

OPINION

Can arbuscular mycorrhizal fungi speed up carbon sequestration by enhanced weathering?

Erik Verbruggen  | Eric Struyf  | Sara Vicca 

Research group PLECO (Plants and Ecosystems), Department of Biology, University of Antwerp, Wilrijk, Belgium

Correspondence

Erik Verbruggen, Research Group PLECO (Plants and Ecosystems), Department of Biology, University of Antwerp, Campus Drie Eiken, Universiteitsplein 1, 2610 Wilrijk, Belgium.

Funding information

BOF; Research Council of the University of Antwerp

Societal Impact Statement

Mitigating climate change and increasing agricultural sustainability are twin challenges society faces in the upcoming decades. One measure that can contribute to reducing atmospheric CO₂ is "enhanced weathering" through application of ground silicates. Here we propose that mycorrhizal fungi may critically contribute to the success of enhanced weathering in agricultural systems. Fundamental lab-based experiments now need to go hand in hand with real-world field trials, with the goal to optimize both decarbonization and environmental sustainability of agricultural ecosystems.

Summary

Arbuscular mycorrhizal fungi have significantly contributed to weathering of the earth's surface since their evolutionary origin 400–500 million years ago. They have been a key player in the global carbon cycle over geological timescales. In order to reach the global warming targets as agreed at the Paris summit in 2015, implementation of negative emission technologies is necessary. Among the options, one of the simplest is "enhanced weathering", where silicate rock is ground into small particles to enhance weathering rate. Here we synthesize the ways by which mycorrhizal fungi interact with these particles when applied to agricultural fields, and suggest they may stimulate weathering by various direct and indirect mechanisms. We conclude that because the intensity with which mycorrhiza interact with soil is tightly related to plant provisioning of photosynthates in exchange for soil-derived nutrients, weathering rates and hence carbon sequestration are likely to increase with agricultural activities that stimulate plant reliance on and investment in arbuscular mycorrhizal fungi.

KEYWORDS

climate change mitigation, enhanced weathering, geo-engineering, mycorrhizal fungi, sustainable agriculture

1 | INTRODUCTION

Climate change is one of the most pressing environmental and societal issues currently faced by humanity (IPCC, 2018). At the 2015 climate summit in Paris, nearly all world leaders

committed themselves to limit global warming to well below 2°C (UNFCCC, 2015). Achieving this target requires rapid and complete decarbonization of all sectors. Current policies focus on conventional mitigation to reduce emissions, yet scenario analyses and model projections unveiled that conventional mitigation alone

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2021 The Authors. *Plants, People, Planet* © New Phytologist Foundation

will unlikely suffice to limit warming to well below 2°C (Gasser et al., 2015). Safe and scalable negative emission technologies (NETs), which actively remove CO₂ from the atmosphere and ensure long-term sequestration, will therefore be needed in addition to conventional mitigation measures.

A potentially important NET is "enhanced weathering" (EW) of silicate minerals (e.g. Beerling et al., 2020; Fuss et al., 2018; Hartmann et al., 2013; Schuiling & Krijgsman, 2006; Streffer et al., 2018). By EW we mean *the application of ground silicates with the goal to speed up weathering and hence C sequestration*. When silicates weather, CO₂ is bound in aqueous form that eventually precipitates as carbonate, sequestering carbon for millennia. In nature, silicate rocks weather very slowly (geological time scale), mainly because of the limited surface area. The idea behind EW is to speed up this natural process by grinding silicate rocks to fine grains, hence increasing the surface area, and applying it to places where weathering potential is high (Schuiling & Krijgsman, 2006; Hartmann et al., 2013; see also Box 1). Nonetheless, the carbon sequestration rate and potential of this relatively new NET measure remain uncertain (Amann et al., 2020; Kelland et al., 2020) and therefore require urgent further experimental verification.

Silicate weathering depends on both abiotic and biotic influences (Box 1). While much work has been done on the abiotic influences on carbon sequestration potential of EW for different rock types and grain sizes (Haque et al., 2019; Hartmann et al., 2013; Streffer et al., 2018), the role of biota such as plants and microbes in EW has so far rarely been considered (but see: Kelland et al., 2020). Nonetheless, biota currently play and have previously played an important role in determining weathering rates at ecological and evolutionary timescales, respectively (Burghelea et al., 2015; Dontsova et al., 2020; Hoffland et al., 2004). They may thus be crucial for speeding up C sequestration through EW and resolving their influence can crucially aid in selecting the most promising settings and approaches.

2 | THE IMPORTANCE OF MYCORRHIZAL FUNGI IN "ENHANCED WEATHERING"

Mycorrhizal fungi are thought to have significantly increased mineral dissolution rates at evolutionary timescales, as well as in current (unground) rock weathering experiments (e.g.

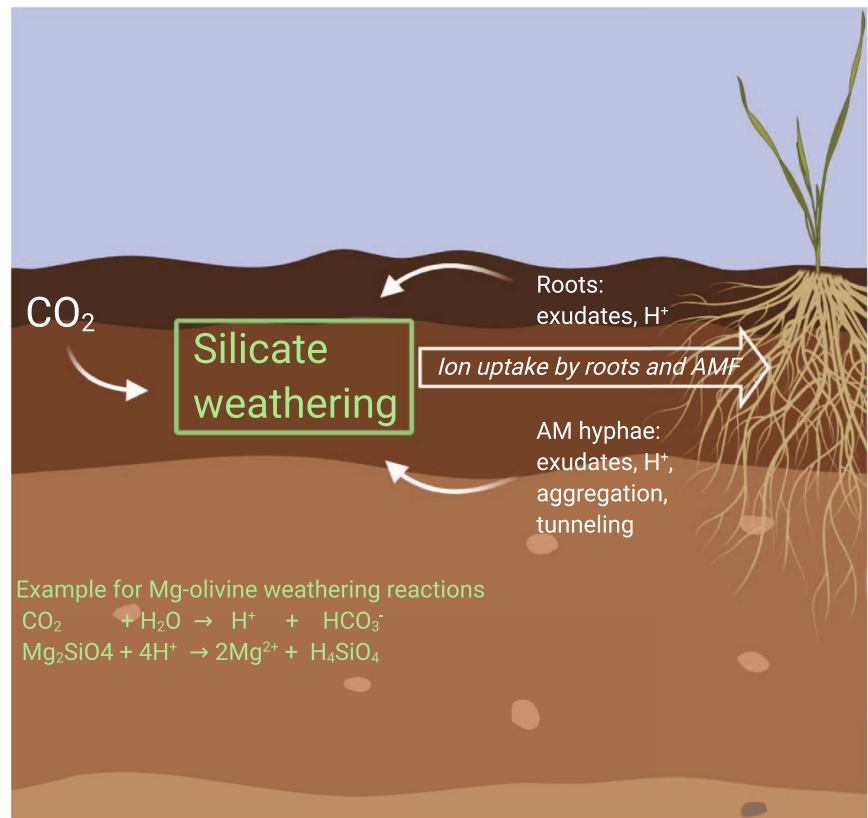
BOX 1 Principles of Enhanced Weathering (EW).

