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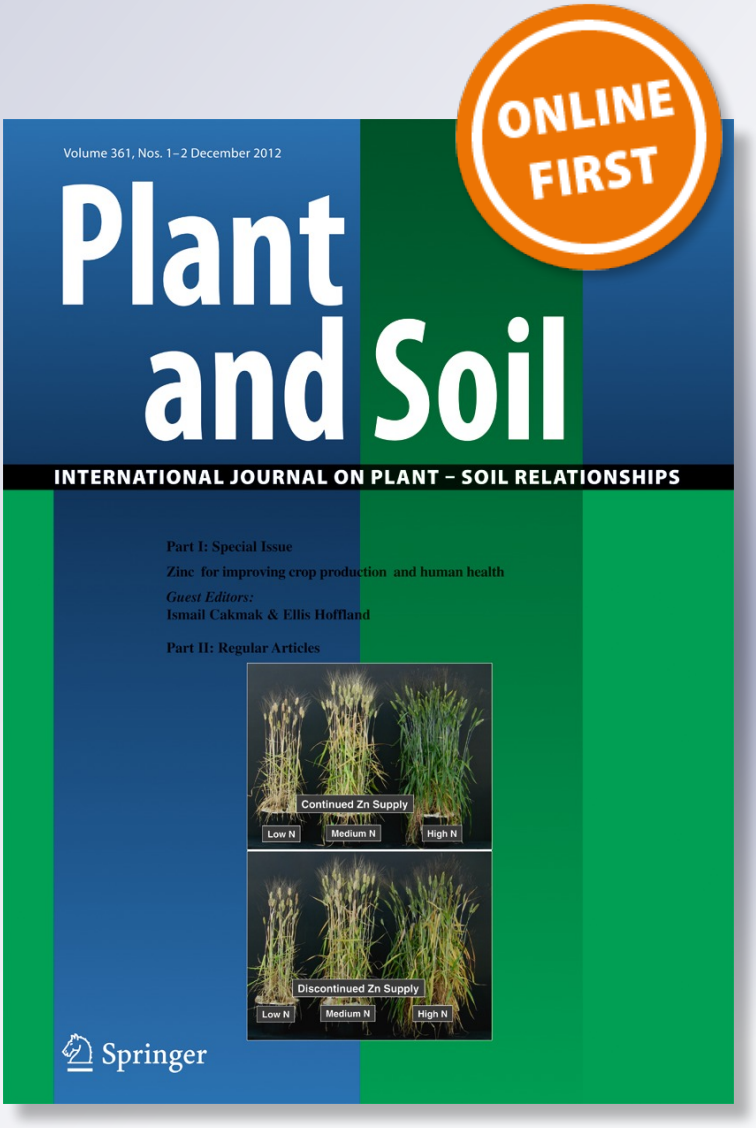
Plant and Soil
An International Journal on Plant-Soil Relationships

ISSN 0032-079X

Plant Soil
DOI 10.1007/s11104-012-1493-z



Springer

Plant Soil
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REGULAR ARTICLE

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Received: 4 May 2012 / Accepted: 5 October 2012

Abstract
Background Soil phosphorus availability declines during long-term ecosystem development on stable land surfaces due to a gradual loss of phosphorus in runoff and transformation of primary mineral phosphate into secondary minerals and organic compounds. These changes have been linked to a reduction in plant biomass as ecosystems age, but the implications for belowground organisms remain unknown.

Methods We constructed a phosphorus budget for the well-studied 120,000 year temperate rainforest chronosequence at Franz Josef, New Zealand. The budget included the amounts of phosphorus in plant biomass, soil microbial biomass, and other soil pools.
Results Soil microbes contained 68–78 % of the total biomass phosphorus (i.e. plant plus microbial) for the majority of the 120,000 year chronosequence. In contrast, plant phosphorus was a relatively small pool that occurred predominantly in wood. This points to the

Responsible Editor: Nico Eisenhauer.

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Published online: 20 November 2012

central role of the microbial biomass in determining phosphorus availability as ecosystems mature, yet also indicates the likelihood of strong competition between plants and saprotrophic microbes for soil phosphorus. *Conclusions* This novel perspective on terrestrial biogeochemistry challenges our understanding of phosphorus cycling by identifying soil microbes as the major biological phosphorus pool during long-term ecosystem development.

