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REVIEW ARTICLE

Phosphorus resorption and tissue longevity of roots and leaves – importance for phosphorus use efficiency and ecosystem phosphorus cycles

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Abstract Plants recycle substantial amounts of phosphorus (P) from senescing tissues, reducing the need to take up P from soils. This paper reviews P recycling in plants, factors that determine its quantitative importance, and evidence that species from low-P ecosystems possess traits that enhance P recycling. It focuses on roots and leaves where most P turnover occurs. Knowledge of root traits and dynamics lags far behind that of leaves, but P concentrations, lifespans, resorption percentages and biomass allocation of roots are all comparable to those of leaves. Relationships among traits that influence P recycling appear more complex in roots than in leaves. Long root lifespans may not be adaptive in soils with very low P availability. At the plant level, the quantitative importance of P resorption to support P requirements decreases with net growth rate and with tissue longevity. Leaf lifespans are negatively correlated with growth rates and resource availability, but root lifespans may not be, indicating that further research into root dynamics and P resorption is essential to understand the role of roots in both P conservation and P acquisition.

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Introduction

Interest in the importance of phosphorus (P) for plants has increased significantly in the past decades, for several important reasons. These include: a greater awareness that many ecosystems in the world are P-limited rather than N-limited (Vitousek et al. 2010); predicted future scarcity of P fertiliser for agricultural and negative environmental impacts P fertilisation (Elser and Bennett 2011); awareness of complex interactions between P, N deposition, high CO_2 and climate change (Fleischer et al. 2019); the realisation that high biodiversity is linked with low P (Laliberté et al. 2013; Wassen et al. 2021); the increased understanding of plant adaptations to low-P soils, including plant–microbe interactions (Lambers 2022).

There has been an impressive body of work into the physiology of P uptake and use by plants in the past decades (Lambers 2022), and there have also been important advances in our knowledge of availability and fluxes of P in ecosystems, in natural and agricultural systems (Bünemann et al., 2010; Simpson et al. 2011). There has, however, been comparatively little integration of the new insights in plant P nutrition and ecosystem P cycling. Such integration can potentially lead to a better understanding of evolutionary drivers, functional diversity, geographical distribution and management implications of plant P nutrition. Current big issues, such as climate change and the need to sustainably increase food production, require integrative approaches, including sophisticated land surface models and crop simulation models. Although progress is being made with the representation of plant P in these models (Goll et al. 2017; Wu et al. 2019), appropriate description of aspects such as soil P availability, plant P stress responses, biomass and nutrient allocation and biomass turnover remain a challenge (Das et al. 2019; Goll et al. 2017; Jiang et al. 2019). An integrated understanding of plant and soil P dynamics is required to respond to important questions such as the effect of P deficiency on elevated-CO_2-stimulated net primary productivity (Ellsworth et al. 2017), or the effect of specific P efficiency traits on crop productivity and P fertiliser requirements (Veneklaas et al. 2012).

Plants that grow on soils with low P availability, whether due to low-P parent material or extreme weathering, require adaptations that lead to enhanced efficiency in the uptake and use of P (Lambers et al. 2006, 2011). I define P uptake efficiency broadly here as the rate of P uptake from low-P soil, per unit root mass. Phosphorus use efficiency is the amount of plant dry mass produced per unit P taken up, which is determined by the efficiency by which P is used in physiological/biochemical processes as well as the residence time of P in the plant (Veneklaas et al. 2012). As will be clear in this paper, accurate measurement of P use efficiency at the whole-plant or whole-ecosystem level is not simple, and as a result, proxy measures have been used by many researchers (e.g., leaf litterfall mass / leaf litterfall P flux; Vitousek 1982), which are useful, but do not account for all aspects of P use efficiency. Implications of plant P efficiency for ecosystem-level P cycling processes are potentially complex: whilst enhanced uptake of P from soils may increase P cycling rates, high P retention in plants will inevitably reduce P cycling through the plant-soil system. Plants lose considerable amounts of nutrients due to tissue turnover, especially the shedding of plant parts such as leaves and fine roots (Chapin et al. 2011). Every unit of P that is retained in the plant is a unit that does not have to be taken up from the soil, to meet the plant's P requirements. The fact that greater P retention reduces P fluxes into the soil, leading to a P decrease in soils that are already low in P, further increases the importance of efficient P uptake. Adaptations for enhanced P uptake in such low-P soils should primarily be considered as mechanisms enabling adequate P uptake to support low to moderate growth rates, rather than mechanisms enabling high P uptake rates and high growth rates. Overall, plants in ecosystems on low-P soils exhibit conservative behaviour which increases internal cycling (within-plant reuse) at the cost of external cycling (tissue turnover – decomposition—mineralisation—uptake). These pathways are also known as the biochemical and biogeochemical cycles (Johnson and Turner 2019).

