1498, 10.1016/S0038-0717(00)00084-5, 2000.

Lal, R.: Soil degradation by erosion, Land Degradation & Development, 12, 519-539, 10.1002/ldr.472, 2001.

Larney, F. J., and Angers, D. A.: The role of organic amendments in soil reclamation: A review, Canadian Journal of Soil Science, 92, 19-38, 10.4141/CJSS2010-064, 2012.

Lashermes, G., Gainvors-Claisse, A., Recous, S., and Bertrand, I.: Enzymatic Strategies and Carbon Use Efficiency of a Litter-Decomposing Fungus Grown on Maize Leaves, Stems, and Roots, Front. Microbiol., 7, 10.3389/fmicb.2016.01315, 2016.

Lavallee, J. M., Conant, R. T., Paul, E. A., and Cotrufo, M. F.: Incorporation of shoot versus root-derived C-13 and N-15 into mineral-associated organic matter fractions: results of a soil slurry incubation with dual-labelled plant material, Biogeochemistry, 137, 379-393, 10.1007/s10533-018-0428-z, 2018.

Lavelle, P., Spain, A., Blouin, M., Brown, G., Decaëns, T., Grimaldi, M., Jiménez, J. J., McKey, D., Mathieu, J., Velasquez, E., and Zangerlé, A.: Ecosystem Engineers in a Self-organized Soil: A Review of Concepts and Future Research Questions, Soil Science, 181, 91-109, 10.1097/ss.0000000000000155, 2016.

Lehmann, J., Rillig, M. C., Thies, J., Masiello, C. A., Hockaday, W. C., and Crowley, D.: Biochar effects on soil biota - A review, Soil Biology & Biochemistry, 43, 1812-1836, 10.1016/j.soilbio.2011.04.022, 2011.

Lehmann, J., and Kleber, M.: The contentious nature of soil organic matter, Nature, 528, 60-68, 10.1038/nature16069, 2015.

Lennon, J. T., and Jones, S. E.: Microbial seed banks: the ecological and evolutionary implications of dormancy, Nat. Rev. Microbiol., 9, 119-130, 10.1038/nrmicro2504, 2011.

Levard, C., Doelsch, E., Basile-Doelsch, I., Abidin, Z., Miche, H., Masion, A., Rose, J., Borschneck, D., and Bottero, J. Y.: Structure and distribution of allophanes, imogolite and proto-imogolite in volcanic soils, Geoderma, 183–184, 100-108, 2012.

Liyanage, A., Grace, P. R., Scheer, C., de Rosa, D., Ranwala, S., and Rowlings, D. W.: Carbon limits non-linear response of nitrous oxide (N2O) to increasing N inputs in a highly-weathered tropical soil in Sri Lanka, Agriculture Ecosystems & Environment, 292, 10.1016/j.agee.2019.106808, 2020.

Manzoni, S., Taylor, P., Richter, A., Porporato, A., and Agren, G. I.: Environmental and stoichiometric controls on microbial carbon-use efficiency in soils, New Phytologist, 196, 79-91, 10.1111/j.1469-8137.2012.04225.x, 2012.

Martin, A., Mariotti, A., Balesdent, J., Lavelle, P., and Vuattoux, R.: Estimate of Organic-Matter Turnover Rate in a Savanna Soil by C-13 Natural Abundance Measurements, Soil Biology & Biochemistry, 22, 517-523, 10.1016/0038-0717(90)90188-6, 1990.

Mathieu, J., Hatté, C., Balesdent, J., and Parent, E.: Deep soil carbon dynamics are driven more by soil type than by climate: a worldwide meta-analysis of radiocarbon profiles, Global Change Biology, 21, 2015.

McNicol, G., and Silver, W. L.: Non-linear response of carbon dioxide and methane emissions to oxygen availability in a drained histosol, Biogeochemistry, 123, 299-306, 10.1007/s10533-015-0075-6, 2015.

Mikutta, R., Kleber, M., Torn, M., and Jahn, R.: Stabilization of Soil Organic Matter: Association with Minerals or Chemical Recalcitrance?, Biogeochemistry, 77, 25-56, 2006.

Miltner, A., Bombach, P., Schmidt-Brucken, B., and Kastner, M.: SOM genesis: microbial biomass as a significant source, Biogeochemistry, 111, 41-55, 2012.

Minasny, B., Malone, B. P., McBratney, A. B., Angers, D. A., Arrouays, D., Chambers, A., Chaplot, V., Chen, Z. S., Cheng, K., Das, B. S., Field, D. J., Gimona, A., Hedley, C. B., Hong, S. Y., Mandal, B., Marchant, B. P., Martin, M., McConkey, B. G., Mulder, V. L., O'Rourke, S., Richer-de-Forges, A. C., Odeh, I., Padarian, J., Paustian, K., Pan, G. X., Poggio, L., Savin, I., Stolbovoy, V., Stockmann, U., Sulaeman, Y., Tsui, C. C., Vagen, T. G., van Wesemael, B., and Winowiecki, L.: Soil carbon 4 per mille, Geoderma, 292, 59-86, 10.1016/j.geoderma.2017.01.002, 2017.

