Plant-soil feedbacks and the resource economics spectrum

Zia Mehrabi[1]

[1]Centre for Sustainable Food Systems and Institute for Resources Environment and Sustainability, University of British Columbia, Canada.

Email: zia.mehrabi@ubc.ca

Summary

- Recent work suggests that resource economic traits might help predict the strength and direction of plant-soil feedback interactions, both in natural systems and in agriculture. However, there are many competing hypotheses to explain the effects of plant resource economics on plant-soil feedbacks.
- Faster-growing plants may have positive fertilizing effects if their tissues are incorporated and mineralized by soil microbes, but may also have negative effects if pathogens build up or fungal symbionts are lost through fertilization. Identifying the direction of effects may be confounded if nutrients are exported through herbivory, leaching, or crop harvesting.
- To determine causality in the effect of plant traits on plant-soil feedbacks it is essential for plant-soil feedback experiments to (1) quantify the mass of nutrients held in standing, or harvested plant biomass, and in losses to other sources in the field, and (2) undertake soil chemistry measurements (e.g. gross and net nitrogen mineralization) of nutrients limiting for plant growth throughout all phases of the feedback cycle.
- If rigorous nutrient budgeting in plant-soil feedback research is more widely practiced this will provide the data needed to synthesise results in comparable ways, and will enable mechanistic insights into the role of plant traits in mediating plant competition in both natural and applied settings.

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.26839v1 | CC BY 4.0 Open Access | rec: 9 Apr 2018, publ: 9 Apr 2018

Main text

Negative plant-soil feedbacks occur when plants culture soil microbiota and influence soil chemistry to the relative disadvantage of their own species [1–3]. This phenomenon has widespread importance in natural systems [2,4,5], and in agriculture where it is a principle driver of crop yield losses [6,7]. Despite its significance, the direction and strength of plant-soil feedbacks has proved extremely difficult to predict [1,8,9]. Previous work has shown that shared evolutionary history is unlikely to be a useful general predictor of plant-soil feedbacks between species [8]. Evidence for directional effects of plant leaf traits on nutrient cycling [10–12] and soil microbial community composition [13–15] on the other hand, suggest that plant functional traits might be used to help mechanistically account for the large unexplained variation in plant-soil feedback witnessed across different taxa and experimental settings.

It has been hypothesised that fast-growing resource-exploitative species (‘fast species’) with highly decomposable tissues replenish nutrients quicker and have higher fertilizing effects on soil than slow-growing resource conservative species (*see* Ref.16 for experimental evidence to support this idea). Under this scenario we would expect plants to grow better on soil cultured by faster-growing species as result of higher soil nutrient availability (Fig 1). Easy- to-measure aboveground traits (leaf N concentration, leaf P concentration, specific leaf area, leaf dry matter content) have typically been focussed on for their strong links to the plant resource economics spectrum [18,19] and their importance in driving soil nutrient status and food web structure [11–13,15]. The net effect of fast versus slow plant strategies on plant-soil feedbacks will however be influenced by the interactions with soil organisms, and mobilisation (or inputs) and immobilisation (or withdrawals) of soil nutrients, mediated through both aboveground and belowground organs [10,20]. Recent evidence suggests some consistency between below ground resource acquisition traits and plant-soil feedback effects [21].

However, just knowing the resource economics traits of species interacting in the soil medium is not by itself enough to use resource economic spectrum for mechanistic prediction of plant-soil interactions. For determination of the effects of resource economics, we need complementary nutrient budgeting in plant-soil feedback studies. There are two aspects that are of high importance: (1) quantification of the mass of nutrients held in standing, or harvested plant biomass from the culture phase (or in losses to other sources such as leaching or herbivores), and (2) soil chemistry measurements (both gross and net nitrogen mineralization, for example) of nutrients limiting for plant growth throughout the feedback cycle. Both of these aspects are needed to understand the operation and importance of plant-resource economics in interspecific plant-soil feedbacks.