Silicate weathering is controlled by abiotic factors such as precipitation, temperature, CO₂, and pH of the (soil) water, as well as biotic interactions (Figure 1). Increases in precipitation, temperature, and CO₂ typically stimulate weathering rate, while the effect of H⁺ depends on the soil pH: at a low pH (< 4.5) an increase in H⁺ concentration can increase mineral dissolution, while up to a pH of about 8 the effect is neutral (Drever, 1994). In the rhizosphere however, H⁺ release due to uptake of base cations can locally reduce pH by multiple units compared to bulk soil (e.g. Gómez-Suárez et al., 2020), and thus still increase mineral dissolution even in case of higher bulk soil pH. The weathering process involves the dissolution of silicates which consumes H⁺, releases geogenic nutrients such as P, Ca, Mg, K, and Si (depending on the source material) and increases the alkalinity of the environment. In response, the chemical equilibrium between dissolved CO₂ and bicarbonate shifts slightly towards the latter, so additional CO₂ can be taken up from the atmosphere. Weathering products can precipitate in the soil, sequestering carbon in secondary carbonate minerals. The geogenic nutrients can also be taken up by plants and microbes. Weathering products can leave the system when they are transported to inland waters and the ocean. Bicarbonates entering the ocean can counter ocean acidification (Hartmann et al., 2013; Meysman & Montserrat, 2017). On the other hand, the slow process (Renforth & Henderson, 2017) of carbonate precipitation in the ocean will eventually release some (max. 50%) of the initially sequestered CO₂ back into the atmosphere (Hartmann et al., 2013).

Many silicate sources can be used for EW. Mafic and ultramafic rocks (like basalt) are two of the most logical choices, as they are ubiquitous, have a relatively fast weathering rate, and have the highest content of silicate minerals. They also have higher cation contents than other silicate rocks such as granite or rhyolite, making them more interesting for application in agriculture (Hartmann et al., 2013). Besides these natural silicates, also artificial silicate-containing compounds such as steel slag and concrete demolition may be used for EW (Beerling et al., 2018). According to Renforth (2019), 7 Gt alkaline materials are produced globally each year as a (by-)product of industrial activity. Between 2020 and 2,100, about 560 Gt artificial silicate material could become available, with a theoretical C sequestration potential of 2.9–8.5 Gt CO₂ y⁻¹. Although not all of that waste material may be useful for application in agriculture (due to contaminants), they have the advantage that they do not require mining and their use for EW could be embedded in a circular economy (Beerling et al., 2020).

The global carbon sequestration potential of EW has been estimated at 0.5–5 Gt CO₂ per year in a synthesis study (Fuss et al., 2018) and at 0.5–2 Gt CO₂ per year in a recent nation-by-nation quantitative analysis, including various costs involved (Beerling et al., 2020). However, these estimates are subject to large uncertainties, among others because they are almost exclusively based on extrapolations from lab experiments. Field experiments including interaction with soil and biota are a key research gap that needs urgent attention to verify the true C sequestration potential of EW (Fuss et al., 2018).

FIGURE 1 Illustration of the interaction between biota and silicate weathering. Silicate weathering involves the reaction of the silicate rocks with CO₂ (which can be produced by plants, mycorrhizal fungi or microbes, or be directly drawn from the atmosphere) and water. Plant roots and AM hyphae produce exudates and H⁺, which stimulate silicate weathering. AM hyphae can further influence the weathering rates by stimulating soil aggregation. When silicate materials such as basalt weather, geogenic nutrients are released which can be taken up by plants, AM fungi and microbes



Balogh-Brunstad et al., 2008; Burghel et al., 2015; Hoffland et al., 2004; Zaharescu et al., 2017). Upon the arrival of early land plants, terrestrial weathering is known to have greatly increased. It is thought that the partnering with mycorrhizal fungi aided spread of early land plants (Field et al., 2015). First fossilized fungal spores and hyphae indistinguishable from current arbuscular mycorrhizal fungi date back to 470 million years before present (Redecker et al., 2000), whereas true symbiotic structures such as arbuscules are found in fossil plants approximately 70 million years younger (Remy et al., 1994; Strullu-Derrien et al., 2018). From around that time and onwards, the advent of true roots associated with mycorrhizal fungi is known to have substantially enhanced global carbon cycling, massively increased productivity, and led to greatly ramped up weathering rates (Field et al., 2015; Quirk et al., 2015). The causal influence of mycorrhizas on rock weathering from that time is evident from the mineral weathering tunnels that remain present in the rocks afterwards (Koele et al., 2014; Quirk et al., 2012; Van Schöll et al., 2008).

The extent to which mycorrhizal fungi contribute to weathering may however be context-dependent (Smits & Wallander, 2017). For instance, the mycorrhizal contribution to weathering of apatite, a P-rich mineral, was suggested to depend on the occurrence of P limitation in plants and fungi (Smits et al., 2012), with P limitation stimulating enhanced weathering. Along similar lines, in soils with a high soil organic matter (SOM) content, fungi may preferably scavenge for nutrients in OM and interact less with mineral fractions of soil (Hodge & Fitter, 2010). This may reduce their weathering potential, and dissolved organic carbon originating from SOM may

even retard mineral weathering rates (Smits & Wallander, 2017). Thus far, however, most research on the contemporary influence of mycorrhizal fungi on weathering has focused on forests and ectomycorrhizas, while agricultural land where arbuscular mycorrhizas (AM) dominate is expected to be the primary place for EW application.

Here we focus on the role of AM and list key mechanisms through which they are likely key to influence weathering rates and dynamics when crushed silicates are applied to agricultural soils. These include direct effects via exudation and physical weathering, as well as indirect effect by altering abiotic conditions and through their effect on plants.