Keywords Chronosequence · Franz Josef · Microbial biomass · Phosphorus · Soil

Introduction

On stable land surfaces, and in the absence of major disturbance, phosphorus availability declines during ecosystem development over thousands to millions of years (Walker and Syers 1976; Crews et al. 1995). This occurs through a combination of chemical transformations of soil phosphorus (Walker and Syers 1976; Parfitt et al. 2005; Turner et al. 2007) and its loss in runoff at a greater rate than it is replenished by bedrock weathering or dust deposition from the atmosphere (Hedin et al. 2003). These changes have been linked to a reduction in plant biomass as ecosystems age, termed forest retrogression (Wardle et al. 2004), and appear to be a consistent property of ecosystems, because the same pattern has been observed in chronosequences that have developed under a range of climate conditions and on different geological substrates (Peltzer et al. 2010). The trend towards biological phosphorus limitation as soils age therefore provides a strong conceptual framework within which to evaluate the effects of long-term changes in nutrient availability on biological communities.

Although previous studies have revealed the importance of phosphorus in regulating forest biomass (Wardle et al. 2004) and diversity (Wardle et al. 2008; Wassen et al. 2005), the implications of the decline in phosphorus availability during ecosystem development for belowground microbial communities remain poorly understood (Peltzer et al. 2010). This is of significance because the soil microbial biomass (including saprotrophs and mycorrhizal fungi) plays a central role in the cycling and availability of phosphorus in soils (Richardson and Simpson 2011). Despite this, the microbial phosphorus pool is often assumed to be quantitatively small, because most measurements have been made on agricultural soils that are enriched in phosphorus (Cleveland and Liptzin 2007). Although a few studies have included microbial biomass in whole-ecosystem phosphorus budgets (e.g. Halm et al. 1972; Chapin et al. 1978), this has not been attempted previously for a long-term retrogressive chronosequence.

To address this gap, we constructed a whole-ecosystem phosphorus budget for the 120,000 year Franz Josef post-glacial chronosequence, New Zealand. The budget included estimates of phosphorus in plant biomass, soil microbial biomass, and other soil pools. Our aim was to determine for the first time how phosphorus pools in plants, microbes, and soils, vary during ecosystem development.

Methods

The Franz Josef post-glacial chronosequence is well studied (Walker and Syers 1976; Parfitt et al. 2005; Wardle et al. 2004; Richardson et al. 2004; Turner et al. 2007) and patterns of soil phosphorus and forest biomass are representative of chronosequences more broadly (Peltzer et al. 2010). Briefly, the Franz Josef chronosequence consists of a series of post-glacial schist outwash surfaces up to 120,000 years old on the west coast of the South Island of New Zealand. Mean annual temperature is 10.8 °C and annual rainfall varies from ~6.5 m on young soils in the glacial valley to ~3.5 m on the older sites nearer the coast (Richardson et al. 2004). The sites support mixed conifer–angiosperm forests, with young sites dominated by evergreen angiosperms and older sites supporting an increasing proportion of conifers in the Podocarpaceae (Richardson et al. 2004). The two oldest sites have experienced at least one glacial–interglacial cycle, with deposition of infertile quartz silt loess during the last glaciation (Almond et al. 2001). Despite this, the sequence represents a clear age-related nutrient gradient that influences both above and below-ground biological communities (Allison et al. 2007; Richardson et al. 2004; Wardle et al. 2004; Williamson et al. 2005).

We calculated a phosphorus budget for four key stages of the chronosequence: 5 years, 1000 years, 12,000 years, and 120,000 years. Note that the age of the oldest stage of the sequence (120,000 years)