Monga, O., Bousso, M., Garnier, P., and Pot, V.: 3D geometric structures and biological activity: Application to microbial soil organic matter decomposition in pore space, Ecological Modelling, 216, 291-302, 10.1016/j.ecolmodel.2008.04.015, 2008.

Monga, O., Garnier, P., Pot, V., Coucheney, E., Nunan, N., Otten, W., and Chenu, C.: Simulating microbial degradation of organic matter in a simple porous system using the 3-D diffusion-based model MOSAIC, Biogeosciences, 11, 2201-2209, 10.5194/bg-11-2201-2014, 2014.

Montagnani, L., Badraghi, A., Speak, A. F., Wellstein, C., Borruso, L., Zerbe, S., and Zanotelli, D.: Evidence for a non-linear carbon accumulation pattern along an Alpine glacier retreat chronosequence in Northern Italy, Peerj, 7, 10.7717/peerj.7703, 2019.

Montgomery, D. R.: Soil erosion and agricultural sustainability, Proceedings of the National Academy of Sciences of the United States of America, 104, 13268-13272, 10.1073/pnas.0611508104, 2007.

Mooshammer, M., Wanek, W., Hammerle, I., Fuchslueger, L., Hofhansl, F., Knoltsch, A., Schnecker, J., Takriti, M., Watzka, M., Wild, B., Keiblinger, K. M., Zechmeister-Boltenstern, S., and Richter, A.: Adjustment of microbial nitrogen use efficiency to carbon: nitrogen imbalances regulates soil nitrogen cycling, Nature Communications, 5, 10.1038/ncomms4694, 2014.

Mulder, V. L., Lacoste, M., Martin, M. P., Richer-de-Forges, A., and Arrouays, D.: Understanding large-extent controls of soil organic carbon storage in relation to soil depth and soil-landscape systems, Global Biogeochemical Cycles, 29, 1210-1229, 10.1002/2015GB005178, 2015.

Mulder, V. L., Lacoste, M., Richer-de-Forges, A. C., Martin, M. P., and Arrouays, D.: National versus global modelling the 3D distribution of soil organic carbon in mainland France, Geoderma, 263, 16-34, 10.1016/j.geoderma.2015.08.035, 2016.

Nguyen, C.: Rhizodeposition of organic C by plants: mechanisms and controls, Agronomie, 23, 375-396, 10.1051/agro:2003011, 2003.

Northup, R. R., Yu, Z. S., Dahlgren, R. A., and Vogt, K. A.: Polyphenol Control of Nitrogen Release from Pine Litter, Nature, 377, 227-229, 10.1038/377227a0, 1995.

Pajor, R., Falconer, R., Hapca, S., and Otten, W.: Modelling and quantifying the effect of heterogeneity in soil physical conditions on fungal growth, Biogeosciences, 7, 3731-3740, 10.5194/bg-7-3731-2010, 2010.

Parton, W. J., Schimel, D. S., Cole, C. V., and Ojima, D. S.: Analysis of factors controlling SOM levels in Great Plains grasslands Soil, Soil Science Society of America Journal, 51, 1173-1779, 1987.

Pinheiro, M., Garnier, P., Beguet, J., Laurent, F. M., and Gonod, L. V.: The millimetre-scale distribution of 2,4-D and its degraders drives the fate of 2,4-D at the soil core scale, Soil Biology & Biochemistry, 88, 90-100, 10.1016/j.soilbio.2015.05.008, 2015.

Plante, A. F., Conant, R. T., Paul, E. A., Paustian, K., and Six, J.: Acid hydrolysis of easily dispersed and microaggregate-derived silt- and clay-sized fractions to isolate resistant soil organic matter, Eur. J. Soil Sci., 57, 456-467, doi:10.1111/j.1365-2389.2006.00792.x, 2006.

Poeplau, C., and Katterer, T.: Is soil texture a major controlling factor of root:shoot ratio in cereals?, Eur. J. Soil Sci., 68, 964-970, 10.1111/ejss.12466, 2017.

Qadir, M., and Schubert, S.: Degradation processes and nutrient constraints in sodic soils, Land Degradation & Development, 13, 275-294, 10.1002/ldr.504, 2002.

Rasmussen, C., Heckman, K., Wieder, W. R., Keiluweit, M., Lawrence, C. R., Berhe, A. A., Blankinship, J. C., Crow, S. E.,
50   Druhan, J. L., Pries, C. E. H., Marin-Spiotta, E., Plante, A. F., Schadel, C., Schimel, J. P., Sierra, C. A., Thompson, A., and
Wagai, R.: Beyond clay: towards an improved set of variables for predicting soil organic matter content, Biogeochemistry,
137, 297-306, 10.1007/s10533-018-0424-3, 2018.

Rasse, D., Rumpel, C., and Dignac, M.-F.: Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation, Plant
and Soil, 269, 341-356, 10.1007/s11104-004-0907-y, 2005.

65   Remusat, L., Hatton, P. J., Nico, P. S., Zeller, B., Kleber, M., and Derrien, D.: NanoSIMS Study of Organic Matter Associated
with Soil Aggregates: Advantages, Limitations, and Combination with STXM, Environ. Sci. Technol., 46, 3943-3949,
10.1021/es203745k, 2012.