This paper briefly reviews the topic of P recycling within the plant, describes its role as a mechanism underpinning plant P use efficiency, and explores its likely effects on ecosystem P cycling through reduced fluxes of P in the decomposition process. It focuses on P-limited systems where such interactions are likely to be most tight and have the largest impact on ecosystem function and structure. Special attention is paid to the P dynamics of roots, which are much less studied than aboveground parts.

Uptake and loss of P – from plant to ecosystem fluxes

Ecosystem P cycling is mostly driven by P uptake and P loss of plants (Chapin et al. 2011). In natural systems, atmospheric inputs, weathering, leaching and erosion are generally small relative to biological fluxes associated with plant growth and mortality (Chapin et al. 2011). For most low-P ecosystems it is therefore reasonable to consider their P cycle as a closed cycle for practical purposes. P taken up by plants is derived from decomposing organic material, produced mostly by the plants themselves (and to a smaller extent by heterotrophs which depend on plants). In a steady state, the mean annual P taken up equals the mean annual P decomposed and mineralised, which equals the mean annual P lost from plants through shedding of plant parts or whole-plant mortality. The plant parts that are most short-lived (highest tissue turnover) and have the highest P concentrations are leaves and fine roots (Tang et al. 2018; Johnson and Turner 2019). As summarised below, there is a large body of knowledge on leaf turnover and P, but much less on roots, representing an important gap in our knowledge of plant and ecosystem P dynamics.

The relative amount of biomass that plants invest belowground, and how this varies with nutrient availability and productivity, is still poorly known (Vicca et al. 2018). Plants whose growth is limited by nutrients, including P, allocate more carbon to their roots (Lambers and Oliveira 2019; Poorter et al., 2012) and mycorrhizal partners (Raven et al. 2018). Ecosystems on low-P soil are therefore expected to partition large amounts of carbon belowground. There appear to be important exceptions, however, due to the strong influence of other environmental factors on cycling and uptake rates. Gill and Finzi (2016) used FLUXNET data to estimate below- and aboveground gross primary production, and combined these data with estimates of P mineralisation rates, estimated from P uptake rates (assuming equality). The biomes with the highest ecosystem-level P use efficiency (here defined as gross primary production/net P mineralisation rate), which the authors assumed to indicate P limitation, were the Mediterranean and tropical biomes, which are indeed known to contain many low-P systems (Lambers et al. 2010). Belowground carbon partitioning in the tropical biome was, however, unexpectedly low: 30% of gross primary production compared to an average of 52% for other biomes (Gill and Finzi 2016). The authors suggested that the cost of P acquisition in tropical soils is relatively low due to high temperatures and high N availability, in contrast to Mediterranean systems where seasonal drought and P-fixing soils increase the C-cost of P acquisition.

The difficulty of performing measurements of actual P uptake rates, plant internal P cycling and P mineralisation rates, means that many of our insights into P cycling through ecosystems still come from litterfall studies. Such studies are particularly useful for the study of P fluxes associated with leaf turnover, but unfortunately provide very incomplete estimates of ecosystem P fluxes. Freschet et al. (2013) estimated that roots contribute about half of the annual organic matter input in forest soils, and about a third in grassland soils. Measurements of turnover rates of long-lived plant parts, such as woody twigs and branches, but also coarse roots, are rare. These do contribute to the P cycle and can represent large P pools in high-biomass ecosystems such as forests; they also play a significant role in P dynamics as a store for P, contributing to P supply for new growth after the leafless phase of deciduous trees (Netzer et al. 2017; Zavišić and Polle 2018), and perhaps after severe disturbances such as defoliation due to herbivory or fire. However, they participate much less in plant-soil P dynamics than leaves and fine roots because of their low P concentrations and low rates of growth and decomposition (Johnson and Turner 2019; Weedon et al. 2009). Leaves and roots are therefore the focus of the following section on the importance of plant-internal P re-use in the context of ecosystem P cycling.