was revised from the original 22,000 years reported by Walker and Syers (1976) based on reinterpretation of landforms (Almond et al. 2001). For each stage we calculated the amount of phosphorus on an area basis (g P m^{-2}) contained in plant biomass, soil microbial biomass, and other soil pools. Soil phosphorus pools, including phosphorus in stones, primary mineral phosphate (apatite), organic phosphorus, and secondary mineral phosphate, were calculated to 75 cm depth using values from Walker and Syers (1976) and bulk density values for each horizon from Stevens (1968). Phosphorus in plant biomass was calculated for aboveground wood, roots, and leaves using published values. Foliar phosphorus was estimated from leaf phosphorus concentrations across the chronosequence (Richardson et al. 2005) and specific leaf area (Whitehead et al. 2005) and leaf area index (LAI) derived from normalized difference vegetation index values (NDVI; Whitehead et al. 2005) using an LAI–NDVI relationship established for New Zealand forests (Coops et al. 2002). Phosphorus in aboveground wood was estimated from vegetation height (H) (Richardson et al. 2004; Wardle et al. 2004) converted to wood biomass using $(2.8+0.4H)^2$ (Lefsky et al. 1999) and a global average of wood phosphorus concentration (0.0075 %; Chave et al. 2009) that was similar to values for native New Zealand trees (Levett et al. 1985). Belowground plant biomass was estimated as a fixed proportion (20 %) of aboveground biomass (White et al. 2000), with phosphorus content calculated using a mean root phosphorus concentration (Vitousek and Sanford 1986); this measure for coarse plus fine roots gave a similar, but slightly lower, estimate of belowground phosphorus than using phosphorus concentrations for fine roots sampled along the Franz Josef chronosequence (Holdaway et al. 2011). The estimate of vegetation phosphorus was most sensitive to the 50-fold variation in canopy height across the chronosequence rather than to possible variation in individual parameters.

We added new measurements of soil microbial phosphorus in the top 10 cm of the mineral soil and the organic horizon (where present). This is presumably the region that contains the majority of the microbial biomass (e.g. Fierer et al. 2003), although the oldest soil along the sequence contained relatively high carbon concentrations in deeper parts of the profile (Stevens 1968), raising the possibility that microbial phosphorus was underestimated at this site. Five replicate soil samples were taken at each site over 3 days in the southern hemisphere winter. Soils were sieved <4 mm, small stones and fine roots were removed manually, and the samples were stored at 4 °C prior to analysis. Microbial phosphorus was determined for nine sites along the chronosequence ranging from 60 to 120,000 years, including the four sites for which the whole-ecosystem budgets were calculated. For the surface mineral soil we measured microbial phosphorus directly by chloroform fumigation with phosphorus detection by molybdate colorimetry (Brookes et al. 1982). Values were corrected for phosphate sorption to soil during the extraction and for microbial phosphorus not recovered by fumigation (i.e. using a k_p factor) (Brookes et al. 1982). In the same soils we also determined microbial carbon and nitrogen by standard procedures involving chloroform fumigation and extraction in 0.5 M K_2SO_4 with carbon and nitrogen detection by TOC–TN analyzer (Shimadzu, Columbia, MD) and appropriate corrections for unrecovered biomass (Brookes et al. 1985; Vance et al. 1987).

Chloroform fumigation does not release phosphorus from non-microbial soil organic matter (Brookes et al. 1982), although leaf fragments and fine roots can contribute (Sparling et al. 1985). As this could lead to an overestimation of microbial phosphorus in soil organic horizons, we used total phospholipid fatty acid (PLFA) concentrations measured in both mineral soil (0–10 cm) and organic horizons (methodology and data reported in Allison et al. 2007) to estimate microbial phosphorus in the organic horizon using the PLFA-to-microbial-carbon ratio of the mineral soil. This assumes a close relationship between total PLFA and microbial carbon concentrations determined by fumigation extraction (e.g. Fierer et al. 2003), and a constant microbial carbon to phosphorus ratio between organic and mineral horizons at a site (e.g. Sparling et al. 1994).

We corrected the original organic phosphorus values presented in Walker and Syers (1976) by subtracting the amount of microbial phosphorus, based on the assumption that most microbial phosphorus in unmanaged soils occurs in organic forms (Magid et al. 1996). Microbial phosphorus concentrations were too low to measure on the youngest soil, so these were estimated from microbial phosphorus data for a 60 year old site, assuming a constant total organic carbon-to-microbial phosphorus ratio (as observed from the positive linear relationship between total carbon and microbial

phosphorus in surface soils along the sequence). Total organic carbon concentrations for all samples along the sequence were reported previously (Allison et al. 2007).