Resat, H., Bailey, V., McCue, L. A., and Konopka, A.: Modeling Microbial Dynamics in Heterogeneous Environments: Growth
on Soil Carbon Sources, Microbial Ecology, 63, 883-897, 10.1007/s00248-011-9965-x, 2012.

70   Rochette, P., and Angers, D. A.: Soil surface carbon dioxide fluxes induced by spring, summer, and fall moldboard plowing in
a sandy loam, Soil Science Society of America Journal, 63, 621-628, 10.2136/sssaj1999.03615995006300030027x, 1999.

Rovira, A. D., and Greacen, E. L.: The effect of aggregate disruption on the activity of microorganisms in the soil

, Australian Journal of Agricultural Research, 8, 659-673, 1957.

Rowley, M. C., Grand, S., and Verrecchia, É. P.: Calcium-mediated stabilisation of soil organic carbon, Biogeochemistry, 137,
75   27-49, 10.1007/s10533-017-0410-1, 2018.

Ruamps, L. S., Nunan, N., Pouteau, V., Leloup, J., Raynaud, X., Roy, V., and Chenu, C.: Regulation of soil organic C
mineralisation at the pore scale, Fems Microbiology Ecology, 86, 26-35, 10.1111/1574-6941.12078, 2013.

Sallih, Z., and Bottner, P.: Effect of Wheat (Triticum-Aestivum) Roots on Mineralization Rates of Soil Organic-Matter, Biology
and Fertility of Soils, 7, 67-70, 1988.

80   Schimel, J.: SOIL CARBON Microbes and global carbon, Nature Climate Change, 3, 867-868, 2013.

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M., Kogel-Knabner, I.,
Lehmann, J., Manning, D. A. C., Nannipieri, P., Rasse, D. P., Weiner, S., and Trumbore, S. E.: Persistence of soil organic
matter as an ecosystem property, Nature, 478, 49-56, 2011.

Senesi, N., and Plaza, C.: Role of humification processes in recycling organic wastes of various nature and sources as soil
85   amendments, Clean-Soil Air Water, 35, 26-41, 10.1002/clen.200600018, 2007.

Shan, J., Brune, A., and Ji, R.: Selective digestion of the proteinaceous component of humic substances by the geophagous
earthworms Metaphire guillelmi and Amynthas corrugatus, Soil Biology & Biochemistry, 42, 1455-1462,
10.1016/j.soilbio.2010.05.008, 2010.

Shen, C. C., Xiong, J. B., Zhang, H. Y., Feng, Y. Z., Lin, X. G., Li, X. Y., Liang, W. J., and Chu, H. Y.: Soil pH drives the
90   spatial distribution of bacterial communities along elevation on Changbai Mountain, Soil Biology & Biochemistry, 57, 204-211,
10.1016/j.soilbio.2012.07.013, 2013.

Sierra, C. A., Trumbore, S. E., Davidson, E. A., Vicca, S., and Janssens, I.: Sensitivity of decomposition rates of soil organic
matter with respect to simultaneous changes in temperature and moisture, Journal of Advances in Modeling Earth Systems,
7, 335-356, 10.1002/2014MS000358, 2015.

95   Sinsabaugh, R. L., Manzoni, S., Moorhead, D. L., and Richter, A.: Carbon use efficiency of microbial communities:
stoichiometry, methodology and modelling, Ecology Letters, 16, 930-939, 10.1111/ele.12113, 2013.

Sinsabaugh, R. L., Belnap, J., Findlay, S. G., Shah, J. J. F., Hill, B. H., Kuehn, K. A., Kuske, C. R., Litvak, M. E., Martinez, N.
G., Moorhead, D. L., and Warnock, D. D.: Extracellular enzyme kinetics scale with resource availability, Biogeochemistry,
121, 287-304, 10.1007/s10533-014-0030-y, 2014.

00   Sistla, S. A., Moore, J. C., Simpson, R. T., Gough, L., Shaver, G. R., and Schimel, J. P.: Long-term warming restructures
Arctic tundra without changing net soil carbon storage, Nature, 497, 615-+, 10.1038/nature12129, 2013.

Six, J., Elliott, E. T., Paustian, K., and Doran, J. W.: Aggregation and Soil Organic Matter Accumulation in Cultivated and
Native Grassland Soils, Soil Sci Soc Am J, 62, 1367–1377 1998.

67

Six, J., Conant, E., Paul, E. A., and Paustian, K.: Stabilization mechanisms of soil organic matter : implications for C-saturation of soils, Plant and Soil, 241, 155-176, 2002.

Stahl, C., Fontaine, S., Klumpp, K., Picon-Cochard, C., Grise, M. M., Dezecache, C., Ponchant, L., Freycon, V., Blanc, L., Bonal, D., Burban, B., Soussana, J. F., and Blanfort, V.: Continuous soil carbon storage of old permanent pastures in Amazonia, Global Change Biology, 23, 3382-3392, 10.1111/gcb.13573, 2017.

