#RootsNotShoots – Joel Williams

Introduction

In recent times there has been growing interest in the potential of soils to sequester carbon from the atmosphere and there has been an increased number of studies investigating the dynamics of soil organic matter [SOM], particularly in the past decade or so. Even without highlighting the benefits of carbon sequestration for climate change, there are many ecosystem and agronomic benefits to building SOM levels which can improve both production and profitability – clearly a major win-win. Many new ideas and new paradigms are emerging and perhaps challenging some of the previous ideas about SOM. For example, it has been suggested that 'humus' as we study it in the lab, does not really exist in the soil and that it is exclusively a product of the extraction process[1] – in other words, the properties of humus and humic substances measured in the lab are not the same as in the soil, before it was extracted out. Alternative ways to consider SOM have been proposed based on water solubility or separating it into different fractions based on particle size and its attachment to soil mineral surfaces[2]. The focus of this article will not cover this nuanced discussion, but perhaps this is something that could be explored in a future article. Instead we will take a step back and with a more practical focus, consider the influence of different plant materials [shoots, roots and exudates] as they enter the soil and interact with the chemical, physical and biological properties of the soil on its way to forming SOM.

Microbial Transformation Carbon Inputs

Before we get to key focus of this article and tease out the intricacies of plant litter integration, we must first highlight the role of soil organisms in processing and transforming these carbon [C] inputs into SOM. Being photosynthetic organisms, plants provide the initial C inputs to the soil however it is the fungal and bacterial bodies, their various metabolic by-products and particularly their dead bodies [microbial necromass] that are the primary C containing constituents of the more stable fractions of the SOM pool[3–7]. So if microbes are key drivers of SOM formation, how can we help facilitate this process? What is their preferred food source? How do we improve the efficiency of growing their living biomass so that it can eventually contribute to SOM via its death and decay processes? Here we must differentiate between high quality and low quality food sources and that particularly comes down to the C:N ratio. N-rich substrates (low C:N) are more easily digested by microbes, so it with a greater efficiency in which they can assimilate these substrates into their living biomass. Recent studies highlight that low C:N ratio inputs play a particularly important role in forming SOM that binds to mineral surfaces and these are also part of the more stable SOM pools[8–10]. It appears that the better quality C inputs play a more important role so let's explore the different qualities of plant derived C inputs.

Roots Not Shoots

Rightly so, we have traditionally placed significant focus on stubble retention and maintaining shoot litter on the surface of the soil for a host of important reasons – protecting the soil from erosion, conserving soil moisture, providing habitat for soil dwellers and to build SOM. However, there is a significant body of evidence that highlights that although those surface shoots do help to build SOM [mainly indirectly], there is a much more efficient pathway, but we must shift our attention to belowground residues – roots not shoots[11–16].

One particular study reviewed a selection of other studies that have explored this relationship between roots vs shoots. Figure 1 summarises their findings and highlights what percentage of above- or below- ground carbon was captured into SOM. Overall, they suggest that root inputs are approximately five times more likely than shoot inputs to become integrated into SOM[16].

Table 1: Proportion of aboveground and belowground biomass contributing to SOM formation in agricultural field studies performed in situ using primarily isotopic approaches[16]