Results

There was a rapid depletion of primary mineral phosphate in both stones and the fine earth fraction (< 2 mm), and a parallel accumulation of phosphorus in secondary minerals and organic compounds (Fig. 1, Table 1). Only a small proportion of the total profile weight of phosphorus was in the organic horizon at any site (≤ 4 %; Table 2). Ecosystem phosphorus in organic forms, including dead soil organic matter, plants, and microbes, increased from < 1 % of the total phosphorus in the youngest soil (5 years) to > 40 % in the oldest soil (120,000 years). These changes confirm a progressive switch from a system dominated by dissolution of inorganic phosphorus in primary minerals driven by weathering, to mineralization of organic phosphorus driven by biological processes. Particularly striking, although not widely recognized, is the rapid decline of the stone fraction and its contribution to phosphorus availability during ecosystem development through weathering and the release of primary mineral phosphate.

For living tissue, phosphorus in plant biomass constituted a relatively small pool throughout the sequence (0.5–4.9 g P m^{-2}; Fig. 1; Table 1). Plant phosphorus was mostly contained in woody tissue in the late phosphorus-limited stages of the chronosequence (Table 1). In contrast, the soil microbial biomass contained 3.9–10.3 g P m^{-2} in mature soils, which represented 68–78 % of the total biomass phosphorus (Fig. 1; Table 1). Microbial phosphorus was therefore several times greater than phosphorus in vegetation for the majority of the 120,000 year chronosequence. The organic horizon contained only ~8 % of the total microbial phosphorus in the 1000 and 120,000 year soils, but 26 % in the 12,000 year soil, reflecting the thickness of the organic horizon at this site (Table 2).

Aside from the early stages of the chronosequence, microbial nutrient concentrations in mineral soil varied little over 120,000 years of ecosystem development (Fig. 2). For soils between 500 and 60,000 years old, microbial carbon, nitrogen, and phosphorus concentrations were ~1500 mg C kg^{-1}, ~300 mgN kg^{-1}, and ~150 mg P kg^{-1}, respectively (Fig. 2). Concentrations of all microbial nutrients were lower in younger soils, and there was a small decline in microbial phosphorus in the oldest soil (Fig. 2c).

The relatively consistent concentrations of nutrients in microbial biomass resulted in stable carbon to nitrogen and carbon to phosphorus ratios for the majority of the sequence (Fig. 2d). For all soils between 130 and 60,000 years, mean microbial carbon to phosphorus molar ratios were ~30 and microbial nitrogen to phosphorus molar ratios were ~5 (Fig. 2d). Ratios were higher in young (60 year) and old (120,000 year) soils (Fig. 2d).

Discussion

Previous studies of ecosystem development have revealed the importance of total phosphorus in regulating plant biomass (Wardle et al. 2004), as well as the increasing importance of organic phosphorus as soils age (Walker and Syers 1976; Turner et al. 2007), but have not recognized the quantitative significance of the soil microbial phosphorus pool. This is perhaps because measurements have been made on agricultural systems, where microbial biomass typically contains < 5 % of the total soil phosphorus (Brookes et al. 1982; Cleveland and Liptzin 2007).

The remarkable finding that soil microbial biomass contains much more phosphorus than plant biomass for the majority of the 120,000 years of ecosystem development at Franz Josef is linked to the disparity between the concentrations of phosphorus in plant and microbial tissues. For example, the mean phosphorus concentrations (dry weight basis) for soil microbes were reported to be 5.4 mg P g^{-1} in fungi and 19 mg P g^{-1} in bacteria (Brookes et al. 1982). In contrast, the global average phosphorus concentration in wood is approximately 0.08 mg P g^{-1} (Chave et al. 2009), which is similar to values reported for New Zealand broadleaf–podocarp forests (Levett et al. 1985). For live leaves, community-level phosphorus concentrations range between 0.5 and 1.6 mg P g^{-1} along the Franz Josef chronosequence, with the lowest concentrations on the oldest sites (Richardson et al. 2004). Microbes therefore contain substantially greater phosphorus concentrations than plants throughout the sequence.