Re-use of P by leaves and fine roots

High P use efficiency of plants in low-P ecosystems is achieved to a large extent by long residence times of P in the plant (Veneklaas et al. 2012). Residence times are determined by two factors: the longevity of the tissue containing the P, and the proportion of the P that is retained upon senescence, through recycling within the plant. The ecology of leaf lifespans is relatively well-known, and this trait is one of the key functional traits in the leaf economics spectrum (Wright et al. 2004). Fine roots have lifespans of similar duration, but data are much scarcer, and probably less reliable for methodological reasons. How do leaves and fine roots compare in terms of lifespans, P concentrations and P resorption fraction?

Tissue lifespans

A broad comparison of leaf and fine root lifespans using published data indicates similarly wide ranges of lifespan for both tissues, but on average fine roots have lifespans that are almost twice as long as those of leaves (Fig. 1). The median values for these datasets are 6.0 months for leaves and 11.0 months for fine roots. In low-productive systems, these values may converge. The meta-analysis of Chen et al. (2019) showed that while the *biomass* of fine roots and leaves scaled isometrically, fine root *production* increased less rapidly than leaf production as ecosystem net primary productivity increased. These authors concluded that this trend is likely due to differences in leaf and root turnover, i.e., faster leaf turnover in more productive systems. De Kauwe et al. (2014) reported that root lifespans were 1.5 and 2.1 times

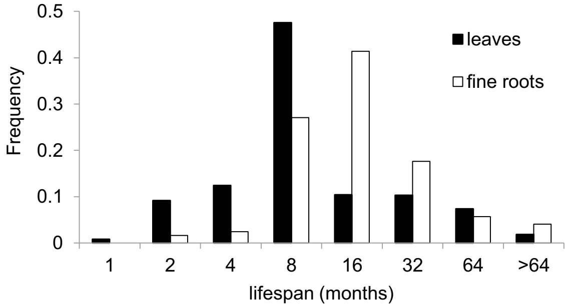

Fig. 1 Frequency distribution of lifespans of leaves and fine roots in global datasets. Data for leaves ($n = 4847$) sourced from the TRY database (Kattge et al. 2020). Data for fine roots ($n = 244$) sourced from the GRooT database (Guerrero-Ramirez et al. 2021). All data were used, irrespective of growth forms, taxa, geography etc. Numbers on the X axis indicate the upper boundaries of the lifespan classes. Note logarithmic increase

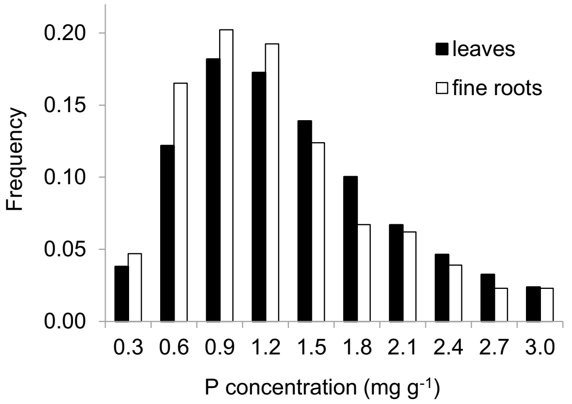

Fig. 2 Frequency distribution of phosphorus (P) concentrations in leaves and fine roots in global datasets. Data for leaves ($n = 50{,}996$) sourced from the TRY database (Kattge et al. 2020). Data for fine roots ($n = 2742$) sourced from the GRooT database (Guerrero-Ramirez et al. 2021). All data were used, irrespective of growth forms, taxa, geography etc. Numbers on the X axis indicate the upper boundaries of the P concentration classes. Values > 3 mg g^{-1} were omitted

longer than leaf lifespans in two productive temperate forests. Less productive systems may have shorter root lifespans than leaf lifespans, but patterns in root traits are not correlated with productivity in simple ways (Carmona et al. 2021), as discussed below.