2.1 | Direct

Arbuscular mycorrhizal fungi are obligate symbionts of most land plant species (Brundrett & Tedersoo, 2018). They colonize roots and extend into the soil where they scavenge for nutrients such as PO₄²⁻, NH₄⁺, K, and Zn, while relying on their host plant for carbon and energy (Smith & Read, 2008). Their finely branched hyphae (1–10 µm diameter) greatly increase the bioactive surface area compared to roots, meaning that a plant that invests its C in fungal biomass instead of roots greatly expands its root-depletion zone. These traits of AM fungi are likely to influence rock weathering. The mechanisms by which they do are diverse. AM fungi can cover and tunnel into mineral surfaces and serve as efficient sinks for ions released from the minerals (Quirk

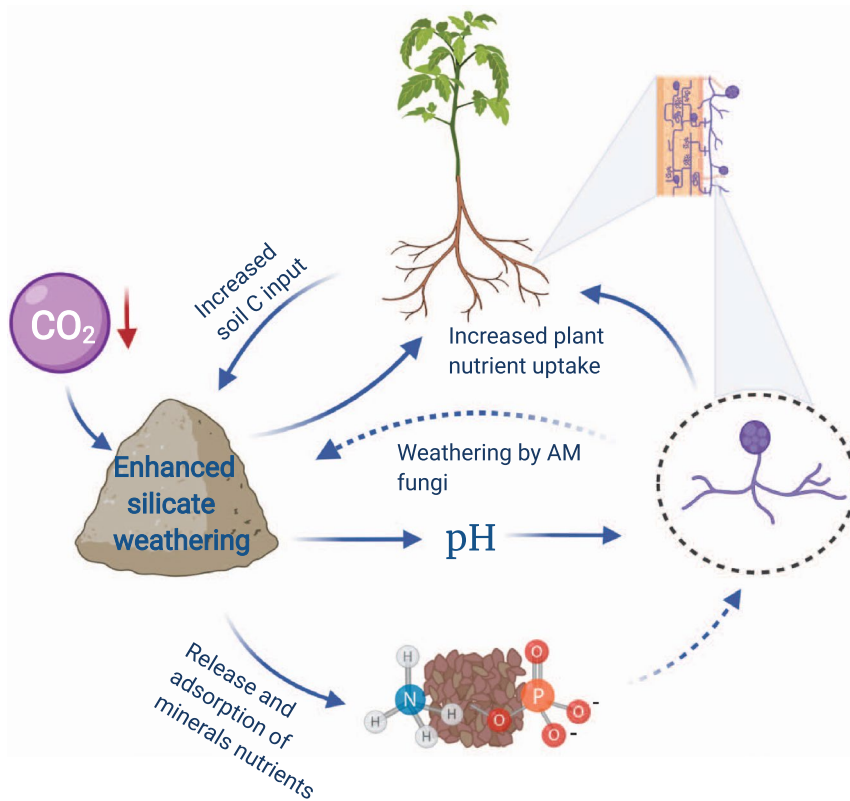


FIGURE 2 Path-diagram for the anticipated interactions between silicate application, AM fungi, and weathering in agricultural soils. Blue arrows indicate anticipated positive effects, with dashed arrows indicating crucial paths to be resolved. Weathering increases soil buffering capacity through release of carbonates and cations, mitigating soil acidification. See the main text for elaboration on main interdependencies

et al., 2015; Smith & Read, 2008; Figure 2). This activity creates chemical disequilibria across large areas of rock surface fueling its weathering (e.g. Taylor et al., 2009). Furthermore, exuded sugars, and organic acids by AM hyphae (Hooker et al., 2007; Toljander et al., 2007) or the rich diversity of bacteria living on their surfaces (Agnolucci et al., 2015), can act as chelators that destabilize mineral surfaces increasing weathering potential. Moreover, turnover of organic compounds, hyphae, and bacteria associated with them increases respiration (Olsson & Johnson, 2005) on rock surfaces, which further stimulates silicate weathering. Other mechanisms by which AM fungi stimulate weathering are acidification related with preferential NH_4^+ uptake (Cheng et al., 2012), and enhanced soil aggregation (Rillig et al., 2015). The latter can create local anoxia and steep micro-environmental gradients (Sextstone et al., 1985) that can increase weathering (Zaharescu et al., 2020). Simultaneously however, lock-up of minerals and reduced respiration inside aggregates may retard weathering rates.

2.2 | Indirect

Plants invest substantial amounts of carbon belowground to obtain nutrients and other resources. Especially in agricultural settings, root-derived C will be a substantial fraction of total soil C inputs and thus a major driver of EW. Plant roots release CO₂ and organic acids, creating physicochemical conditions that accelerate the dissolution of silicate minerals (Dontsova et al., 2020). AM fungi can

have a strong effect on these belowground plant processes. Ven et al. (2019) found, for example, that AM fungi stimulated plant growth and increased the total belowground carbon flux in an experiment with maize plants. Burghlea et al. (2018) even suggested that AM fungi can enhance root exudation especially in substrates that are difficult to weather. These results align with a generally positive effect of AM fungi on plant growth (Lekberg & Koide, 2005) which, despite a trend towards decreased root to shoot ratio (Veresoglou et al., 2012) is likely to increase the total amount of C entering soil (Figure 2).

3 | WILL AM FUNGI CONTRIBUTE TO "ENHANCED WEATHERING" IN AN AGRICULTURAL SETTING?

As indicated above, there are numerous ways by which AM fungi can increase weathering of minerals. However, most studies on the influence of biota on mineral weathering measure effects of plant roots and their symbionts on a relatively large piece of mineral that is inserted into growth media (e.g., Bonneville et al., 2011), or use pure basalt growth media (e.g., Burghellea et al., 2015), where nutrient availability and physicochemical properties are dictated by the mineral itself. In contrast, in the practice of EW, ground silicates are added to the soil, creating a very different setting than what is simulated in those growth media. For instance, available nutrient levels are generally larger in soils than in primary minerals, due to agricultural fertilization and general accrual of SOM during pedogenesis

(e.g., Menge et al., 2012). While application of silicates holds potential to replace (some of) the fertilizer that is typically required for sustained agricultural productivity, can we expect AM fungi to also stimulate weathering in an agricultural setting? In other words, is the biotic and abiotic context conducive to silicate weathering by AM fungi?

3.1 | AM fungi in agriculture: can a stronger alliance be forged?