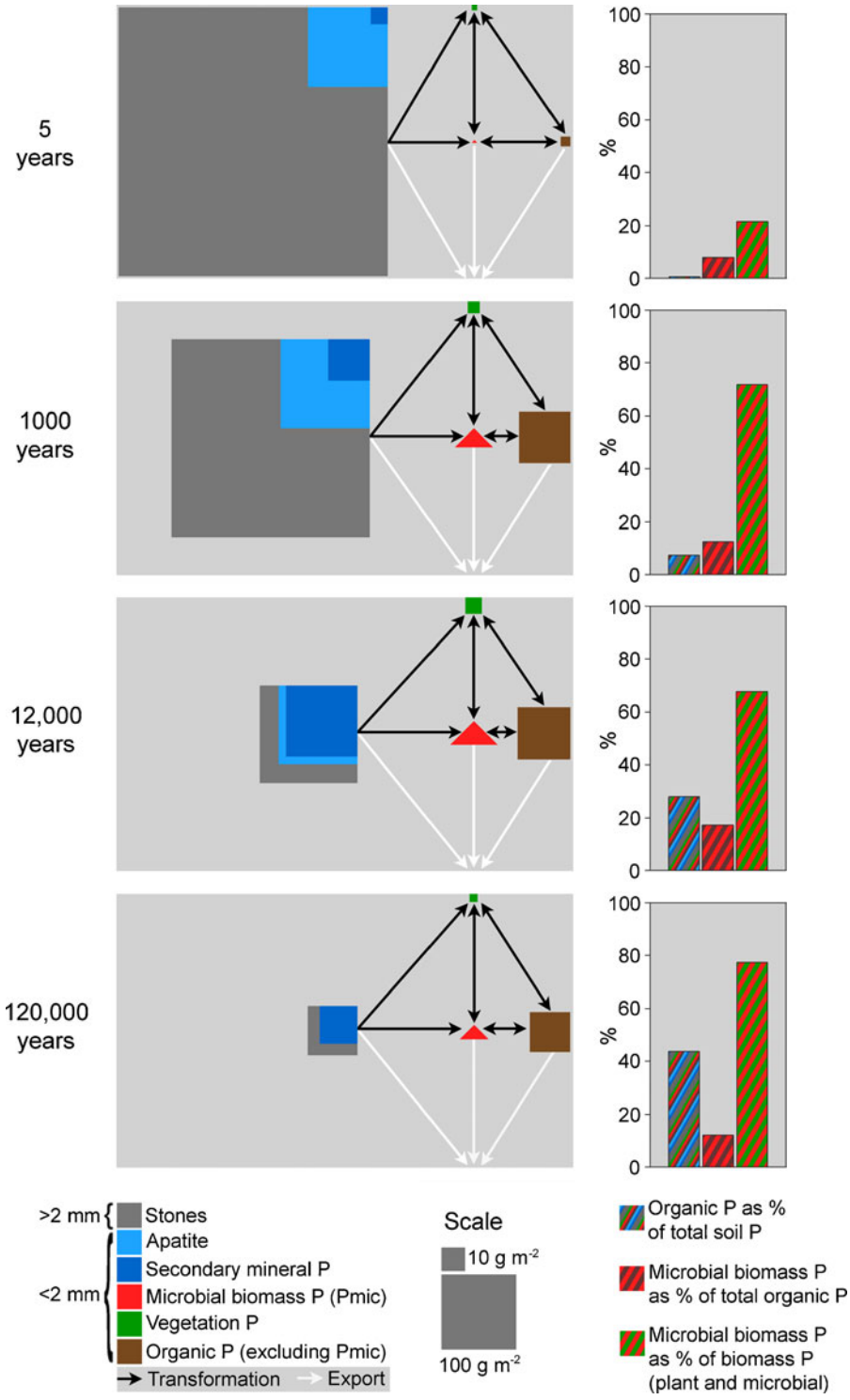

Fig. 1 Changes in ecosystem phosphorus pools along the 120,000-year Franz Josef soil chronosequence, New Zealand. The area of each scale box represents the amount of phosphorus in the respective pool on an area basis to 0.75 m depth (g P m^{-2}). Note the central role of the microbial biomass in the system; its representation as a triangle emphasizes the three axes of interactions and transfers between the other major pools, including with plants via mycorrhizal fungi (the apex of the triangle), weathering of mineral phosphorus (the left-facing point of the triangle) and mineralization of organic phosphorus (the right facing point). Bar graphs show (from left to right) organic phosphorus (i.e. phosphorus in soil organic matter, microbes, and vegetation) as a percentage of the total ecosystem phosphorus, microbial phosphorus as a percentage of the soil organic phosphorus (i.e. phosphorus in organic matter and microbes), and microbial phosphorus as a percentage of the total biomass phosphorus (i.e. phosphorus in microbes and vegetation)