Why nutrient budgeting is needed is easily understood by considering two simple experiments. In the first experiment the researcher grows species A in soil during a culture phase, harvests the plant biomass, then grows a species B on that same soil in a feedback phase, and at the end of the experiment records species B's biomass. In the second experiment, the researcher grows species A on soil, tills the biomass back into the soil, and then grows and records species B's biomass on that soil. All else equal (ignoring other biotic interactions), we might expect that the export of nutrients in the culture phase of experiment 1 would lead to less accumulation of biomass of species B during the feedback phase in experiment 1 than in experiment 2. If species A was more exploitative, particularly for nitrogen, and was able to extract nutrients quicker during its growth, we would expect this fitness difference to be even greater. This simple model example shows how nutrient export in plant-soil feedback experiments, or in the field, would lead to the complete opposite conclusions of the impacts of resource economic traits on plant-soil feedbacks than would be expected under the classical hypothesis, where plants in general benefit from the nutrient cycling effects of fast growing species (e.g. Fig 1). Extensions of these simple interactions could be made to other definitions of plant-soil feedback related to population level processes[22] – but whatever the formulation, the key problem remains: without proper nutrient budgeting in experiments, particularly during the culture phase, researchers will be left in the dark as to the expected effect of plant resource economics on plant-soil feedbacks.

The lack of accounting for nutrients dynamics furthermore makes it hard to tease apart the competing hypotheses on the impacts of resource economics on plant-soil feedbacks. Yes, on the one hand, positive effects of fast species might be explained by their fertilizing effects and chemistry legacies, or due to proliferation of microbes involved in nutrient mobilisation in fast soils [14,16,17]. But, on the other hand nutrient increase driven proliferation of pathogens [23], losses of beneficial fungi [14,24,25], investment in growth vs. defence, phytotoxic effects of highly decomposable tissue inputs [26,27], or disruptions or lags to recycling of plant materials [20], would all drive the effect of plant strategy on plant-soil feedbacks in the opposite direction, with plants performing worse on soil cultured by faster species. Separating out the relevance of each of these hypotheses will require targeted experimentation by plant-soil feedback researchers. While different types of experimental design may be needed for specific questions and systems, nutrient budgeting is a key baseline requirement for all.

Whilst there have already been calls for better coverage of belowground resource economics [10,28], inclusion of more realistic timescales of growth responses phases in plant-soil feedback experiments [29,30], and identification of biota responsible for pathogenic or symbiotic effects [31], improved nutrient budgeting in plant-soil feedback studies has received less attention. The gold standard should be to have the nutrient dynamics of the experimental system accounted for. Only once that has been done will it be possible to determine the degree of utility of the fast-slow resource economics for predicting the net effects of interspecific plant-soil feedbacks across different studies and environments, and understanding how we can better translate plant-soil feedback work into applied settings, such as agriculture.

Acknowledgements

Many thanks to Paul Kardol, Owen Lewis, Richard Bardgett, Peter Long, Sean Tuck, Kathy Willis, Peter Reich, and Jens Kattge, for their helpful comments on early drafts of this manuscript, and to Natascha Mehrabi for help with the graphics. ZM was supported by the BBRSC (BB/J014427/1).