Tissue concentrations

Phosphorus concentrations are strikingly similar in leaves and fine roots, at a global level (Fig. 2), presumably because both tissues have high metabolic activities. Median P concentrations in the dataset shown in Fig. 2 are 1.25 mg g^{-1} for leaves and 1.10 mg g^{-1} for roots. There are fundamental anatomical and morphological differences between leaves and roots, reflecting not only the different functions of these organs, but also the contrasting environments in which they are placed. Such differences are reflected in traits like tissue specific density, which is generally higher for leaves than for fine roots: median values for leaves are 0.19 and 0.42 g cm^{-3} for herbaceous species and evergreen woody species respectively (Poorter et al. 2009), whereas the median value for fine roots is 0.20 g cm^{-3} (Guerrero-Ramirez et al. 2021). Since higher density is likely due to smaller cells, thicker cell walls, cuticles etc., P concentrations in the cytoplasm of leaf cells are probably somewhat higher than in root cells. Within tissues, different cell types can have quite different P concentrations: for example, Hayes et al. (2018) reported up to 6.5-fold higher P concentrations in photosynthetic compared to non-photosynthetic cells in leaves of West Australian sclerophyll species. Such variation may explain some of the variation in whole-tissue P and may influence potential resorption efficiency.

Resorption

Based on a global review, mean P resorption from senescing leaves is 65% (Vergutz et al. 2012). In 73 Australian sclerophylls, which have lower P concentrations, higher LMA and longer lifespans than the global average, mean P resorption is 63% (Wright and Westoby 2003). In this study there was no significant correlation between P resorption and lifespan (or LMA), suggesting that some species may achieve P conservation through high resorption, others through long lifespans, and others through both traits.

In contrast to leaves, data availability for resorption of P from roots is very limited. Based on a comparison of P concentrations in live and dead roots, Yuan et al. (2011) estimated that on average 27% of P had been resorbed from senescing roots. In a study of 40 subarctic species, Freschet et al. (2010) reported 57% P resorption for fine roots, very similar to the 63% P resorption they found for leaves. Two woody species from highly P-impoverished

Australian ecosystems had a P resorption of 95% and 89% from their specialised cluster roots (Shane et al. 2004; Teste et al. 2020). There remains large uncertainty about resorption estimates for roots, mainly for methodological reasons (Kunkle et al. 2009), which can lead to both underestimates and overestimates. Such issues include mass loss during senescence, microbial consumption, leaching prior to and during sample preparation, and contamination with soil. There is no known physiological or anatomical reason why P resorption from fine roots should be less efficient than from leaves, and biochemical P fractions are also broadly similar (Chapin and Bieleski 1982). From an evolutionary perspective, high P resorption from senescing fine roots is expected, especially in soils with low P availability. In such soils, live roots may contain more P than what they can take up from the low-P soil over their lifespan, as illustrated by a model in the section 'Root P resorption is essential in low-P soils'.

Does the benefit of P resorption vary with growth rate?

Resorption can contribute significant amounts of P for newly grown tissues, but this contribution does vary with ontogeny and growth rate. In young seedlings, seed reserves are an important P source (White and Veneklaas 2012). Only when the first-grown tissues start the senescence process, resorbed P becomes available for new tissue, although some P can be resorbed from developing and mature leaves, e.g., by reducing ribosomal P or replacing phospholipids by galacto- and sulfolipids (Lambers et al. 2012; Netzer et al. 2018; Sulpice et al. 2014), especially under P-limiting conditions. In young plants that are in an exponential growth phase, the contribution of resorption to the plant's P requirement is smaller than the percentage of P resorbed from senescing tissue, because the amount of senescing tissue is smaller than the amount of growing tissue at all times. Faster growth reduces the contribution that resorption can make to the plant's P requirements. Counterintuitively perhaps, so do longer lifespans (Fig. 3). However, since fast-growing plants tend to have tissues with short lifespans (Reich 2014), the model shown in Fig. 3 suggests that the actual plant-level importance of resorption could be quite similar for fast-growing plants with short tissue lifespans and slow-growing plants with longer tissue lifespans. As discussed below, lifespans of leaves do indeed correlate negatively with growth rates, but since this is not clear for fine roots, an increased research effort in belowground turnover and resorption is warranted.