Concentrations of carbon, nitrogen, and phosphorus in microbial biomass varied little along the chronosequence, although there was evidence for a decline in microbial phosphorus in the oldest soil, perhaps attributable to the previously reported increase in the fungal to bacterial ratio in the late stages of the

Table 1 Phosphorus pools (g P m^{-2}) in plants and soils along the Franz Josef post-glacial chronosequence, New Zealand

Surface age[a]	Profile number[b]	Plant biomass P				Soil (profile to 75 cm including the organic horizon)						
Years		Wood	Leaf	Root	Total	Total P[c]	Total P (>2 mm)	Total P (<2 mm)	Apatite (<2 mm)	Secondary P (<2 mm)	Organic P (<2 mm)[d]	Microbial P (<2 mm)
5	I	0.07	0.34	0.10	0.51	1292.0	1177.0	115.0	108.0	5.2	1.7	0.14
1000	LW1	1.17	0.41	1.04	2.62	753.0	558.0	194.2	109.6	31.1	46.8	6.66
12000	M1	2.48	0.25	2.18	4.90	229.0	59.0	169.6	19.5	90.4	49.4	10.31
120000	Ok2	0.49	0.19	0.45	1.13	76.0	18.0	58.0	0.0	25.7	28.4	3.89

[a] Year five is equivalent to year zero in Walker and Syers (1976)

[b] Profile numbers are from Stevens (1968)

[c] Including stones >2 mm

[d] Soil organic phosphorus does not include microbial phosphorus

sequence (Allison et al. 2007). Wardle and Ghani (1995) also observed that microbial biomass in mineral and organic horizons determined by substrate-induced respiration increased early on in the sequence and declined in the oldest soil, a similar pattern to that reported here for microbial carbon and nitrogen determined by fumigation–extraction. The stable microbial nutrient concentrations are consistent with the recent suggestion that microbial element stoichiometry is constrained across ecosystems worldwide (Cleveland and Liptzin 2007). For example, the global mean (± standard error) microbial carbon to phosphorus molar ratio in forest soils is 74.0±6.2, while the mean microbial nitrogen to phosphorus molar ratio is 8.9±0.8 (data from Table 1 in Cleveland and Liptzin 2007). For all soils along the Franz Josef chronosequence, the mean microbial carbon to phosphorus molar ratio was 36.2±2.8 and the mean microbial nitrogen to phosphorus molar ratio was 5.9±0.7. Although there are few comparable data on soil microbial nutrients in the Franz Josef region, a study of organic and surface mineral soils supporting native *Nothofagus* forest in New Zealand reported microbial nitrogen to phosphorus molar ratios < 5 (Sparling et al. 1994). Our values therefore indicate that the microbial biomass along the Franz Josef chronosequence is relatively rich in phosphorus compared to forest soils worldwide, but is similar to at least one other site under native forest in New Zealand. This hints at persistent nitrogen limitation of soil microbes throughout ecosystem development in New Zealand temperate rain forests.

There have been three previous assessments of microbial phosphorus concentrations along soil chronosequences. Lajtha and Schlesinger (1988) studied a sequence of Aridisols ranging in age from ~1000 to > 25,000 years old in the Basin and Range physiographic province in the Southwestern United States. However, microbial phosphorus concentrations determined by chloroform fumigation and anion-exchange resins were small and variation along the sequence was not reported. Torn et al. (2005) studied a series of soils developed on basaltic lava on the Hawaiian Islands ranging from 300 to 4.1 million years old. Microbial phosphorus concentrations peaked after 150,000 years in both organic and mineral soil horizons,

Table 2 Proportional distribution of total and microbial phosphorus by organic versus mineral soil horizons for four key stages along the Franz Josef chronosequence, New Zealand

