

OPINION

Soil extracellular enzymes for climate-smart and resource-efficient agroecosystems: Research priorities

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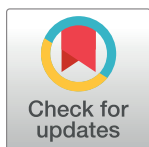
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Global demands for plant biomass are expected to grow substantially over the coming decades, driven by a rapidly growing world population and an ever-increasing demand for food, fibre and fuel. Most of this biomass will come from agricultural systems, with demands for crop yields expected to increase by over 50% between 2005 and 2050 [1]. To sustainably intensify agricultural systems, higher biomass production should be achieved without concomitant increases in fertilizer inputs and without increasing greenhouse gas (GHG) emissions or depleting soil carbon (C) and nitrogen (N) stocks. Achieving this goal in a changing climate will be one of the grand challenges of the 21st century [2].

Recent studies suggest that managing soil microorganisms is a promising technology for developing climate-smart and resource-efficient agroecosystems [3]. For example, soil microorganisms play a key role in enhancing plant nutrient acquisition [4], improving tolerance to drought stress [5], and reducing GHG emissions [6]. Despite the large potential, the relations between microbially mediated C and nutrient cycling, environmental conditions and cropping managements are still largely unclear, limiting the application of microbial technologies. For example, efforts to inoculate plant-growth-promoting microbes often fail due to a lack of acclimatization and competition with indigenous microbes [3]. Measurements on soil microorganisms are also time-consuming, costly, and involve strict requirements regarding laboratory equipment and storage conditions of soil samples. These challenges call for reliable, cheap, and simple methods to quantify the role of soil microbes in key environmental processes relevant to agricultural ecosystems.

Soil extracellular enzymes (EEs) are produced by plants and microbes to catalyse the degradation of organic matter in order to acquire energy and nutrients to support their growth [7]. Plants and microorganisms preferentially invest metabolic resources for EEs production to acquire the nutrients that are limiting their growth [8]. Therefore, EEs can be used to track changes in microbially mediated soil C and nutrient cycling. For example, several recent studies identified a number of hydrolytic and oxidative EEs with strong impacts on soil C and nutrient cycling [9, 10], suggesting the potential to protect soil C stocks and reduce fertilizer inputs if we could manage these EEs. Similarly, soil EEs play important roles in regulating soil N₂O emission and nitrate leaching [11]. These studies strongly suggest the need for research to identify keystone soil EEs for climate-smart and resource-efficient agroecosystems and to determine the mechanisms through which they operate.



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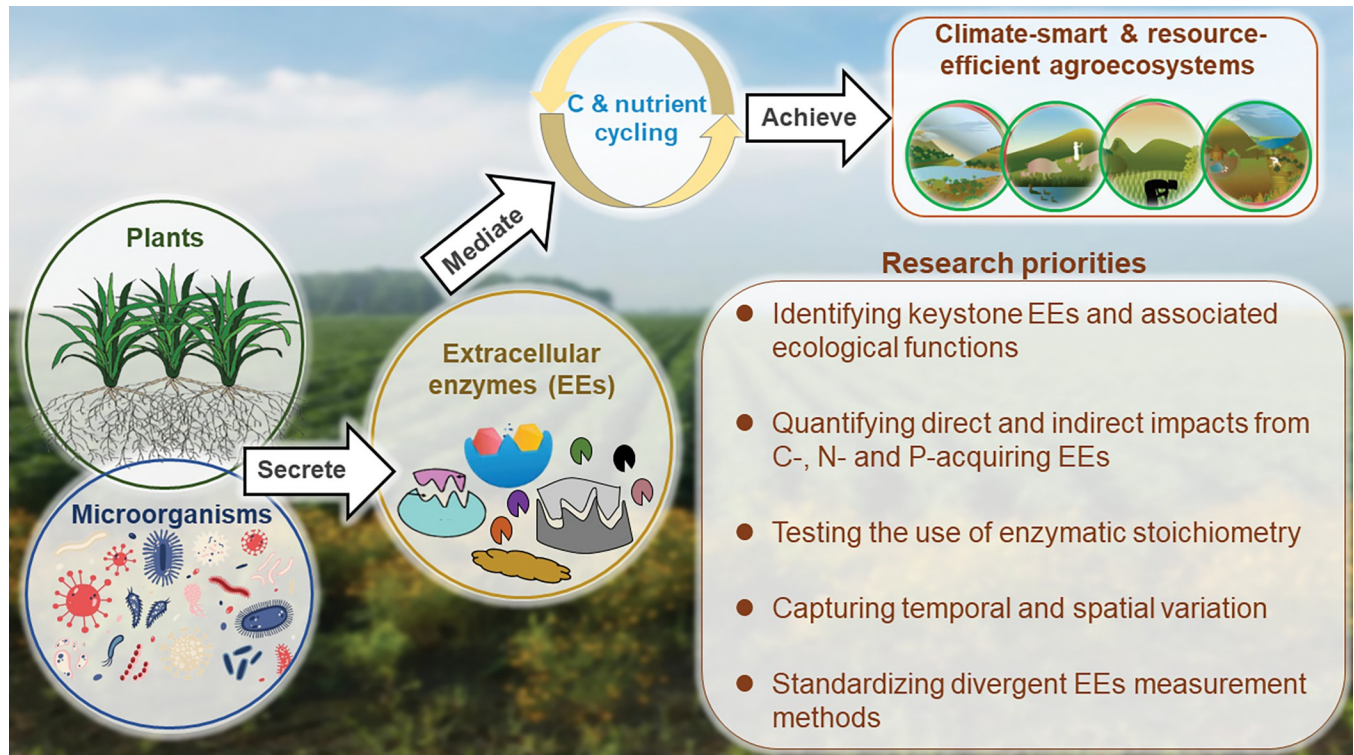