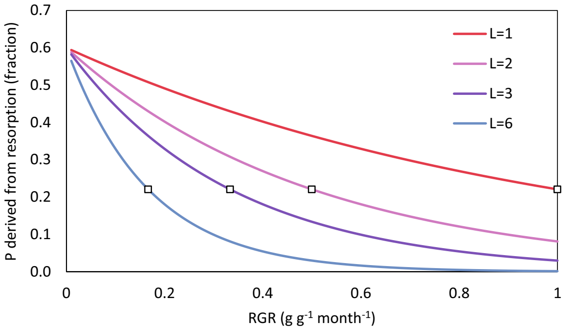

Fig. 3 Estimated fraction of phosphorus (P) that can be derived from resorption of P from senesced tissues into new growth, at different relative growth rates (RGR, g g^{-1} month^{-1}), for different mean tissue lifespans (L = 1, 2, 3, 6 months), for a resorption fraction of 0.6. Estimates were calculated for exponentially growing plants, with plant P content $P_p = P_0 * e^{(RGR*t)}$, where t is time, P_0 is plant P content at t = 0, and RGR is the relative growth rate. P becomes available from resorption of senesced tissues (P_r) when the tissue reaches its lifespan L, which is described by the same equation with a lag of L, multiplied by the resorption fraction rf: $P_r = rf*P_0* e^{(RGR*(t-L))}$. The total (plant-level) fraction of P derived from resorption is calculated as the ratio of P_r and P_p: $P_r/P_p = rf*e^{(-RGR*L)}$. The square symbols on each line indicate points where L = 1/RGR, highlighting that the inverse relationship between L and RGR can result in plant-level resorption being largely invariant with growth rate (for a given resorption fraction)

Is internal re-use of P greater in low-P, low-productive ecosystems?

Trait trends

Comprehensive assessment of plant-level P resorption along P-availability gradients is not possible because data on resorption efficiencies, leaf and root lifespans and biomass partitioning are scarce. Many studies have reported that there is no clear relationship between resorption efficiency and leaf or soil nutrient status (e.g., Aerts 1996), and there is ample evidence that several other factors contribute to variation in resorption efficiencies between species and between sites. Such factors include phylogeny, plant functional types, environmental conditions during senescence, plant sink strength for nutrients during senescence, and methodological issues such as uncertainty about leaf mass loss (Killingbeck 2004; Kobe et al. 2005; Vergutz et al. 2012). However, the global dataset for live and senesced leaves clearly indicates that P resorption is higher in species that have low P concentrations (Vergutz et al. 2012). It is worth noting that this trend also highlights the fact that such species have high proficiency, i.e., they reduce the P concentration in senesced leaves to extremely low levels (Killingbeck 2004). These observations point to an adaptive response related to soil P availability. Negative correlations between P resorption and soil P availability confirm this pattern for a West Australian soil chronosequence (Hayes et al. 2014) and for 102 French forest systems (Achat et al. 2018). A meta-analysis of fertilisation studies showed that P resorption decreased with increasing P availability (Yuan and Chen 2015). Whilst the available evidence does indicate that percentage P resorption varies significantly and adaptively, variation in tissue longevity is larger (Eckstein et al. 1999) and may therefore offer greater potential for P conservation in plants. Leaf P resorption percentages vary from 20–90%, but leaf life spans vary from less than 1 month to more than 5 years (Fig. 1).

Evidence for leaves suggests that lifespans are longer in low-P systems (Reich 2014). These leaves are often thick and tough, and therefore have high Leaf Mass per Area (LMA). In contrast, fine roots in low-P environments are not necessarily thick, tough and long-lived (Weemstra et al. 2016). Specific Root Length (SRL), a trait that can be considered a morphological analogue of LMA (or rather, its inverse: Specific Leaf Area), does not correlate in a simple way with resource availability and growth rates (Weemstra et al. 2016, 2020; Wen et al. 2022).

Root traits and P economy

Current thinking about root traits (Bergmann et al. 2020; Carmona et al. 2021; Comas et al. 2012; Laughlin et al. 2021; Weemstra et al. 2016) is that the complex trait relationships of roots (compared to the simpler 'fast-slow' or 'acquisitive-conservative' spectrum in leaves; Reich 2014) can be attributed to the diverse functions of roots in resource acquisition and the large number of factors in soils influencing root structure and function. Phosphorus uptake is one of the important functions of fine roots, affected by several soil factors as well as mycorrhizal dependency. In the context of adaptation to P availability, Wen et al. (2019) demonstrated for 16 herbaceous (crop) species that different combinations of fine root traits can lead to similar functional outcomes, due to trade-offs between traits, for example thin, highly branched roots versus mycorrhizal colonisation. Modelling by Weemstra et al. (2020) provided a mechanistic explanation for how the trade-off between SRL and root lifespan (Weemstra et al. 2016) can explain alternative strategies that achieve similar growth rates in trees.