Surface age	Total P (% of total profile P)		Microbial P (% of microbial P in profile)	
Years	Organic horizon	Mineral soil	Organic horizon	Mineral soil
5	0	100	0	100
1000	0.6	99.4	7.4	92.6
12000	4.0	96.0	26.4	73.6
120000	1.9	98.1	8.0	92.0

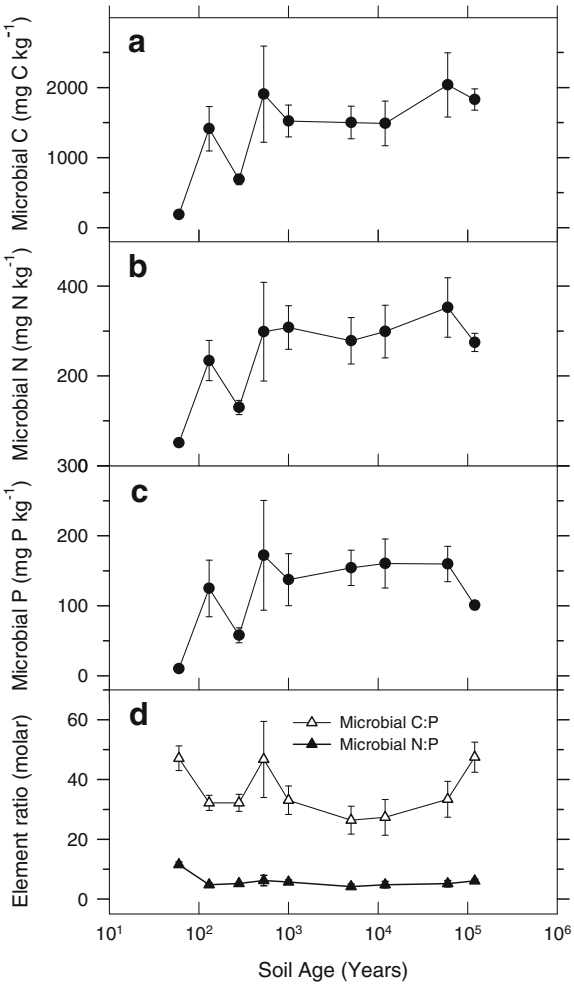

Fig. 2 Soil microbial carbon (**a**), nitrogen (**b**), and phosphorus (**c**), and the molar ratios of carbon and nitrogen to phosphorus (**d**) in mineral soil (0–10 cm) at nine sites along the Franz Josef chronosequence, New Zealand. Values are the mean ± standard error of five replicate samples at each site

and then declined in older soils. However, values were not corrected for phosphate fixation, which might have contributed to the low values on the oldest and presumably most strongly phosphorus-fixing soils, particularly given the long fumigation times used in that study (36–48 h). Lagerström et al. (2009) studied microbial biomass in soils along the Swedish Islands sequence, in which fire frequency is determined by island size, resulting in 'younger' soils on larger islands that burn less frequently and 'older' soils on small islands that burn rarely. Microbial phosphorus concentrations were between 298 and 545 mg P kg^{-1}, with highest concentrations on intermediate-sized islands, and microbial nitrogen to phosphorus ratios were < 4 on a molar basis. Together with our data for the Franz Josef chronosequence, these results suggest a consistent pattern of change in microbial phosphorus during pedogenesis under a range of geological and climatic conditions.

The studies discussed above did not determine pools of phosphorus in microbes and plants, so we cannot assess whether the dominance of the microbial phosphorus pool observed at Franz Josef also occurs along other chronosequences. However, the generality of the phenomenon is hinted at by a simple calculation based on global estimates of plant and microbial phosphorus. Combining the global estimate of soil microbial carbon of 13.9 Gt (Wardle 1992, p. 341) with the global mean carbon to phosphorus ratio in microbial biomass of 23.1 on a mass basis (Cleveland and Liptzin 2007) yields a global microbial phosphorus estimate of 0.60 Gt. Comparing this with the global estimate of plant phosphorus of 0.39 Gt (Wang et al. 2010) indicates that the global microbial phosphorus pool is 54 % greater than the global plant phosphorus pool and accounts for 60 % of the total biomass phosphorus. Although this calculation requires further verification, it does suggest that our findings are broadly applicable to ecosystems worldwide.

