

Growing soil organic carbon in dryland agricultural systems

Mark Farrell^{A,B,C,*} and Gupta Vadakattu^{A,B}

For full list of author affiliations and declarations see end of paper

***Correspondence to:**

Mark Farrell
CSIRO Agriculture & Food, Karna
Country, Locked Bag 2, Glen Osmond,
SA 5064, Australia
Email: mark.farrell@csiro.au

ABSTRACT

Soil organic carbon (SOC) plays a crucial role in dryland agricultural systems, improving resilience, productivity and delivering a range of ecosystem services including carbon (C) sequestration and broader ecosystem health. Although the net primary production (NPP) is the principal source of C inputs to soil, plant–microbe interactions can help increase NPP and stimulate plant C inputs to the soil through a variety of mechanisms. Additionally, the soil microbial community plays a crucial role in the loss (CO₂ respiration) and stabilisation of SOC. With improved understanding of soil microbiomes and plant–microbe interactions, there are new emerging strategies in which microorganisms may be harnessed either directly or indirectly to increase the amount of C added and stabilised in dryland soils.

Sources of carbon, the role of microorganisms and the impacts of management practices

The primary source of carbon (C) inputs to soil is net primary production (NPP) by photosynthetic fixation of atmospheric CO₂ to plant biomass and exudates¹ (Fig. 1). Although exogenous inputs in the form of organic amendments, such as manures, composts and biochars, may be locally relevant they are not typically available in regionally or nationally significant quantities, and typically involve the diversion of C that has already been removed from the atmosphere; thus they are not the concern of this paper. In dryland systems that account for ~45% of global land area² and typically receive < 500 mm of annual rainfall, water availability is the governing factor that limits NPP and thus flows of C to the soil organic C (SOC) pool. Soil microorganisms process C inputs from plants – famously described by David Jenkinson as ‘The eye of the needle’³ – with a proportion of the C lost through microbial respiration to CO₂, and the remainder retained in microbial biomass. This partitioning is termed carbon-use efficiency (CUE).⁴ In turn, microbial biomass is itself subsequently further cycled upon cell death.

Over the past three decades, our understanding of the processes involved in SOC stabilisation have evolved greatly. The traditional view of chemical recalcitrance driving persistence has been largely replaced by multiple lines of evidence that point towards physical and chemical protection of kinetically unstable compounds within aggregates and upon clay particles.⁵ Although emerging research suggests that direct stabilisation of plant C inputs may have been underestimated,⁶ it is understood that the soil microbial community plays a pivotal role in both stabilisation and loss of C in soils. Indeed, in low CUE situations, over 90% of C from fresh inputs may be respired⁷ (Fig. 1).

Soil organic C does not exist in isolation. It is a component of soil organic matter (SOM), and has been shown to broadly conform to Redfield’s stoichiometric ratio, having fairly consistent proportions of C:N:P:S.⁸ Plant C inputs typically contain far greater C:nutrient ratios than microbial biomass or stabilised SOM. Thus, in order to build SOC, nutrients are also required, and the availability of nutrients in ratios broadly representative of SOM typically increases microbial CUE,⁴ although clay content and the size of the extant microbial biomass can be more important drivers.⁹

Modern management practices in dryland systems often seek to maximise water availability for the target crop through the adoption of zero tillage, stubble retention as a mulch and the control of summer weeds. Each of these practices can have a direct or indirect effect on the inputs to and losses of SOC. Additionally, in dryland cropping systems such as those predominantly found across the Australian wheatbelt, nitrogen (N) is frequently a limiting factor for crop production because of conservative application rates that target individual season profitability and may ‘mine’ mineralised N from SOM,¹⁰ resulting in increased losses of SOC by mineralisation.