Stamati, F. E., Nikolaidis, N. P., Banwart, S., and Blum, W. E. H.: A coupled carbon, aggregation, and structure turnover (CAST) model for topsoils, Geoderma, 211, 51-64, 10.1016/j.geoderma.2013.06.014, 2013.

Sutton, R., and Sposito, G.: Molecular Structure in Soil Humic Substances: The New View, Environ. Sci. Technol., 39, 9009-9015, 2005.

Tamrat, W. Z., Rose, J., Grauby, O., Doelsch, E., Levard, C., Chaurand, P., and Basile-Doelsch, I.: Composition and molecular scale structure of nanophases formed by precipitation of biotite weathering products, Geochimica et Cosmochimica Acta, 229, 53-64, https://doi.org/10.1016/j.gca.2018.03.012, 2018.

Tamrat, W. Z., Rose, J., Grauby, O., Doelsch, E., Levard, C., Chaurand, P., and Basile-Doelsch, I.: Soil organo-mineral associations formed by co-precipitation of Fe, Si and Al in presence of organic ligands, Geochimica et Cosmochimica Acta, 260, 15-28, https://doi.org/10.1016/j.gca.2019.05.043, 2019.

Terrat, S., Horrigue, W., Dequietd, S., Saby, N. P. A., Lelievre, M., Nowak, V., Tripied, J., Regnier, T., Jolivet, C., Arrouays, D., Wincker, P., Cruaud, C., Karimi, B., Bispo, A., Maron, P. A., Prevost-Boure, N. C., and Ranjard, L.: Mapping and predictive variations of soil bacterial richness across France, Plos One, 12, 10.1371/journal.pone.0186766, 2017.

Torn, M. S., Trumbore, S. E., Chadwick, O. A., Vistousek, P. M., and Hendricks, D. M.: Mineral control of soil organic carbon and turnover, Nature, London, 389, 170-173, 1997.

Torsvik, V., and Ovreas, L.: Microbial diversity and function in soil: from genes to ecosystems, Current Opinion in Microbiology, 5, 240-245, 10.1016/S1369-5274(02)00324-7, 2002.

Trap, J., Bonkowski, M., Plassard, C., Villenave, C., and Blanchart, E.: Ecological importance of soil bacterivores for ecosystem functions, Plant and Soil, 398, 1-24, 10.1007/s11104-015-2671-6, 2016.

van Groenigen, J. W., van Kessel, C., Hungate, B. A., Oenema, O., Powlson, D. S., and van Groenigen, K. J.: Sequestering Soil Organic Carbon: A Nitrogen Dilemma, Environ. Sci. Technol., 51, 4738-4739, 10.1021/acs.est.7b01427, 2017.

VandenBygaart, A. J.: Comments on soil carbon 4 per mille by Minasny et al. 2017, Geoderma, 309, 113-114, 10.1016/j.geoderma.2017.05.024, 2018.

Vidal, A., Quenea, K., Alexis, M., and Derenne, S.: Molecular fate of root and shoot litter on incorporation and decomposition in earthworm casts, Organic Geochemistry, 101, 1-10, 10.1016/j.orggeochem.2016.08.003, 2016.

Vogel, C., Mueller, C., Höschen, C., Buegger, F., Heister, K., Schulz, S., Schloter, M., and Kögel-Knabner, I.: Submicron structures provide preferential spots for carbon and nitrogen sequestration in soils, Nat Commun, 5, 10.1038/ncomms3947, 2014.

Vogel, L. E., Makowski, D., Garnier, P., Vieublé-Gonod, L., Coquet, Y., Raynaud, X., Nunan, N., Chenu, C., Falconer, R., and Pot, V.: Modeling the effect of soil meso- and macropores topology on the biodegradation of a soluble carbon substrate, Advances in Water Resources, 83, 123-136, http://dx.doi.org/10.1016/j.advwatres.2015.05.020, 2015.

von Luetzow, M., Kogel-Knabner, I., Ludwig, B., Matzner, E., Flessa, H., Ekschmitt, K., Guggenberger, G., Marschner, B., and Kalbitz, K.: Stabilization mechanisms of organic matter in four temperate soils: Development and application of a conceptual model, Journal of Plant Nutrition and Soil Science-Zeitschrift Fur Pflanzenernahrung Und Bodenkunde, 171, 111-124, 2008.

Wen, Y., Su, L. M., Qin, W. C., Fu, L., He, J., and Zhao, Y. H.: Linear and non-linear relationships between soil sorption and hydrophobicity: Model, validation and influencing factors, Chemosphere, 86, 634-640, 10.1016/j.chemosphere.2011.11.001, 2012.

West, T. O., and Six, J.: Considering the influence of sequestration duration and carbon saturation on estimates of soil carbon capacity, Climatic Change, 80, 25-41, 10.1007/s10584-006-9173-8, 2007.