AM fungi are often suppressed in terms of abundance and diversity under conventional agricultural practices compared to natural systems (Banerjee et al., 2019; Verbruggen et al., 2012; Xiang et al., 2014), which imposes serious limits on their weathering potential. Extraradical hyphal densities (those hyphae that extend into the soil from roots) may be particularly suppressed (Verbruggen & Kiers, 2010), with field studies reporting 2.49 m/g under barley (Thirkell et al., 2019), average of 2.65 m/g across 50 maize fields in northern China (Xiang et al., 2014), and active hyphae ranging from approximately 2.5 to 10 m/g under maize (Miller et al., 1995). This contrasts with values >10 m/g typically found in non-agricultural settings (Antoninka et al., 2011). However, large variation exists under both settings and extraradical mycorrhizal density is expected to increase with elevated CO₂ (Antoninka et al., 2011; Quirk et al., 2015). Given the large variation, agriculture does offer a unique opportunity to control and optimize conditions that stimulate AM-mediated weathering rates. If negative effects of conventional agricultural practices on AM fungi can be ameliorated, agricultural systems may be the ideal systems to practice EW, as they offer the opportunity to manipulate e.g., plant species and variety, tillage, or fertilization rate and type, all of which are known to strongly affect AM fungal performance (e.g. Field et al., 2020). While densities on par with natural systems may not be reached, the tractability of man-made agricultural systems can help tune weathering rates and AM fungal activities in ways impossible in other ecosystems, once we know the important gears to turn.

Apart from tractability, organic matter contents of agricultural soil are usually low compared to the forests where most research on mycorrhizal weathering has been performed thus far (Finlay et al., 2009), stimulating interaction of AM fungi with the mineral soil component (Smits et al., 2014). Furthermore, the unbalanced removal of biomass and nutrients that is intrinsic to most agricultural systems, holds potential to stimulate the interactions with soil when AM fungi explore it in search of nutrients. For instance, the relative limitation of N versus P can greatly affect the plant growth response to AM fungi (Hoeksema et al., 2010) and productivity of AM fungi themselves (Johnson et al., 2015).

Thus, apart from the opportunity offered by agricultural fields in terms of area and accessibility, optimization of agricultural practices could foster AM fungi to help maximize CO₂ removal from the air using silicate materials. This may not only benefit climate, but could also improve crop yields and nutritional value as well as their pest

and drought resistance, all of which can be promoted by AM fungi (Lekberg & Koide, 2005; Verlinden et al., 2018; Rillig et al., 2019; but see Ryan & Graham, 2018), the availability of Si (e.g. Epstein, 2009), and by application of ground silicates (Beerling et al., 2018; Haque et al., 2019). Intriguingly, Frew et al. (2017) found the effect of AM fungi on pest resistance of sugarcane crops to be intricately related to soil Si availability: under low Si conditions, soil AM fungi reduced root palatability to an important root herbivore by increasing root concentration of Si. Agricultural soils are often strongly depleted in biogenic soil Si, promoting the need for plants to acquire Si directly from mineral weathering sources (Vandevenne et al., 2015). New experiments are needed to explore the potential of plant-AM optimization for maximizing C sequestration by EW, while also assessing important side-effects and especially the relation to crop yield.

3.2 | How will AM fungi respond to ground silicate applications?

Until now we have especially focused on the effects of AM fungi on EW, and we argue it requires specific agricultural practices to stimulate their activity in order to maximize weathering and carbon uptake. Could application of ground silicates be a step in this process? How can we expect AM fungi to respond to application of a large quantity of ground minerals such as basalt rock? First of all, silicate addition will increase pH, which may affect AM fungal abundance and diversity. When moving from acidic to neutral or slightly alkaline pH, AM fungal root colonization (Frater et al., 2018) and species richness (Verbruggen et al., 2012) generally increase. A common agricultural practice that is most analogous to silicate application is the application of ground limestone (liming). Liming can significantly increase root colonization by AM fungi, due to its increase in pH and/or immobilization of phosphate (Heyburn et al., 2017). In a long-term fertilization study of grassland, liming was found to increase AM fungal extraradical hyphal density, which was reduced when P was co-applied, indicating pH and P availability can have opposing effects (Sochorová et al., 2016).

What can we expect for silicate application? Studies are few, but a recent study by Kelland et al. (2020) showed that AM fungi actively colonize basalt-filled root-excluding mesh bags under Sorghum. Similar mesh bags filled with basalt under AM trees have likewise been shown to result in more than twofold AM fungal densities compared to mesh bags filled with granite or quartz (Quirk et al., 2012). Another recent test found that ground concrete demolition and dolerite can increase root AM fungal colonization, dependent on its mixing ratio with sand (Son et al., 2020). Therefore, limited data suggest that AM fungal growth may be positively affected by these applications. It is known that organic and slow-release fertilizers often benefit abundance and diversity of AM fungi, probably by increasing plant reliance on the fungi for nutrient procurement, whereas mineral fertilizers tend to have a negative effect (Gryndler et al., 2006; Van Geel et al., 2016). Ground silicates such as basalt will be a source for some nutrients but can be an (initial) sink for others by formation

of organo-mineral complexes and chemical adsorption. Ground silicates can adsorb a variety of ions such as ammonium and phosphate, although the efficiency strongly depends on type of rock (Landis & Craw, 2003; Witter & Kirchmann, 1989). While initially reducing nutrient availability, then, the additions may act like slow-release fertilizers and focus biological activity such as nutrient scavenging by mycorrhizal hyphae on their surfaces. Such effect is analogous to applications of biochar or expanded clay, for instance, whose surfaces are highly attractive to AM fungi thereby stimulating their abundance (Bukovská et al., 2016; Hammer et al., 2014).

4 | CONCLUSIONS

Given the clear potential that silicate addition holds with respect to climate change mitigation, and the important role mycorrhizas are likely to play in the process, we push for more research on this exciting subject. We here argue that explicit consideration of the biota involved in the weathering process, among which AM fungi are key players, will be essential to understand the drivers of weathering rates in the field and to maximize climate gains from this technique. In line with recent calls (e.g., Yona et al., 2020), aside from calculating theoretical weathering rates, greenhouse gas fluxes and in situ weathering should be followed-up to determine the true effects of the implementation of mitigating practices. In field and lab settings, research is now needed to measure the response of AM fungi and weathering rates to high quantities of silicates, and especially their co-dependence on soil characteristics and agricultural practices such as fertilization and tillage. In doing so, we may be able to (a) prioritize the most promising sites for application of silicates, (b) optimize agricultural practices for EW, sustainability, and yield, and (c) accurately estimate greenhouse gas emission responses to ground silicate application that may be far apart from initial assumptions.

ACKNOWLEDGEMENTS

We want to thank Ivan Janssens for previous inspiring conversations that contributed to the ideas presented here. We also thank BOF and the Research Council of the University of Antwerp for financial support.

AUTHOR CONTRIBUTIONS

EV and SV have equally contributed to the conception and first-draft of the MS. EV, ES, and SV have subsequently jointly edited and finalized the MS.