References

1. Van der Putten, W. H. *et al.* Plant-soil feedbacks: The past, the present and future challenges. *J. Ecol.* **101,** 265–276 (2013).
2. Mangan, S. A *et al.* Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* **466,** 752–755 (2010).
3. Kulmatiski, A., Beard, K. H., Stevens, J. R. & Cobbold, S. M. Plant-soil feedbacks: A meta-analytical review. *Ecol. Lett.* **11,** 980–992 (2008).
4. Petermann, J. S., Fergus, A. J. F., Turnbull, L. a. & Schmid, B. Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology* **89,** 2399–2406 (2008).
5. Bagchi, R. *et al.* Testing the Janzen-Connell mechanism: Pathogens cause overcompensating density dependence in a tropical tree. *Ecol. Lett.* **13,** 1262–1269 (2010).
6. Dick, R. P. A review: long-term effects of agricultural systems on soil biochemical and microbial parameters. *Agric. Ecosyst. Environ.* **40,** 25–36 (1992).
7. Bennett, A. J., Bending, G. D., Chandler, D., Hilton, S. & Mills, P. Meeting the demand for crop production: The challenge of yield decline in crops grown in short rotations. *Biol. Rev.* **87,** 52–71 (2012).
8. Mehrabi, Z. & Tuck, S. L. Relatedness is a poor predictor of negative plant – soil feedbacks. *New Phytol.* **205**,1071-5 (2015).
9. Kardol, P., Veen, G., Tests, F. & Perring, M. Peeking into the black box: a trait- based approach to predicting plant –soil feedbacks. *New Phytol.* **206,** 1–4 (2015).
10. Freschet, G. T. *et al.* Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. *J. Ecol.* **101,** 943–952 (2013).
11. Cornwell, W. K. *et al.* Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol. Lett.* **11,** 1065–1071 (2008).
12. De Deyn, G. B., Cornelissen, J. H. C. & Bardgett, R. D. Plant functional traits and soil

carbon sequestration in contrasting biomes. *Ecol. Lett.* **11,** 516–531 (2008).

13. de Vries, F. T. *et al.* Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. *Ecol. Lett.* **15,** 1230–1239 (2012).
14. Grigulis, K. *et al.* Relative contributions of plant traits and soil microbial properties to mountain grassland ecosystem services. *J. Ecol.* **101,** 47–57 (2013).
15. Van Der Heijden, M. G. a, Bardgett, R. D. & Van Straalen, N. M. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.* **11,** 296–310 (2008).
16. Baxendale, C., Orwin, K. H., Poly, F., Pommier, T. & Bardgett, R. D. Are plant-soil feedback responses explained by plant traits? *New Phytol.* **204**, 408-423 (2014).
17. Ke, P., Miki, T. & Ding, T. The soil microbial community predicts the importance of plant traits in plant–soil feedback. *New Phytol.* **206**, 329–341 (2014).
18. Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428,** 821–827 (2004).
19. Reich, P. B. The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *J. Ecol.* **102,** 275–301 (2014).
20. Hobbie, S. E. Plant species effects on nutrient cycling: revisiting litter feedbacks. *Trends Ecol. Evol.* **30,** 357–363 (2015).
21. Teste, F. P. *et al.* Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science* **355,** 173–176 (2017).
22. Ke, P. & Miki, T. Incorporating the soil environment and microbial community into plant competition theory. *Front. Microbiol.* **6,** 1–16 (2015).
23. Veresoglou, S. D., Barto, E. K., Menexes, G. & Rillig, M. C. Fertilization affects severity of disease caused by fungal plant pathogens. *Plant Pathol.* **62,** 961–969 (2013).
24. Hoeksema, J. D. *et al.* A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecol. Lett.* **13,** 394–407 (2010).
25. Orwin, K. H. *et al.* Linkages of plant traits to soil properties and the functioning of temperate grassland. *J. Ecol.* **98,** 1074–1083 (2010).
26. Bonanomi, G., Sicurezza, M. G., Caporaso, S., Esposito, A. & Mazzoleni, S. Phytotoxicity dynamics of decaying plant materials. *New Phytol.* **169,** 571–578 (2006).
27. Bonanomi, G. *et al.* Phytotoxicity, not nitrogen immobilization, explains plant litter inhibitory effects: Evidence from solid-state 13C NMR spectroscopy. *New Phytol.* **191,** 1018–1030 (2011).
28. Bardgett, R. D., Mommer, L. & Vries, F. T. De. Going underground : root traits as drivers of ecosystem processes. *Trends Ecol. Evol.* **29,** 692–699 (2014).
29. Hawkes, C. V., Kivlin, S. N., Du, J. & Eviner, V. T. The temporal development and additivity of plant-soil feedback in perennial grasses. *Plant Soil* **369,** 141–150 (2013).
30. Kardol, P., De Deyn, G. B., Laliberté, E., Mariotte, P. & Hawkes, C. V. Biotic plant-soil feedbacks across temporal scales. *J. Ecol.* **101,** 309–315 (2013).
31. Bever, J. D. *et al.* Rooting theories of plant community ecology in microbial interactions. *Trends Ecol. Evol.* **25,** 468–478 (2010).