White, R. E., Davidson, B., Lam, S. K., and Chen, D. L.: A critique of the paper 'Soil carbon 4 per mille' by Minasny et al.
50 (2017), Geoderma, 309, 115-117, 10.1016/j.geoderma.2017.05.025, 2018.
Wiesmeier, M., Urbanski, L., Hobley, E., Lang, B., von Lützow, M., Marin-Spiotta, E., van Wesemael, B., Rabot, E., Ließ, M.,
Garcia-Franco, N., Wollschläger, U., Vogel, H.-J., and Kögel-Knabner, I.: Soil organic carbon storage as a key function of
soils - A review of drivers and indicators at various scales, Geoderma, 333, 149-162,
https://doi.org/10.1016/j.geoderma.2018.07.026, 2019.
55 Zangerle, A., Pando, A., and Lavelle, P.: Do earthworms and roots cooperate to build soil macroaggregates? A microcosm
experiment, Geoderma, 167-68, 303-309, 10.1016/j.geoderma.2011.09.004, 2011.
Zimmerman, A. R., Chorover, J., Goyne, K. W., and Brantley, S. L.: Protection of Mesopore-Adsorbed Organic Matter from
Enzymatic Degradation, Environ. Sci. Technol., 38, 4542-4548, 10.1021/es035340+, 2004.

50

Table 1: Possible non-linear mechanisms of carbon decomposition or accumulation. Due to these mechanisms, decomposition rates are dependent on the amounts of carbon supplied or present. These processes can interact with each other.

MAIN NON-LINEAR MECHANISMS
Effect of organic matter on physical properties that affect biodegradation rates: - Water properties (porosity, wettability, evaporation, mulch) - Ground temperature (porosity, thermal conductivity, albedo, mulch)
Minerals/organic matter ratio modulating carbon stabilization
Physical protection ("glue" role of organic matter and microbial polysaccharides) favoring organomineral associations
Exsudation release of complexing organic acids that destabilize organomineral associations
Priming effect: stimulation of the biodegradation of stabilized organic matter by the energy supply from fresh matter
Carbon use efficiency depending on nutrients available to microorganisms
Toxicity of biodegradation byproducts to microbes (e.g. antibacterial litter, phenols)
Organic matter resources for fauna that promote organomineral stabilization (earthworms)

Factor changes (increase ↗, decrease ↘)		Effect on the intensity of the mechanism involved (increase ↗, decrease ↘, increase or decrease ↗↘)		Effect on carbon storage	Consideration in models Century, RothC
↗	Carbon input flux	↗	Source of organic matter	↗↗	Yes
↗	Decomposable carbon input flux	↗	Mineralization of old C by the priming effect	↘	No
↗	Biodegradabily of C input (plants, organic wastes)	↗	Carbon use efficiency	↗	No
		↗↘	Sorption, associations with minerals	↗↘	No
↗	Soil temperature	↗	Microbial activity	↘↘	Yes, all mechanisms combined
		↘	Sorption		
		↗	Diffusion		
↗	Water content (except pO2)	↗	Microbial growth and mobility	↘	Yes, all mechanisms combined
		↘	Sorption		
		↗	Diffusion and transfer		
↘	O2 (anaeroby)	↘	Microbial activity	↗	Yes
		↘	Oxydative degradation		No
	Granulometry:	↘	Diffusion and transfer	↗	Yes, all mechanisms combined
↘	Mineral size	↗	Sorption		
	Mineralogy : - Short range order phases	↗	Coprecipitation	↗↗	No
↗	- Al, Fe, Ca complexes	↗	Complexation	↗	No
		↗	Sorption	↗	No
	- 2:1 phyllosilicates	↘	Transfer	↗	No
		=	Microbial activity (4.5 <pH< 8.3)	0	No
		↗	Charge of organic and mineral surfaces	↗	No
↗	pH	↗↘	Destabilization of organomineral associations	↗↘	No
		↘	Free Al	↘	No
		↗	Exchangeable Ca	↗	No
		↗	Fauna		
↗	Ionic species in soil solution	↗	Al^{3+}, Ca^{2+} concentration	↗	No
		↗	Na^+ concentration (salty soil)	↘	No
		↗	Decomposition of high C/N organic residue	↘	Yes
↗	N, P, S availability	↘	Priming effect	↗	No
		↗↘	Carbon use efficiency		No
		↗	Antibacterial compounds	↗	No
↗	Activities of specific organisms, biodiversity	↗	Bacteriovorous predators	↗	No
		↗	Mycorrhizal symbiosis	↗↘	No
		↗	Earthworms (association with minerals)	↗	No
↗	Biotic/abiotic interactions (exudates, excreta)	↗	Dissolution of short range order minerals	↗↘	No
		↘	Local pH	↗↘	No