Received: 17 January 2023

Accepted: 2 February 2023

Published: 20 February 2023

Cite this:

Farrell M and Vadakattu G (2023)
Microbiology Australia
44(1), 18–21. doi:10.1071/MA23005

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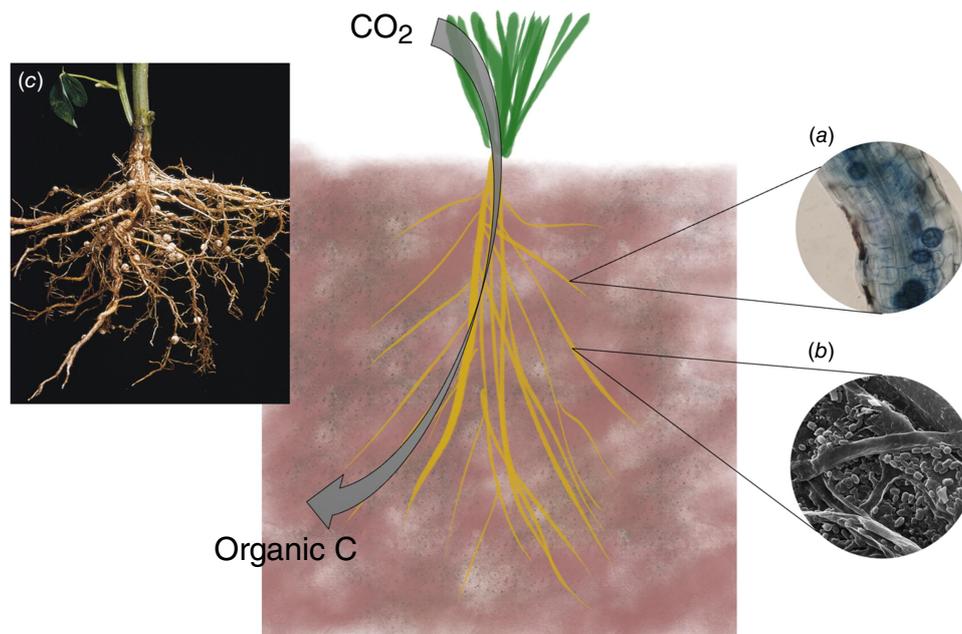


Fig. 1. Conceptual diagram of carbon flow from the atmosphere by the plant to the soil. Photosynthesis fixes atmospheric CO₂, which then enters the soil by above- and below-ground litter and rhizodeposits. Symbiotic fungi such as mycorrhizae (a), plant growth promoting rhizobacteria (b) or, in the case of legumes, rhizobia (c) modulate plant C inputs to the soil by facilitating greater root exploration, N₂ fixation, greater plant productivity and, especially in the case of mycorrhizae, the deposition of their own necromass.

Against this background, a number of practices are emerging that seek to deliver more C to the soil through increasing the proportion of time a living plant is present in the system (e.g. by using cover crops in otherwise fallow periods¹¹), harnessing plant traits that increase C delivery below ground,¹² or manipulating the soil, rhizosphere or root microbiome to increase the stabilisation of plant C inputs.

Progress to date

The most widespread type of biological amendment in regular use in dryland agriculture are rhizobia inocula – N₂ fixing symbionts of legume crops. Tightly optimised for legume crop type and often soil properties, rhizobia can fix 20–25 kg N Mg dry matter⁻¹ year⁻¹ in dryland systems.¹³ Because of the lower C:N ratio of legume-derived organic matter inputs, higher CUE and thus greater retention of legume-derived C may be expected.

However, rhizobia are, by and large, the exception. Although there are a multitude of biological amendments available, including both active inocula and biostimulant products, consistency of results remains poor.¹⁴ Unlike the highly specific and well-understood legume–*Rhizobium* symbiosis that is harnessed to perform an exclusive function, many commercially available microbial inocula have more generalist target outcomes. In a lot of cases, including those with reported aims of increasing SOC, mechanisms and modes of action have often remained unclear or poorly verified. Additionally, there is a need to improve mechanisms of application that protect microbial inoculants from the harsh soil environment prior to their colonisation of the

root and rhizosphere. It is necessary to develop strategies for effective inoculation methods, so that single species or consortia of microorganisms of interest can gain an advantage in colonisation efficiency over native microbiomes in the field environment. This may present a significant challenge given that native microbial communities are highly adapted to their environment.