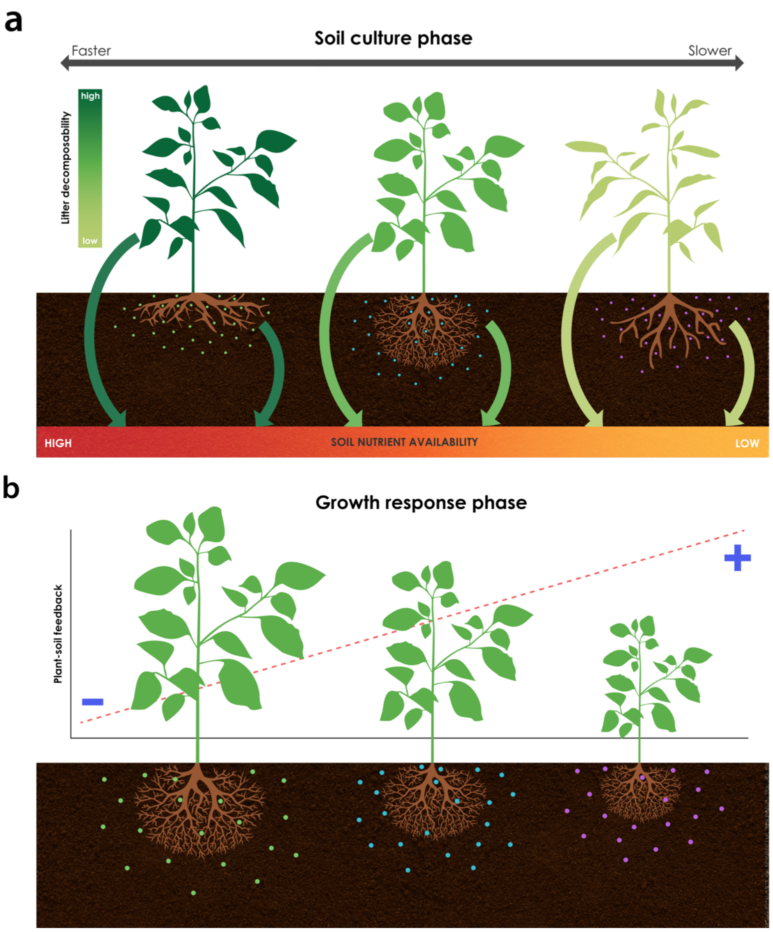

Figure 1. The classic hypothesis on the relationship between the plant resource economics spectrum and nutrient driven plant-soil driven feedbacks a) ‘Faster’ plants with highly decomposable litter inputs are expected to culture soils to have higher nutrient availability than ‘slower’ plants with lower litter decomposability b) All else being equal, plant growth of a given species is expected to increase on soil cultured by heterospecifics that are ‘faster’ and decrease on soils cultured by heterospecifics that are ‘slower’ relative to that of similar strategy conspecifics. Plant-soil feedback may be defined in different ways, but for illustration here it is defined as the average species fitness (e.g. proxied with biomass) accumulated on conspecific soil minus its average fitness accumulated on heterospecific soil.

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.26839v1 | CC BY 4.0 Open Access | rec: 9 Apr 2018, publ: 9 Apr 2018