70

71
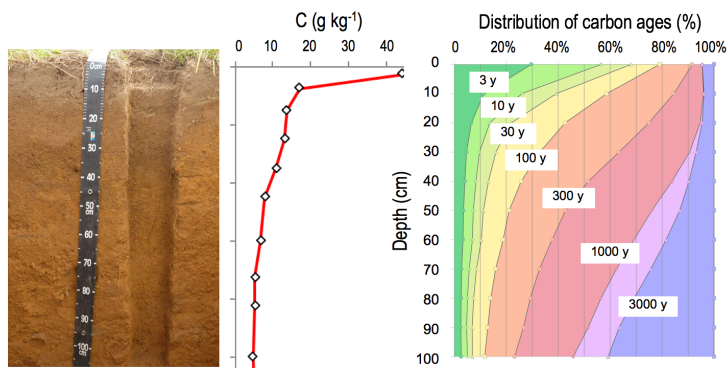
Figure 1: Grassland soil profile (left panel). The vertical distribution of organic carbon in this soil (central panel). A current distribution of carbon ages (right panel, based on data from Balesdent et al. (2018))
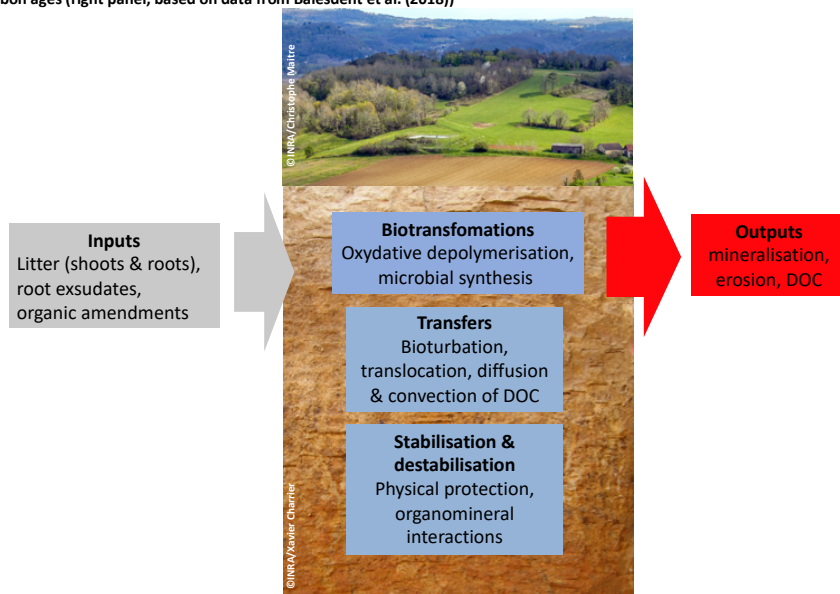