An important approach to potentially improve the efficacy of microbial inocula and biostimulants in dryland agricultural systems is to develop a clearer understanding of the limits to crop productivity and thus C inputs. Aligned with this, a better understanding of interactive effects of multiple management interventions across several seasons and rotations on plant C inputs by NPP and microbial stabilisation of C inputs is required. Hallama *et al.*¹¹ concluded that cover crops increased mycorrhizal abundance, leading to improved colonisation of the main crop and subsequent provision of nutrients. However, although appropriate application of fungicides may control crop disease and increase crop yield and C inputs of an existing crop, fungicides may also negatively affect non-target fungal functions,¹⁵ including potentially beneficial mycorrhizae, and this is particularly the case for anti-fungal seed coatings.

A promising future?

Recent plant root research has improved our understanding of the diversity of root traits and their contribution to plant and ecosystem functioning.¹⁶ Coupled with this is the progress in understanding root–microbiome interactions both in terms of the drivers of microbiome function and the potential

consequences of manipulating microbiomes to stimulate root growth, health and biogeochemical processes – including C turnover and stabilisation.¹⁷ It is suggested that root architectural traits known to increase below-ground plant-derived C inputs are important drivers of microbial community structure and biomass, which in turn contribute to turnover and stabilisation of freshly added C.

A number of microbial genera and species generally referred to as plant-growth promoting rhizobacteria (PGPR; e.g. *Pseudomonas*, *Azospirillum*, *Bacillus* spp.) have been shown to produce phytohormones (e.g. auxins, gibberellins and cytokinin) and other quorum sensing molecules¹⁸ that promote root growth (lateral root formation, root hair development), thus expanding rhizosphere and rhizodeposit C addition. PGPR may also benefit root growth and functioning through establishment of rhizobial and mycorrhizal symbioses, protection from soil-borne root pathogens and by eliciting plant defences including induced systemic resistance. Beneficial effects from such interactions, in particular from introduced organisms, depend upon the correct microbe–plant combination and the expression of the required functional traits (e.g. producing optimal concentrations of hormones at the appropriate time). Therefore, harnessing this type of root–microbe interaction requires a deeper understanding of the complex feedback mechanisms associated with the abundances of specific microbial species, the types and concentrations of chemical signals, and genetic and environmental controls for functional expression.¹⁸

Despite extensive research demonstrating potential benefits from the symbiotic associations between arbuscular mycorrhizae and agricultural crops, practical applications of these associations are yet to be utilised, largely because the complex influences of edaphic and environmental factors in field environments are not well understood. In Australian dryland agricultural soils with low SOM concentrations, arbuscular mycorrhizae can make a significant contribution to improving plant C inputs and turnover processes through their extensive hyphal networks combined with enzymatic, metabolic and nutrient acquisition capabilities and effects on C translocation below-ground.¹⁶

Plant genotype may play a significant role in the recruitment, assembly and activities of the rhizosphere microbiome. The composition of highly diverse rhizosphere microbiomes is largely selected by the host plant but primarily modulated by soil type.¹⁹ For example, a core root microbiome dominated by a restricted group of bacterial taxa has been found in multiple phyla growing in close proximity. This suggests shared functionality relating to traits in the core root bacterial communities and opportunities for a targeted approach to manipulate root growth across a broad spectrum of plant types.²⁰ Crop-based variations in rhizosphere microbiomes have been well documented, with diverse rotations being shown to increase disease suppression and avoid negative legacies.²¹ Recent evidence has shown that structural or taxonomic diversification of rhizosphere-associated microbial communities exists within crop varieties and between wild and domesticated accessions of many crops (barley, wheat, maize, pearl millet and arabidopsis) – that is, root-associated microbiomes have greater heritable variation.²² Such differences in root traits and microbiomes

could contribute to variability among cultivars for soil C cycling and SOC sequestration potential. A strong relationship between phylogenetic distance and rhizosphere microbiome dissimilarity is reported for different species in both monocotyledons and dicotyledons.²³