Fig 1. Schematic figure highlighting the critical roles of soil extracellular enzymes for climate-smart and resource-efficient agroecosystems.

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Most research on soil EEs to date has been conducted in natural ecosystems [8] and scientists have only recently started to explore the role of EEs in agroecosystems [12]. Here we highlight several research priorities that need to be addressed to improve our understanding of the role of soil EEs in agricultural soils (Fig 1). First, there is an urgent need to identify which EEs are playing key roles in minimizing environmental impacts and increasing resilience to climate extremes. Because of technological limitations it remains unclear how many kinds of EEs are actually present in soils [13], making it difficult to identify core EEs for climate-smart and resource-efficient agroecosystems. Thus, more research is needed to identify a wider range of soil EEs, and to link these enzymes to their ecological functions.

Second, there is a need to identify direct and particularly the indirect links between C-, N- and P-acquiring EEs in relation to a range of ecological functions. For example, the majority of studies exploring the enzymatic mechanisms associated with soil C cycling are primarily focusing on C-acquiring EEs, whereas the effects from N- and P-acquiring EEs on soil C dynamics remain elusive even though they also break down C compounds [10]. However, C-, N- and P-acquiring EEs are rarely simultaneously investigated in the same experiment platform in relation to their ecological functions.

Third, there is a need to test the use of enzymatic stoichiometry to identify the relative nutrient limitations in agroecosystems. Ecoenzymatic stoichiometry is defined as the relative activity of extracellular enzymes involved in C, N, and P cycling, and it is often used to identify microbial relative nutrient limitation. This approach has been applied successfully in natural ecosystems [8]. However, patterns of enzymatic stoichiometry may change due to the fertilizer application and the complexity of agricultural managements; caution is therefore required when applying this knowledge in agroecosystems.

Fourth, there is an urgent need to capture temporal variation in soil EE activity and to optimize the measurement frequency to capture this variation. Previous studies on soil EEs often measured enzyme activity only once per year, which makes it difficult to link EEs to ecosystem processes with clear seasonal variations, such as GHG emissions. Indeed, seasonal variations in the activity of EEs may be larger than treatment effects and temporal variation can differ strongly between treatments [14]. Therefore, to better capture the hotspots of enzyme activity, increased measurement frequency is required.

Finally, there is a need to develop standardised EEs measurement methods. Absolute EEs activity and treatment effects depend on numerous choices, e.g. the use of fresh vs. air-dried soil samples, incubation temperature, and adjustment of soil pH [15]. Previous studies on soil EEs applied a wide range of measurement methods [15], making it difficult to compare data across sites and to synthesize findings.

Bridging natural and agricultural science has contributed to important insights to support sustainable intensification of agroecosystems. In this context, soil EEs present a novel approach to understand the intricate plant-soil-microbial feedbacks and their ecological functions, as well as a promising tool to develop climate-smart and resource-efficient agroecosystems. Because of the wide range of expertise involved in this effort, extensive interdisciplinary collaborations between microbiologists, modellers, and data analysts are urgently needed.