Vegetation type or treatment	Belowground carbon inputs retained in SOM (%)	Aboveground carbon inputs retained in SOM (%)	Ratio	Reference
Conventional agriculture	35%	4.8%	7.4	Kong & Six 2010
Low-input agriculture	65%	4.9%	13.2	Kong & Six 2010
Organic agriculture	91%	3.6%	25.6	Kong & Six 2010
Mixed C_3 and C_4 crops	36%	4.0%	9.0	Ghafoor et al. 2017
Mixed C_3 and C_4 fertilized crops	18%	10%	1.8	Ghafoor et al. 2017
Maize	61%	5.0%	12.2	Mazzilli et al. 2015
Soybean	80%	3.0%	26.7	Mazzilli et al. 2015
Rye cover crop, 5 months	26%	5.2%	5.0	Austin et al. 2017
Rye cover crop, 12 months	27%	3.5%	7.7	Austin et al. 2017
Rye cover crop	24%	5.9%	4.1	Austin et al. 2017
Maize	21%	12%	1.7	Bolinder et al. 1999
Maize	38%	11%	3.5	Balesdent & Balabane 1996
Maize	73%	14%	5.1	Clapp et al. 2000
Maize, fertilized	58%	16%	3.6	Clapp et al. 2000
Vetch	49%	13%	3.7	Puget & Drinkwater 2001
Maize	34%	8.0%	4.3	Barber 1979
Mix C_3 and C_4 crops	39%	17%	2.3	Kätterer et al. 2011
Average, median	46%, 39%	8.3%, 6.6%	8.1, 5.0	

There are a few nuanced factors involved but overall, there is no magic secret as to why roots have a disproportionate influence rather than shoots – the primary driver is simply the fact that roots reside in the soil and that's where the bulk of the living biota are also found. So the spatial accessibility and point of entry of roots and exudates[15] to the soil biology means they are more effectively processed into microbial biomass as compared to surface shoot-C which is far more prone to being oxidised off into the atmosphere as CO_2. Additionally, the constant drip feed of root exudates stimulates more steady assimilation and lower microbial respiration as compared to larger but infrequent C additions which can induce greater respiration losses[15]. Down in the soil, root-C is also far more likely to be entangled and embedded within aggregates where it is physically protected from oxidation and occluded from microbial degradation[17].

What about Root Exudates?

So if root litter plays a more important role than shoot litter, the next logical question would lead us to – what about root exudates? How much of a contribution do root exudates make toward building SOM? It appears that root exudates may have historically been rather overlooked in many studies exploring SOM dynamics – and there are two key reasons for this. Firstly, the sampling of root exudates 'in situ' is incredibly difficult hence making them extremely hard to study[18]; and secondly, previous thinking was that root exudates were unlikely to ever be stabilised into SOM as they were too labile [structurally simple] and not recalcitrant [structurally complex] enough. However, this paradigm that only complex forms of carbon are more important for soil carbon sequestration has been displaced by a growing body of evidence that recalcitrance [or complexity] is not solely the most important factor for carbon stabilisation in soils[17,19–21]. These recalcitrant carbon compounds [plant litters] have a lower carbon use efficiency [CUE] than root exudates[22–24]. In other words, what that means is that it is easier and less metabolically expensive for microbes to consume root exudate carbon than it is plant litter carbon – as exudates are easier to digest, they can be readily assimilated and this more efficiently increases the overall microbial biomass. Degrading this plant litter comes at an energetic cost as microbes cannot assimilate it 'as is'. They have to synthesise and excrete extracellular enzymes first, which externally digest the complex litter into smaller components, which only then can be assimilated. Consequently, the synthesis of these extracellular enzymes costs or wastes microbial energy and overall they produce less microbial biomass per unit of C when feeding on litter vs exudates[22–24]. How more or less efficiently different C inputs grow microbial biomass is a critical factor because as was discussed earlier, it is dead microbial biomass that contributes so significantly to the genesis of SOM[4] and root exudates are estimated to fuel more than 50% of belowground foodweb activity[25–27]. Succinctly put, the more efficiently we produce microbial biomass, the more efficiently we ultimately sequester SOM and root exudates have a higher CUE than litter inputs. Again, I must stress that litter inputs still play a role and are still important overall to create the microclimate for the soil, but here I am focussing on 'efficiencies' and in this context, gains are to be had by shifting thinking belowground.