Figure 2: The different processes that control carbon storage in soils (DOC: dissolved organic carbon)
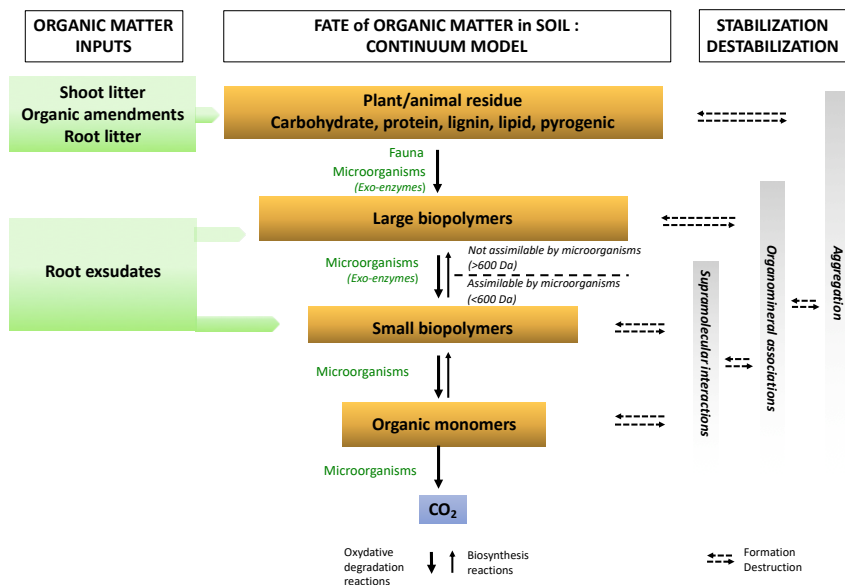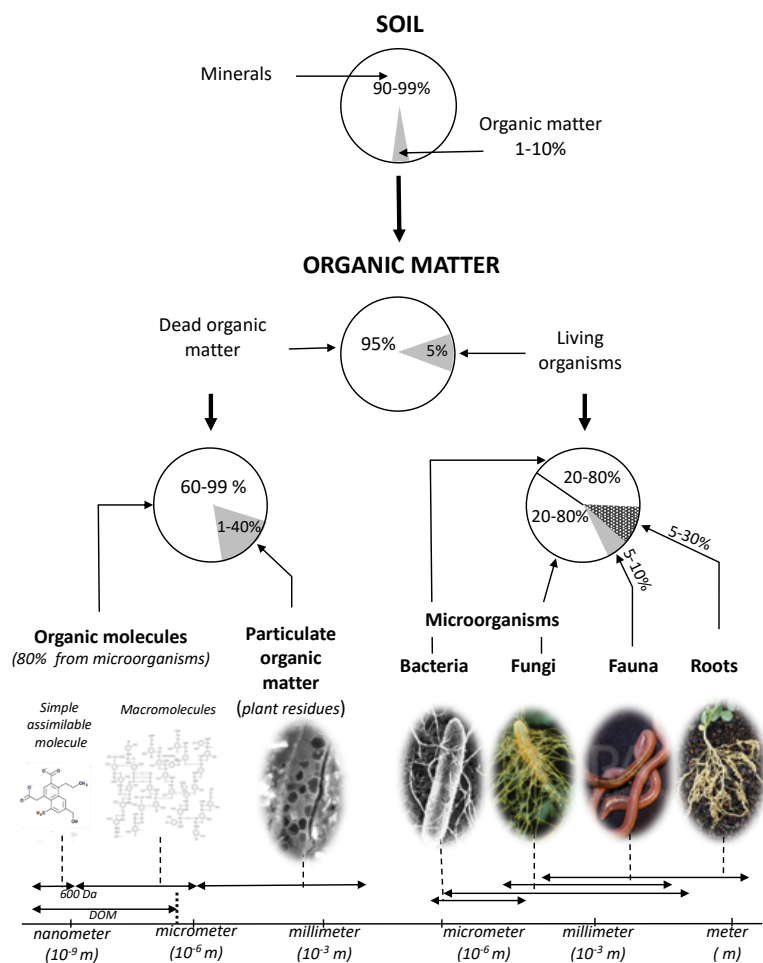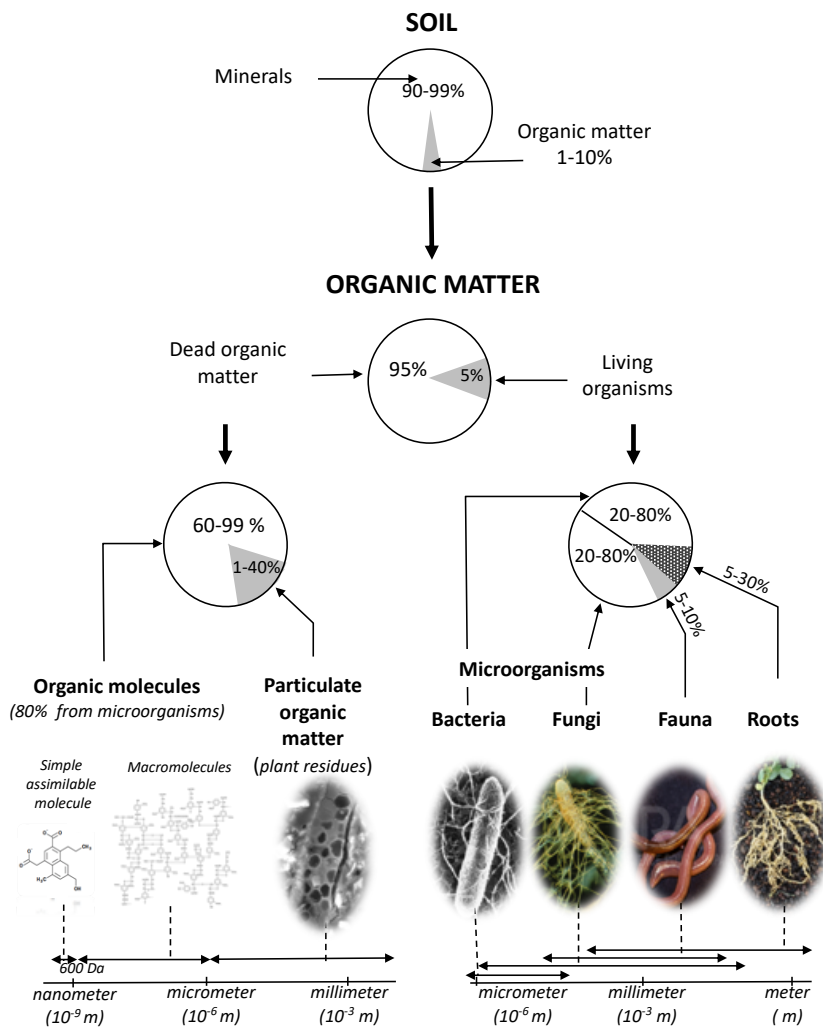
72

Figure 3: Representation of the soil OM biotransformation continuum model (adapted from Lehmann and Kleber (2015)). Organic matter enters the soil surface and deeper horizons in different forms. It is continuously degraded from plant and animal debris to the smallest molecules by the decomposer community. 600 Da (approximately 1 nm) represents the size at which molecules can be absorbed by microorganisms. Simultaneously, the rising oxidation state of the OM carbons increases the water solubility of the compounds, while also enhancing potential protection against further decomposition through greater reactivity to the OM (supramolecular associations), to mineral surfaces (organomineral interactions) and their incorporation into aggregates (aggregation). Solid arrows represent biotic processes and dashed arrows indicate abiotic processes.