As mentioned earlier, N availability is the greatest constraint to Australian dryland wheat production. Engineering crops and synthetic plant–microbe symbioses to introduce N₂ fixation machinery to cereals and other non-legume crops is decades away. Therefore, designer plant–diazotrophic combinations are an attractive option to remove N constraints to production and to increase C inputs in agricultural systems.²⁴ The ecological significance of free-living or associative diazotrophic N₂-fixing bacteria in agricultural soils is becoming more appreciated. A diverse diazotrophic community exists in soils and in below- and above-ground plant parts, and a growing body of evidence suggests that they could be a significant contributor to cereal crop N budgets and thus C inputs.²⁵ This presents an opportunity to harness their capacity in cereal dominated cropping systems.

Although improvements to plant production have been facilitated through breeding and targeted gene manipulation of agricultural crops, there is growing evidence that microorganisms associated with crops can impart positive outcomes on biomass production and biogeochemical processes including C turnover in the vicinity of plant roots. Thus, by understanding the relationship between plants and microbes, more-efficient agricultural systems, particularly in dryland or rainfed cropping regions, could be developed through selection of improved plant genotype–microbiome combinations. Another recent approach is the direct crop application of microbe-to-plant signal molecules, such as isoflavonoids to improve crop tolerance to stresses and enhance plant growth, thus avoiding the constraints related to the successful introduction of microbial inoculants.²⁶

In conclusion, clear potential pathways are emerging by which microorganisms may be harnessed either directly or indirectly to increase the amount of C added and stabilised in dryland soils. These will come from both wider rotation and system-based changes, such as appropriate adoption of cover crops and their feedback effects, and also by targeted plant–microbe interactions and introduction of PGPRs, etc. However, all are underpinned by sustaining or enhancing C inputs from the cash crop, and thus there will be occasions when management to maximise this may involve the targeted use of agrochemicals as part of a sustainable agricultural system.

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Data availability. Data sharing is not applicable as no new data were generated or analysed during this study.

Conflicts of interest. The authors declare that they have no conflicts of interest.

Declaration of funding. The authors received support from the CSIRO Future Science Platform ‘Microbiomes for One-System Health’.

Acknowledgements. Support from the CSIRO Future Science Platform ‘Microbiomes for One-System Health’ is gratefully acknowledged.

Author affiliations

^ACSIRO Agriculture & Food, Kurna Country, Locked Bag 2, Glen Osmond, SA 5064, Australia.

^BCSIRO Microbiomes for One Systems Health Future Science Platform, Kurna Country, Locked Bag 2, Glen Osmond, SA 5064, Australia.

^CUWA School of Agriculture & Environment, The University of Western Australia, Whadjuk Noongar Country, 35 Stirling Highway, Perth, WA 6000, Australia.

Biographies



Dr Mark Farrell is a biogeochemist, with primary interests in carbon and nitrogen cycling in soils, and the impacts of management and environmental change on these processes. Principally working alongside microbiologists, he utilises a range of cutting-edge analytical techniques including nuclear magnetic resonance and mid infrared spectroscopy, as well as stable- and radio-isotopes to understand the composition and flows of carbon and nitrogen through the environment, and how these are moderated by the microbial community.



Dr Gupta Vadakattu investigates on aspects of genetic and functional diversity, functional capability and resilience of soil biota in agricultural soils. Special interests include: genetic, functional and environmental regulators of biological disease suppression in soils, phenotypic and functional diversity of microbiota in the rhizosphere systems, diversity and functional capacity of diazotrophs in annual and perennial crops and turnover to carbon, nutrients and biological health of soils.

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