Going Belowground

What does all this mean from a practical application point of view? How do we interpret the science into applied and actionable strategies to improve SOM? Does the new evidence supersede previous paradigms of soil carbon sequestration or do we need to integrate them together into a consolidated view? Of course, I am not advocating a shift away from stubble retention practices! Stubbles may well be the less 'efficient' way to build SOM but they sure bring hugely significant benefits to overall soil function by protecting the soil and creating an ideal environment for the belowground interactions to work more efficiently. Residues are undoubtedly essential [particularly in dry climates], but perhaps what the emerging evidence suggests is that we need an additional focus on root biomass and maintaining a living root in the soil as well. It's only half the job if we are keeping the soil covered with residue, this aboveground strategy must be matched with a belowground strategy and with equal emphasis and gusto. Perhaps the soil health principle that states 'keep the soil covered with residue *or* living plants' should read ‘keep the soil covered with residue *and* living plants’. Now of course, it is additionally up to each producer to strive to apply this principle within the moisture constraints of their soil type and local climatic conditions. How the principle will be applied should be interpreted and translated into the field conditions on a case by case scenario.

Strategies to improve the overall rooting and belowground potential of the production system might include:

1. Maintain a living root:
    - Integrate Perennials – perennials allocate more C belowground than annuals and being perennial, they maintain a living root in the soil for longer.
    - Cover crops – cocktail covers are an ideal means to select some deep rooted species to encourage greater root biomass production. Cover crops also help to extend the growing season outside of the main cash crop season and hence also help to maintain a living root for longer.
    - Intercropping – intercropping and companion cropping hold great potential as the companion plant could be selected for its belowground rooting behaviours – for example grow the cash crop for its shoots [yield] and the companion for its roots [SOM]. Legumes are a particularly good choice as a companion due to the higher quality residues they input into the soil. Relay intercropping with cash crops can also extend the number of days with living roots in the soil and that means more highly efficient exudates leaking into the soil.
2. Increase the root:shoot ratio:
    - Select varieties of both cash crops and cover crops with better root characteristics – deeper roots, more branching roots and more fine roots are particularly ideal [Figure 1]. Traditional varieties hold particular potential but even modern varieties have much variability in rooting biomass.
    - There is untapped potential to breed new varieties with better rooting characteristics for future production systems. Design with roots in mind and reap the benefits to the production system over the long term. Root biomass might come at a short term cost to shoot biomass but that can be offset under low input production systems – bigger roots mean greater moisture resilience and less inputs required due to greater nutrient scavenging from the soil.
3. Increase plant species diversity:
    - Different plant species have different rooting architectures, root depths, root C:N ratios and this diversity of root biomass all helps via different modes of action.
    - Each different plant species also exudes a distinctive cocktail of root exudates that are unique to that particular species. More plant species will lead to a greater diversity of root exudates entering the soil and that helps to grow a greater diversity microbial biomass which ultimately can be integrated into SOM upon death.
4. Optimise plant Nutrition:
    - Mineral deficiencies will limit photosynthetic potential and it is photosynthesis that drives root biomass and root exudation production. Ensure you are managing all macro and micro minerals and address any limiting factors. Tissue and sap tests are

particularly ideal for in-season monitoring and any shortages can be rapidly addressed via foliar applied solutes.

Figure 1: Einkorn [left] vs modern durum [right] root development. Species or varieties with greater root:shoot ratios can be selected to encourage more belowground carbon allocation. Photo: Edward Dickin

In Summary

Roots make a more important contribution to building SOM than shoots. With the recent interest in building soil carbon levels, it is clear a greater focus on strategies to encourage belowground carbon allocation is required. Traditional efforts focussing solely on maximizing the amount of residues on soils and minimizing physical disturbances such as tillage, may need to be rethought to ensure that the performance of living plants within the system is integrated for both yield and soil functioning. Consequently, the soil health principle of maintaining a living root emerges as a key strategy moving forward along with selecting species or varieties with greater root biomass, designing with more plant species diversity and ensuring plant photosynthetic potential is optimised via overcoming mineral limitations.