SOIL

Minerals → 90-99%

Organic matter
1-10%

ORGANIC MATTER

Dead organic matter → 95% | 5% ← Living organisms

60-99 %
1-40%

20-80%
20-80%
5-10%
5-30%

Organic molecules
(80% from microorganisms)

Particulate organic matter
(*plant residues*)

Microorganisms

Bacteria   **Fungi**   **Fauna**   **Roots**

Simple assimilable molecule   *Macromolecules*

600 Da

DOM

| *nanometer* | *micrometer* | *millimeter* | *micrometer* | *millimeter* | *meter* |
| $(10^{-9} m)$ | $(10^{-6} m)$ | $(10^{-3} m)$ | $(10^{-6} m)$ | $(10^{-3} m)$ | (m) |

74

SOIL

Minerals

90-99%

Organic matter
1-10%

ORGANIC MATTER

Dead organic
matter

95%   5%

Living
organisms

60-99 %

1-40%

20-80%

20-80%

5-30%

5-10%

Organic molecules
(80% from microorganisms)

**Particulate
organic
matter**
(*plant residues*)

Microorganisms

Bacteria   **Fungi**   **Fauna**   **Roots**

*Simple
assimilable
molecule*

Macromolecules

600 Da

nanometer
(10⁻⁹ m)

micrometer
(10⁻⁶ m)

millimeter
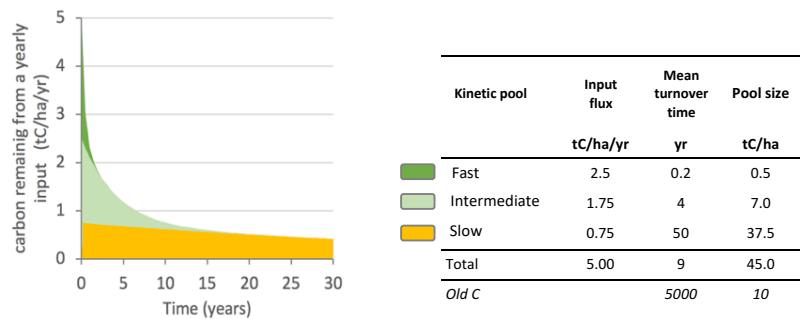(10⁻³ m)

micrometer
(10⁻⁶ m)

millimeter
(10⁻³ m)

meter
(m)

Figure 4: Nature, size range and indicative proportions (<2 mm) of soil organic matter. Organic matter makes up less than 10% of soil constituents. The stock of C in a soil is mainly made up of dead organic matter molecules mainly resulting from the functioning of microorganisms. Adapted from Calvet et al. (2011).

Kinetic pool	Input flux	Mean turnover time	Pool size
	tC/ha/yr	yr	tC/ha
Fast	2.5	0.2	0.5
Intermediate	1.75	4	7.0
Slow	0.75	50	37.5
Total	5.00	9	45.0
Old C		*5000*	*10*

Figure 5: Left side: Simplified kinetic representation of the fate of plant organic inputs in soil (single input event, here 5 tC/ha/year). The kinetics is divided into three mineralization phases: fast, intermediate and slow. Right side: Organic matter can be divided into three corresponding pools, the size of which is represented in the figure by the colored areas. The sizes of the pools inherited from the inputs at year 0 decreases progressively with their own kinetics over 30 years. Pool sizes were calculated based on 30 years of yearly inputs (with fluxes between pools). The numerical values are typical of the 0-30 cm layer of temperate crops. Old carbon represents organic material inherited from a distant past.

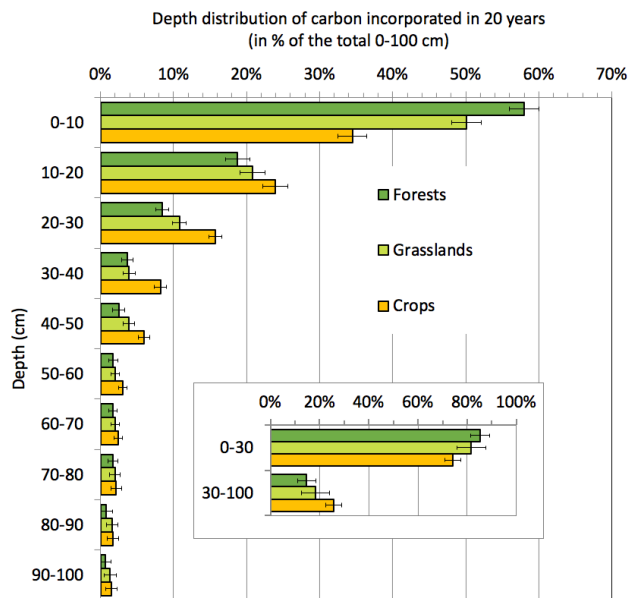**Depth distribution of carbon incorporated in 20 years (in % of the total 0-100 cm)**

Figure 6: Vertical distribution of carbon incorporated by plant matter in the soil in 20 years under average temperate conditions. The data are from the quantification of a recent incorporation of atmosphere-derived carbon atoms into whole-soil profiles, through a meta-analysis of changes in stable carbon isotope signatures at 112 grassland, forest and cropland sites, across different climatic zones, from 1965 to 2015. The quantity (in 10 cm increments) is expressed as a proportion of the total C incorporated in the first meter of soil. The value is a regression mean estimated from climate and land-use conditions. The error bars represent the 95% confidence interval of the estimate. (Based on data from Balesdent et al. (2018)).

"mineral transfer and association processes"?