ORCID

Erik Verbruggen  <https://orcid.org/0000-0001-7015-1515>

Eric Struyf  <https://orcid.org/0000-0001-6833-4136>

Sara Vicca  <https://orcid.org/0000-0001-9812-5837>

REFERENCES

Agnolucci, M., Battini, F., Cristani, C., & Giovannetti, M. (2015). Diverse bacterial communities are recruited on spores of different arbuscular

- mycorrhizal fungal isolates. *Biology and Fertility of Soils*, 51, 379–389. <https://doi.org/10.1007/s00374-014-0989-5>
- Amann, T., Hartmann, J., Struyf, E., de Oliveira Garcia, W., Fischer, E. K., Janssens, I., Meire, P., & Schoelynck, J. (2020). Enhanced Weathering and related element fluxes - A cropland mesocosm approach. *Biogeosciences*, 17(1), 103–119. <https://doi.org/10.5194/bg-17-103-2020>
- Antoninka, A., Reich, P. B., & Johnson, N. C. (2011). Seven years of carbon dioxide enrichment, nitrogen fertilization and plant diversity influence arbuscular mycorrhizal fungi in a grassland ecosystem. *New Phytologist*, 192(1), 200–214. <https://doi.org/10.1111/j.1469-8137.2011.03776.x>
- Balogh-Brunstad, Z., Kent Keller, C., Thomas Dickinson, J., Stevens, F., Li, C. Y., & Bormann, B. T. (2008). Biotite weathering and nutrient uptake by ectomycorrhizal fungus, *Suillus tomentosus*, in liquid-culture experiments. *Geochimica Et Cosmochimica Acta*, 72(11), 2601–2618. <https://doi.org/10.1016/j.gca.2008.04.003>
- Banerjee, S., Walder, F., Büchi, L., Meyer, M., Held, A. Y., Gättinger, A., Keller, T., Charles, R., & van der Heijden, M. G. A. (2019). Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. *ISME Journal*, 13(7), 1722–1736. <https://doi.org/10.1038/s41396-019-0383-2>
- Beerling, D. J., Kantzas, E. P., Lomas, M. R., Wade, P., Eufrazio, R. M., Renforth, P., Sarkar, B., Andrews, M. G., James, R. H., Pearce, C. R., Mercure, J.-F., Pollitt, H., Holden, P. B., Edwards, N. R., Khanna, M., Koh, L., Quegan, S., Pidgeon, N. F., Janssens, I. A., ... Banwart, S. A. (2020). Potential for large-scale CO₂ removal via enhanced rock weathering with croplands. *Nature*, 583(7815), 242–248. <https://doi.org/10.1038/s41586-020-2448-9>
- Beerling, D. J., Leake, J. R., Long, S. P., Scholes, J. D., Ton, J., Nelson, P. N., Bird, M., Kantzas, E., Taylor, L. L., Sarkar, B., Kelland, M., DeLucia, E., Kantola, I., Müller, C., Rau, G., & Hansen, J. (2018). Farming with crops and rocks to address global climate, food and soil security. *Nature Plants*, 4(3), 138–147. <https://doi.org/10.1038/s41477-018-0108-y>
- Bonneville, S., Morgan, D. J., Schmalenberger, A., Bray, A., Brown, A., Banwart, S. A., & Benning, L. G. (2011). Tree-mycorrhiza symbiosis accelerate mineral weathering: Evidences from nanometer-scale elemental fluxes at the hypha-mineral interface. *Geochimica Et Cosmochimica Acta*, 75(22), 6988–7005. <https://doi.org/10.1016/j.gca.2011.08.041>
- Brundrett, M. C., & Tedersoo, L. (2018). Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist*, 220(4), 1108–1115. <https://doi.org/10.1111/nph.14976>
- Bukovská, P., Gryndler, M., Gryndlerová, H., Püschel, D., & Jansa, J. (2016). Organic nitrogen-driven stimulation of arbuscular mycorrhizal fungal hyphae correlates with abundance of ammonia oxidizers. *Frontiers in Microbiology*, 7, 1–15. <https://doi.org/10.3389/fmicb.2016.00711>
- Burghellea, C., Zaharescu, D. G., Dontsova, K., Maier, R., Huxman, T., & Chorover, J. (2015). Mineral nutrient mobilization by plants from rock: Influence of rock type and arbuscular mycorrhiza. *Biogeochemistry*, 124(1–3), 187–203. <https://doi.org/10.1007/s10533-015-0092-5>
- Burghellea, C. I., Dontsova, K., Zaharescu, D. G., Maier, R. M., Huxman, T., Amistadi, M. K., Hunt, E., & Chorover, J. (2018). Trace element mobilization during incipient bioweathering of four rock types. *Geochimica et Cosmochimica Acta*, 234, 98–114. <https://doi.org/10.1016/j.gca.2018.05.011>
- Cheng, L., Booker, F. L., Tu, C., Burkey, K. O., Zhou, L., Shew, H. D., & Hu, S. (2012). Arbuscular mycorrhizal fungi increase organic carbon decomposition under elevated CO₂. *Science*, 337(6098), 1084–1087. <https://doi.org/10.1126/science.1224304>
- Dontsova, K., Balogh-Brunstad, Z., & Chorover, J. (2020). Plants as drivers of rock weathering. In K. Dontsova, Z. Balogh-Brunstad, & G. Le Roux (Eds.), *Biogeochemical cycles: Ecological drivers and environmental impact* (pp. 33–58). John Wiley and Sons. <https://doi.org/10.1002/9781119413332.ch2>