The quantitative importance of the microbial phosphorus pool in even moderately aged ecosystems indicates that microbes must play a far greater role than previously recognized in regulating phosphorus dynamics during ecosystem development. First, microbes, including symbiotic mycorrhizal fungal associations with plant roots, promote phosphorus availability through apatite weathering (Blum et al. 2002; Smits et al. 2012) and recycling from decaying organic matter (Magid et al. 1996; Smith and Read 2008). Phosphorus sequestered in microbial tissue subsequently becomes available to other microbes and plants following cell death. The large size of the microbial phosphorus pool, coupled with the rapid turnover time of soil microbial phosphorus (i.e. ~40 days for temperate agricultural soils; Kouno et al. 2002), suggests that it is an increasingly important source of plant-available phosphorus as soils age.

Second, microbes determine the long-term fate of phosphorus in ecosystems by influencing the rate of soluble phosphorus loss in runoff. Microbes conserve phosphorus by converting it into organic forms in their tissue, particularly during the early period of pedogenesis when there is greatest overall loss of phosphorus

from the ecosystem. However, microbes may promote phosphorus loss by enhancing weathering (see above) and via leaching of organic phosphorus; many organic phosphorus compounds are more mobile in soil than inorganic phosphate (Frossard et al. 1989) and are released from microbial cells following cycles of wetting and drying or freezing and thawing (Turner and Haygarth 2001; Blackwell et al. 2010).

Finally, the disparity between the amounts of phosphorus in plants and microbes in the late stages of the Franz Josef chronosequence indicates the likelihood of intense competition for available phosphorus between autotrophs and saprotrophs in mature soils. This might be expected to increasingly influence the composition of plant communities through time by favoring species with root symbiotic associations adapted to acquire phosphorus from the organic and recalcitrant inorganic forms of phosphorus that dominate the total phosphorus pool in strongly-weathered soils (Lambers et al. 2008; Turner 2008). For example, plants species forming arbuscular mycorrhizas, typical of the majority of land plants and adapted to efficiently scavenge soluble phosphate (Smith and Read 2008), would be expected to decline as ecosystem development proceeds. In contrast, plant species capable of forming ericoid mycorrhizas, which can use a variety of organic phosphorus forms including nucleic acids (Leake and Miles 1996), or plant species that form cluster roots, which are extremely efficient at acquiring phosphorus from infertile soils (Lambers et al. 2008), would be expected to increase in abundance on old soils where competition for phosphorus with microbes is intense. This is consistent with the abundance of members of the Ericaceae and Proteaceae on ancient landscapes, such as the kwongan of Western Australia and the fynbos of South Africa (Lambers et al. 2010).

Furthermore, the progressive loss of phosphorus from soils as ecosystems age may have driven plants and mycorrhizas to evolve more effective mechanisms of mineral weathering and phosphorus recycling. For example, there is evidence that mineral weathering has progressively increased with advancement from arbuscular mycorrhizal to later independently-evolved ectomycorrhizal fungi, and from gymnosperm to angiosperm hosts with both fungal groups (Quirk et al. 2012). This has far-reaching consequences for global biogeochemical cycles, including feed-backs between the geosphere and atmosphere via the geochemical carbon cycle over multi-million year timescales (Taylor et al. 2009).

In summary, our results indicate that microbial biomass can be the dominant biotic phosphorus pool for > 100,000 years of ecosystem development, far exceeding the amount of phosphorus in vegetation. This finding challenges our understanding of phosphorus cycling in natural systems and provides a novel framework for understanding plant–microbe interactions in space and time. The results are likely to apply broadly to ecosystems worldwide given the similarity of changes in phosphorus during pedogenesis in contrasting ecosystems (Parfitt et al. 2005; Peltzer et al. 2010; Turner et al. 2012). They also have important implications for the development of sustainable agronomic systems in light of the impending depletion of rock phosphate reserves for fertilizer production worldwide (Cordell et al. 2009).

Acknowledgements This manuscript is a product of an ARC–NZ Network for Vegetation Function workshop held at the University of Western Australia. We thank V.J. Allison, S.J. Davies, A.E. Herre, E. Laliberté and P. Thrall for their contributions.

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