Author Contributions

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References

1. Alexandratos N, Bruinsma J. World agriculture towards 2030/2050: the 2012 revision. 2012. <https://ageconsearch.umn.edu/record/288998>
2. Cassman KG, Grassini P. A global perspective on sustainable intensification research. *Nature Sustainability*. 2020; 3(4), 262–268. <https://doi.org/10.1038/s41893-020-0507-8>
3. Trivedi P, Mattupalli C, Eversole K, Leach JE. Enabling sustainable agriculture through understanding and enhancement of microbiomes. *New Phytologist*. 2021; 230, 2129–2147. <https://doi.org/10.1111/nph.17319> PMID: 33657660
4. Oldroyd GED. Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. *Nature Reviews Microbiology*. 2013; 11, 252–263. <https://doi.org/10.1038/nrmicro2990> PMID: 23493145
5. Rubin RL, van Groenigen KJ, Hungate BA. Plant growth promoting rhizobacteria are more effective under drought: a meta-analysis. *Plant and Soil*. 2017; 416, 309–323. <https://doi.org/10.1007/s11104-017-3199-8>
6. Itakura M, Uchida Y, Akiyama H, Hoshino YT, Shimomura Y, Morimoto S, et al. Mitigation of nitrous oxide emissions from soils by Bradyrhizobium japonicum inoculation. *Nature Climate Change*. 2013; 3, 208–212. <https://doi.org/10.1038/nclimate17347>
7. Allison SD, Vitousek PM. Responses of extracellular enzymes to simple and complex nutrient inputs. *Soil Biology and Biochemistry*. 2005; 37, 937–944. <https://doi.org/10.1016/j.soilbio.2004.09.014>
8. Sinsabaugh RL, Hill BH, Follstad Shah JJ. Ecoenzymatic stoichiometry of microbial organic nutrient acquisition in soil and sediment. *Nature*. 2009; 462, 795–798. <https://doi.org/10.1038/nature08632> PMID: 20010687
9. Chen J, Luo Y, van Groenigen KJ, Hungate BA, Cao J, Zhou X, et al. A keystone microbial enzyme for nitrogen control of soil carbon storage. *Science Advances*. 2018; 4, eaaq1689. <https://doi.org/10.1126/sciadv.aaq1689> PMID: 30140736
10. Chen J, van Groenigen KJ, Hungate BA, Terrer C, van Groenigen J-W, Maestre FT, et al. Long-term nitrogen loading alleviates phosphorus limitation in terrestrial ecosystems. *Global Change Biology*. 2020; 26, 5077–5086. <https://doi.org/10.1111/gcb.15218> PMID: 32529708

11. Richardson D, Felgate H, Watmough N, Thomson A, Baggs E. Mitigating release of the potent greenhouse gas N₂O from the nitrogen cycle—could enzymic regulation hold the key? *Trends in Biotechnology*. 2009; 27, 388–397. <https://doi.org/10.1016/j.tibtech.2009.03.009> PMID: 19497629
12. Luis Moreno J, Bastida F, Díaz-López M, Li Y, Zhou Y, López-Mondéjar R., et al. Response of soil chemical properties, enzyme activities and microbial communities to biochar application and climate change in a Mediterranean agroecosystem. *Geoderma*. 2022; 407, 115536. <https://doi.org/10.1016/j.geoderma.2021.115536>
13. Caldwell BA. Enzyme activities as a component of soil biodiversity: A review. *Pedobiologia*. 2005; 49, 637–644. <https://doi.org/10.1016/j.pedobi.2005.06.003>
14. Machmuller MB, Mohan JE, Minucci JM, Phillips CA, Wurzbürger N. Season, but not experimental warming, affects the activity and temperature sensitivity of extracellular enzymes. *Biogeochemistry*. 2016; 131, 255–265. <https://doi.org/10.1007/s10533-016-0277-6>
15. Wallenstein MD, Weintraub MN. Emerging tools for measuring and modeling the in situ activity of soil extracellular enzymes. *Soil Biology and Biochemistry*. 2008; 40, 2098–2106. <https://doi.org/10.1016/j.soilbio.2008.01.024>