References

1. The contentious nature of soil organic matter. (2015). doi: 10.1038/nature16069
2. Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. (2019). doi:10.1111/gcb.14859
3. Fate of gram-negative bacterial biomass in soil - Mineralization and contribution to SOM. (2006). doi: 10.1016/j.soilbio.2006.04.047
4. SOM genesis: Microbial biomass as a significant source. (2012). doi: 10.1038/NGEO2520
5. Fate of ectomycorrhizal fungal biomass in a soil bioreactor system and its contribution to soil organic matter formation. (2015). doi: 10.1016/j.soilbio.2015.05.012
6. Quantitative assessment of microbial necromass contribution to soil organic matter. (2019). doi: 10.1111/gcb.14781
7. Mineral surface-reactive metabolites secreted during fungal decomposition contribute to the formation of soil organic matter. (2017). doi: 10.1111/1462-2920.13990
8. Nitrogen-rich microbial products provide new organo-mineral associations for the stabilization of soil organic matter. (2018). doi: 10.1111/gcb.14009
9. Soil Organic Carbon Stabilization: Mapping Carbon Speciation from Intact Microaggregates. (2018). doi: 10.1021/acs.est.8b03095
10. Soil organic matter is stabilized by organo-mineral associations through two key processes: The role of the carbon to nitrogen ratio. (2020). doi: 10.1016/j.geoderma.2019.113974
11. Greater humification of belowground than aboveground biomass carbon into particulate soil organic matter in no-till corn and soybean crops. (2015). doi: 10.1016/j.soilbio.2015.02.014
12. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. (2005). doi: 10.1007/s11104-004-0907-y
13. Below-ground carbon inputs contribute more than above-ground inputs to soil carbon accrual in a bioenergy poplar plantation. (2019). doi: 10.1007/s11104-018-3850-z
14. The root of the matter: Linking root traits and soil organic matter stabilization processes. (2018). doi: 10.1016/j.soilbio.2018.02.016
15. Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. (2018). doi:10.1038/s41561-018-0258-6
16. The Ecology of Soil Carbon: Pools, Vulnerabilities, and Biotic and Abiotic Controls. (2017). doi: 10.1146/annurev-ecolsys-112414-054234
17. Soil organic matter turnover is governed by accessibility not recalcitrance. (2012). doi: 10.1111/j.1365-2486.2012.02665.x
18. Sampling root exudates – Mission impossible? (2018). doi: 10.1016/j.rhisph.2018.06.004
19. How relevant is recalcitrance for the stabilization of organic matter in soils? (2008). doi: 10.1002/jpln.200700049
20. Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: Results from long-term field experiments. (2009). doi: 10.1111/j.1461-0248.2009.01303.x
21. Sub-micron level investigation reveals the inaccessibility of stabilized carbon in soil microaggregates. (2018). doi: 10.1038/s41598-018-34981-9

22. Evidence for the primacy of living root inputs, not root or shoot litter, in forming soil organic carbon. (2019). doi: 10.1111/nph.15361
23. Leveraging a New Understanding of how Belowground Food Webs Stabilize Soil Organic Matter to Promote Ecological Intensification of Agriculture. (2018). doi:10.1016/b978-0-12-812766-7.00004-4
24. Managing Agroecosystems for Soil Microbial Carbon Use Efficiency: Ecological Unknowns, Potential Outcomes, and a Path Forward. (2019). doi: 10.3389/FMICB.2019.01146
25. Exploring carbon flow through the root channel in a temperate forest soil food web. (2014). doi: 10.1016/j.soilbio.2014.05.005
26. The carbon we do not see - The impact of low molecular weight compounds on carbon dynamics and respiration in forest soils: A review. (2005). doi: 10.1016/j.soilbio.2004.06.010
27. The underestimated importance of belowground carbon input for forest soil animal food webs. (2007). doi: 10.1111/j.1461-0248.2007.01064.x