- Drever, J. I. (1994). The effect of land plants on weathering rates of silicate minerals. *Geochimica Et Cosmochimica Acta*, 58(10), 2325–2332. [https://doi.org/10.1016/0016-7037\(94\)90013-2](https://doi.org/10.1016/0016-7037(94)90013-2)
- Epstein, E. (2009). Silicon: Its manifold roles in plants. *Annals of Applied Biology*, 155(2), 155–160. <https://doi.org/10.1111/j.1744-7348.2009.00343.x>
- Field, K. J., Daniell, T., Johnson, D., & Helgason, T. (2020). Mycorrhizas for a changing world: Sustainability, conservation, and society. *Plants, People, Planet*, 2(2), 98–103. <https://doi.org/10.1002/ppp3.10092>
- Field, K. J., Pressel, S., Duckett, J. G., Rimington, W. R., & Bidartondo, M. I. (2015). Symbiotic options for the conquest of land. *Trends in Ecology and Evolution*, 30(8), 477–486. <https://doi.org/10.1016/j.tree.2015.05.007>
- Finlay, R., Wallander, H., Smits, M., Holmstrom, S., van Hees, P., Lian, B., & Rosling, A. (2009). The role of fungi in biogenic weathering in boreal forest soils. *Fungal Biology Reviews*, 23(4), 101–106. <https://doi.org/10.1016/j.fbr.2010.03.002>
- Frater, P. N., Borer, E. T., Fay, P. A., Jin, V., Knaeble, B., Seabloom, E., & Harpole, W. S. (2018). Nutrients and environment influence arbuscular mycorrhizal colonization both independently and interactively in *Schizachyrium scoparium*. *Plant and Soil*, 425(1–2), 493–506. <https://doi.org/10.1007/s11104-018-3597-6>
- Frew, A., Powell, J. R., Allsopp, P. G., Sallam, N., & Johnson, S. N. (2017). Arbuscular mycorrhizal fungi promote silicon accumulation in plant roots, reducing the impacts of root herbivory. *Plant and Soil*, 419, 423–433. <https://doi.org/10.1007/s11104-017-3357-z>
- Fuss, S., Lamb, W. F., Callaghan, M. W., Hilaire, J., Creutzig, F., Amann, T., Beringer, T., de Oliveira Garcia, W., Hartmann, J., Khanna, T., Luderer, G., Nemet, G. F., Rogelj, J., Smith, P., Vicente, J. L. V., Wilcox, J., del Mar Zamora Dominguez, M., & Minx, J. C. (2018). Negative emissions - Part 2: Costs, potentials and side effects. *Environmental Research Letters*, 13, 063002. <https://doi.org/10.1088/1748-9326/aabf9f>
- Gasser, T., Guivarch, C., Tachiiri, K., Jones, C. D., & Ciais, P. (2015). Negative emissions physically needed to keep global warming below 2°C. *Nature Communications*, 6, 7958. <https://doi.org/10.1038/ncomms8958>
- Gómez-Suárez, A. D., Nobile, C., Faucon, M. P., Pourret, O., & Houben, D. (2020). Fertilizer potential of struvite as affected by nitrogen form in the rhizosphere. *Sustainability*, 12, 2212. <https://doi.org/10.3390/su12062212>
- Gryndler, M., Larsen, J., Hršelová, H., Řezáčová, V., Gryndlerová, H., & Kubát, J. (2006). Organic and mineral fertilization, respectively, increase and decrease the development of external mycelium of arbuscular mycorrhizal fungi in a long-term field experiment. *Mycorrhiza*, 16(3), 159–166. <https://doi.org/10.1007/s00572-005-0027-4>
- Hammer, E. C., Balogh-Brunstad, Z., Jakobsen, I., Olsson, P. A., Stipp, S. L. S., & Rillig, M. C. (2014). A mycorrhizal fungus grows on biochar and captures phosphorus from its surfaces. *Soil Biology and Biochemistry*, 77, 252–260. <https://doi.org/10.1016/j.soilbio.2014.06.012>
- Haque, F., Chiang, Y. W., & Santos, R. M. (2019). Alkaline mineral soil amendment: A climate change stabilization wedge? *Energies*, 12(12), 2299. <https://doi.org/10.3390/en12122299>
- Haque, F., Santos, R. M., Dutta, A., Thimmanagari, M., & Chiang, Y. W. (2019). Co-benefits of wollastonite weathering in agriculture: CO₂ sequestration and promoted plant growth. *ACS Omega*, 4(1), 1425–1433. <https://doi.org/10.1021/acsomega.8b02477>
- Hartmann, J., West, A. J., Renforth, P., Köhler, P., De La Rocha, C. L., Wolf-Gladrow, D. A., Dürr, H. A., & Scheffran, J. (2013). Enhanced chemical weathering as a geoengineering strategy to reduce atmospheric carbon dioxide, supply nutrients, and mitigate ocean acidification. *Reviews of Geophysics*, 51(2), 113–149. <https://doi.org/10.1002/rog.20004>
- Heyburn, J., McKenzie, P., Crawley, M. J., & Fornara, D. A. (2017). Long-term belowground effects of grassland management: The key role of liming. *Ecological Applications*, 27(7), 2001–2012. <https://doi.org/10.1002/eap.1585>
- Hodge, A., & Fitter, A. H. (2010). Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 13754–13759. <https://doi.org/10.1073/pnas.1005874107>
- Hoeksema, J. D., Chaudhary, V. B., Gehring, C. A., Johnson, N. C., Karst, J., Koide, R. T., Pringle, A., Zabinski, C., Bever, J. D., Moore, J. C., Wilson, G. W. T., Klironomos, J. N., & Umbanhowar, J. (2010). A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters*, 13(3), 394–407. <https://doi.org/10.1111/j.1461-0248.2009.01430.x>
- Hoffland, E., Kuyper, T. W., Wallander, H., Plassard, C., Gorbushina, A. A., Haslewandter, K., & van Breemen, N. (2004). The role of fungi in weathering. *Frontiers in Ecology and the Environment*, 2(5), 258–264. [https://doi.org/10.1890/1540-9295\(2004\)002](https://doi.org/10.1890/1540-9295(2004)002)
- Hooker, J. E., Piatti, P., Cheshire, M. V., & Watson, C. A. (2007). Polysaccharides and monosaccharides in the hyphosphere of the arbuscular mycorrhizal fungi *Glomus* E3 and *Glomus* tenue. *Soil Biology and Biochemistry*, 39(2), 680–683. <https://doi.org/10.1016/j.soilbio.2006.08.006>
- IPCC. (2018). *Global warming of 1.5°C*. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change.
- Johnson, N. C., Wilson, G. W. T., Wilson, J. A., Miller, R. M., & Bowker, M. A. (2015). Mycorrhizal phenotypes and the Law of the Minimum. *New Phytologist*, 205, 1473–1484. <https://doi.org/10.1111/nph.13172>
- Kelland, M. E., Wade, P. W., Lewis, A. L., Taylor, L. L., Sarkar, B., Andrews, M. G., & Beerling, D. J. (2020). Increased yield and CO₂ sequestration potential with the C4 cereal *Sorghum bicolor* cultivated in basaltic rock dust-amended agricultural soil. *Global Change Biology*, 26(6), 3658–3676. <https://doi.org/10.1111/gcb.15089>
- Koele, N., Dickie, I. A., Blum, J. D., Gleason, J. D., & de Graaf, L. (2014). Ecological significance of mineral weathering in ectomycorrhizal and arbuscular mycorrhizal ecosystems from a field-based comparison. *Soil Biology and Biochemistry*, 69, 63–70. <https://doi.org/10.1016/j.soilbio.2013.10.041>
- Landis, C. A., & Craw, D. (2003). Phosphate minerals formed by reaction of bird guano with basalt at Cooks Head Rock and Green Island, Otago, New Zealand. *Journal of the Royal Society of New Zealand*, 33(1), 487–495. <https://doi.org/10.1080/03014223.2003.9517739>
- Lekberg, Y., & Koide, R. T. (2005). Is plant performance limited by abundance of arbuscular mycorrhizal fungi? A meta-analysis of studies published between 1988 and 2003. *New Phytologist*, 168(1), 189–204. <https://doi.org/10.1111/j.1469-8137.2005.01490.x>
- Menge, D. N. L., Hedin, L. O., & Pacala, S. W. (2012). Nitrogen and phosphorus limitation over long-term ecosystem development in terrestrial ecosystems. *PLoS One*, 7(8), e42045. <https://doi.org/10.1371/journal.pone.0042045>
- Meysman, F. J. R., & Montserrat, F. (2017). Negative CO₂ emissions via enhanced silicate weathering in coastal environments. *Biology Letters*, 13, 20160905. <https://doi.org/10.1098/rsbl.2016.0905>
- Miller, M. H., McGonigle, T. P., & Addy, H. D. (1995). Functional ecology of vesicular arbuscular mycorrhizas as influenced by phosphate fertilization and tillage in an agricultural ecosystem. *Critical Reviews in Biotechnology*, 15(3–4), 241–255. <https://doi.org/10.3109/07388559509147411>
- Olsson, P. A., & Johnson, N. C. (2005). Tracking carbon from the atmosphere to the rhizosphere. *Ecology Letters*, 8, 1264–1270. <https://doi.org/10.1111/j.1461-0248.2005.00831.x>
- Quirk, J., Beerling, D. J., Banwart, S. A., Kakonyi, G., Romero-Gonzalez, M. E., & Leake, J. R. (2012). Evolution of trees and mycorrhizal fungi

- intensifies silicate mineral weathering. *Biology Letters*, 8(6), 1006–1011. <https://doi.org/10.1098/rsbl.2012.0503>
- Quirk, J., Leake, J. R., Johnson, D. A., Taylor, L. L., Saccone, L., & Beerling, D. J. (2015). Constraining the role of early land plants in Palaeozoic weathering and global cooling. *Proceedings. Biological Sciences/ the Royal Society*, 282(1813), 20151115. <https://doi.org/10.1098/rspb.2015.1115>
- Redecker, D., Kodner, R., & Graham, L. E. (2000). Glomalean fungi from the Ordovician. *Science*, 289(5486), 1920–1921.
- Remy, W., Taylor, T. N., Hass, H., & Kerp, H. (1994). Four hundred-million-year-old vesicular arbuscular mycorrhizae. *Proceedings of the National Academy of Sciences*, 91, 11841–11843. <https://doi.org/10.1073/pnas.91.25.11841>
- Renforth, P. (2019). The negative emission potential of alkaline materials. *Nature Communications*, 10(1), 1401. <https://doi.org/10.1038/s41467-019-09475-5>
- Renforth, P., & Henderson, G. (2017). Assessing ocean alkalinity for carbon sequestration. *Reviews of Geophysics*, 55(3), 636–674. <https://doi.org/10.1002/2016RG000533>
- Rillig, M. C., Aguilar-Trigueros, C. A., Bergmann, J., Verbruggen, E., Veresoglou, S. D., & Lehmann, A. (2015). Plant root and mycorrhizal fungal traits for understanding soil aggregation. *New Phytologist*, 205, 1385–1388. <https://doi.org/10.1111/nph.13045>
- Rillig, M. C., Aguilar-Trigueros, C. A., Camenzind, T., Cavagnaro, T. R., Degruene, F., Hohmann, P., Lammel, D. R., Mansour, I., Roy, J., Heijden, M. G. A., & Yang, G. (2019). Why farmers should manage the arbuscular mycorrhizal symbiosis. *New Phytologist*, 222(3), 1171–1175. <https://doi.org/10.1111/nph.15602>
- Ryan, M. H., & Graham, J. H. (2018). Little evidence that farmers should consider abundance or diversity of arbuscular mycorrhizal fungi when managing crops. *New Phytologist*, 220, 1092–1107. <https://doi.org/10.1111/nph.15308>
- Schuilting, R. D., & Krijgsman, P. (2006). Enhanced weathering: An effective and cheap tool to sequester CO₂. *Climatic Change*, 74(1–3), 349–354. <https://doi.org/10.1007/s10584-005-3485-y>
- Sexstone, A. J., Revsbech, N. P., Parkin, T. B., & Tiedje, J. M. (1985). Direct measurement of oxygen profiles and denitrification rates in soil aggregates. *Soil Science Society of America Journal*, 49(3), 645–651. <https://doi.org/10.2136/sssaj1985.03615995004900030024x>
- Smith, S. E., & Read, D. J. (2008). *Mycorrhizal symbiosis*, 3rd ed. Academic Press.
- Smits, M. M., Bonneville, S., Benning, L. G., Banwart, S. A., & Leake, J. R. (2012). Plant-driven weathering of apatite - the role of an ectomycorrhizal fungus. *Geobiology*, 10(5), 445–456. <https://doi.org/10.1111/j.1472-4669.2012.00331.x>
- Smits, M. M., Johansson, L., & Wallander, H. (2014). Soil fungi appear to have a retarding rather than a stimulating role on soil apatite weathering. *Plant and Soil*, 385(1–2), 217–228. <https://doi.org/10.1007/s11104-014-2222-6>
- Smits, M. M., & Wallander, H. (2017). Role of mycorrhizal symbiosis in mineral weathering and nutrient mining from soil parent material. In N. C. Johnson, C. A. Gehring, & J. Jansa (Eds.), *Mycorrhizal mediation of soil* (first, pp. 35–46). Elsevier. <https://doi.org/10.1016/B978-0-12-804312-7.00003-6>
- Sochorová, L., Jansa, J., Verbruggen, E., Hejman, M., Schellberg, J., Kiers, E. T., & Collins, N. C. (2016). Long-term agricultural management maximizing hay production can significantly reduce belowground C storage. *Agriculture, Ecosystems and Environment*, 220, 104–114. <https://doi.org/10.1016/j.agee.2015.12.026>
- Son, Y., Stott, K., Manning, D. A. C., & Cooper, J. M. (2020). Carbon sequestration in artificial silicate soils facilitated by arbuscular mycorrhizal fungi and glomalin-related soil protein. *European Journal of Soil Science*, in press. <https://doi.org/10.1111/ejss.13058>
- Strefler, J., Amann, T., Bauer, N., Kriegler, E., & Hartmann, J. (2018). Potential and costs of carbon dioxide removal by enhanced weathering of rocks. *Environmental Research Letters*, 13(034010). <https://doi.org/10.1088/1748-9326/aaa9c4>
- Strullu-Derrien, C., Selosse, M. A., Kenrick, P., & Martin, F. M. (2018). The origin and evolution of mycorrhizal symbioses: From palaeomycology to phylogenomics. *New Phytologist*, 220(4), 1012–1030. <https://doi.org/10.1111/nph.15076>
- Taylor, L. L., Leake, J. R., Quirk, J., Hardy, K., Banwart, S. A., & Beerling, D. J. (2009). Biological weathering and the long-term carbon cycle: Integrating mycorrhizal evolution and function into the current paradigm. *Geobiology*, 7(2), 171–191. <https://doi.org/10.1111/j.1472-4669.2009.00194.x>
- Thirkell, T., Cameron, D., & Hodge, A. (2019). Contrasting nitrogen fertilisation rates alter mycorrhizal contribution to barley nutrition in a field trial. *Frontiers in Plant Science*, 10, 1–9. <https://doi.org/10.3389/fpls.2019.01312>
- Toljander, J. F., Lindahl, B. D., Paul, L. R., Elfstrand, M., & Finlay, R. D. (2007). Influence of arbuscular mycorrhizal mycelial exudates on soil bacterial growth and community structure. *FEMS Microbiology Ecology*, 61(2), 295–304. <https://doi.org/10.1111/j.1574-6941.2007.00337.x>
- UNFCCC. (2015). *Adoption of the Paris Agreement, 21st conference of the parties*. United Nations.
- Van Geel, M., De Beenhouwer, M., Ceulemans, T., Caes, K., Ceustermans, A. N., Bylemans, D., Gomand, A., Lievens, B., & Honnay, O. (2016). Application of slow-release phosphorus fertilizers increases arbuscular mycorrhizal fungal diversity in the roots of apple trees. *Plant and Soil*, 402(1–2), 291–301. <https://doi.org/10.1007/s11104-015-2777-x>
- Van Schöll, L., Kuyper, T. W., Smits, M. M., Landeweert, R., Hoffland, E., & Breemen, N. V. (2008). Rock-eating mycorrhizas: Their role in plant nutrition and biogeochemical cycles. *Plant and Soil*, 303(1–2), 35–47. <https://doi.org/10.1007/s11104-007-9513-0>
- Vandevenne, F. I., Barão, L., Ronchi, B., Govers, G., Meire, P., Kelly, E. F., & Struyf, E. (2015). Silicon pools in human impacted soils of temperate zones. *Global Biogeochemical Cycles*, 29, 1439–1450. <https://doi.org/10.1002/2014GB005049>
- Ven, A., Verlinden, M. S., Verbruggen, E., & Vicca, S. (2019). Experimental evidence that phosphorus fertilization and arbuscular mycorrhizal symbiosis can reduce the carbon cost of phosphorus uptake. *Functional Ecology*, 33, 2215–2225. <https://doi.org/10.1111/1365-2435.13452>
- Verbruggen, E., & Kiers, E. T. (2010). Evolutionary ecology of mycorrhizal functional diversity in agricultural systems. *Evolutionary Applications*, 3(5–6), 547–560. <https://doi.org/10.1111/j.1752-4571.2010.00145.x>
- Verbruggen, E., Van Der Heijden, M. G. A., Weedon, J. T., Kowalchuk, G. A., & Rölting, W. F. M. (2012). Community assembly, species richness and nestedness of arbuscular mycorrhizal fungi in agricultural soils. *Molecular Ecology*, 21, 2341–2353. <https://doi.org/10.1111/j.1365-294X.2012.05534.x>
- Veresoglou, S. D., Meneses, G., & Rillig, M. C. (2012). Do arbuscular mycorrhizal fungi affect the allometric partition of host plant biomass to shoots and roots? A meta-analysis of studies from 1990 to 2010. *Mycorrhiza*, 22(3), 227–235. <https://doi.org/10.1007/s00572-011-0398-7>
- Verlinden, M. S., Ven, A., Verbruggen, E., Janssens, I. A., Wallander, H., & Vicca, S. (2018). Favorable effect of mycorrhizae on biomass production efficiency exceeds their carbon cost in a fertilization experiment. *Ecology*, 99(11), 2525–2534. <https://doi.org/10.1002/ecy.2502>
- Witter, E., & Kirchmann, H. (1989). Peat, zeolite and basalt as adsorbents of ammoniacal nitrogen during manure decomposition. *Plant and Soil*, 115(1), 43–52. <https://doi.org/10.1007/BF02220693>
- Xiang, D., Verbruggen, E., Hu, Y., Veresoglou, S. D., Rillig, M. C., Zhou, W., Xu, T., Li, H., Hao, Z., Chen, Y., & Chen, B. (2014). Land use influences arbuscular mycorrhizal fungal communities in the farming-pastoral ecotone of northern China. *New Phytologist*, 204, 968–978. <https://doi.org/10.1111/nph.12961>

- Yona, L., Cashore, B., Jackson, R. B., Ometto, J., & Bradford, M. A. (2020). Refining national greenhouse gas inventories. *Ambio*, 49(10), 1581–1586. <https://doi.org/10.1007/s13280-019-01312-9>
- Zaharescu, D. G., Burghilea, C. I., Dontsova, K., Presler, J. K., Maier, R. M., Huxman, T., Domanik, K. J., Hunt, E. A., Amistadi, M. K., Gaddis, E. E., Palacios-Menendez, M. A., Vaquera-Ibarra, M. O., & Chorover, J. (2017). Ecosystem composition controls the fate of rare earth elements during incipient soil genesis. *Scientific Reports*, 7, 1–15. <https://doi.org/10.1038/srep43208>
- Zaharescu, D. G., Burghilea, C. I., Dontsova, K., Reinhard, C. T., Chorover, J., & Lybrand, R. (2020). Biological weathering in the terrestrial system. In K. Dontsova, Z. Balogh-Brunstad, & G. Le Roux (Eds.),

Biogeochemical cycles: Ecological drivers and environmental impact (pp. 1–32). John Wiley and Sons. <https://doi.org/10.1002/9781119413332.ch1>

How to cite this article: Verbruggen, E., Struyf, E., & Vicca, S. (2021). Can arbuscular mycorrhizal fungi speed up carbon sequestration by enhanced weathering? *Plants, People, Planet*, 3(5), 445–453. <https://doi.org/10.1002/ppp3.10179>