Phosphorus uptake rates, and efficient use of carbon and P for root function, are influenced by both SRL and root lifespan. Thus, the trade-off between SRL and root lifespan has led to some species adapting to low-P soils by having high SRL and others by having longer root lifespan. Long root lifespan provides longer lifetime return on investment of carbon and P in these tissues, as is the case for leaves. In contrast, high SRL allows greater root length per unit dry mass, which means that larger volumes of soil can be explored for P with greater root surface area (Laliberté, 2017). One of the constraints on root lifespan may be the fact that P is not very mobile in soils, which means that once a root has depleted the available P in its rhizosphere, very little additional P gain can be expected from a longer lifespan. An extreme adaptation in very low-P soils is the morphology and physiology of the proteoid or cluster roots, which have very closely spaced thin rootlets that 'mine' the available P, and only last ~ 3 weeks (Shane et al. 2004; Teste et al. 2018). They exemplify highly acquisitive traits in very conservative species adapted to low-P environments (cf. Wen et al. 2022). Mycorrhizal symbionts may facilitate longer root lifespans by removing the constraint that roots can only take up P from the soil nearest to its surface. As such it is an example of trait interactions that may contribute to the recently described 'collaboration' gradient in the root economics space, orthogonal to classic conservation (slow-fast) gradient (Bergmann et al. 2020). These two gradients or dimensions are present in all biomes (Bergmann et al. 2020). Inclusion of P concentrations and P resorption traits in the root economic spaces may enhance our insights in trait coordination.

Root P resorption is essential in low-P soils

The large biomass investment in roots, their relatively fast turnover and high P concentrations would indicate that resorption of P from senescing roots is likely quantitatively important. Another perspective on the need to resorb P is to consider the balance between P invested in roots and P taken up by those roots. Soil P concentrations are much lower than root P concentrations, and since P is not very mobile in soils the root can only take up P to a certain (small) distance from the root. It is thus vital that roots take up that soil P very efficiently, to justify the investment of a root in that volume of soil, from a P balance perspective. Once this P has been taken up, there is little gain in extending the root's lifespan. The model calculations shown in Fig. 4 demonstrate that in low-P soils, efficient resorption of P upon senescence is also vital to ensure a favourable P balance, especially for roots with larger diameters. In low-P soils, optimum P balance is achieved at thinner diameters.

Functional diversity and plant-soil feedbacks

Global patterns in leaf and root traits hide the large inter-species differences that exist within plant communities. All species in low-P ecosystems are adapted to low P availability through efficient uptake and use of P, but even in these systems there is a wide spectrum of combinations of traits that influence plant P economies (Lambers et al. 2011). As a result, ecosystems are characterised by spatial variation in plant P content, P fluxes and soil P concentrations (and forms). Plants with lower P concentrations and higher P resorption rates produce litter with a very low P content. They may thus create patches with low P fluxes in litter and soil, which will influence the ability of this and other species to thrive. Resorption and tissue longevity, above- and belowground, are therefore an example of a mechanism underlying plant-soil feedbacks, with potential consequences for the evolution and maintenance of biodiversity (Teste et al. 2017).

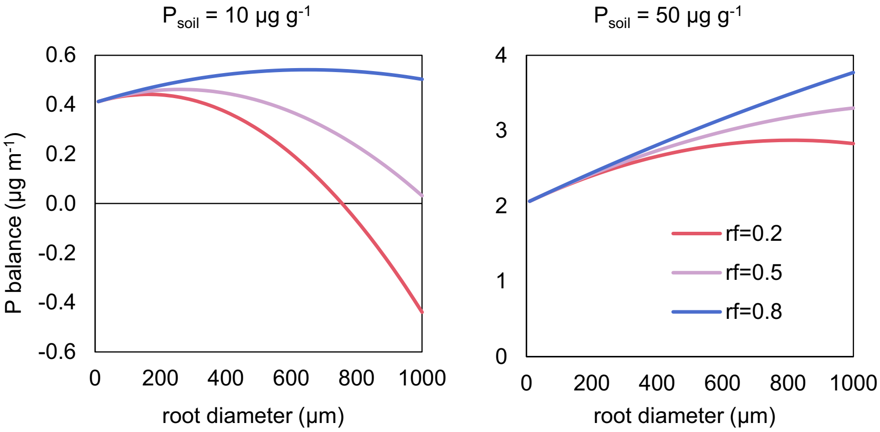

Fig. 4 Net P balance for roots of different diameters and different P resorption fractions (rf = 0.2, 0.5, 0.8) in soils with available P concentrations of 10 or 50 µg g^{-1} dry soil. The model assumes that roots can take up all available P from their rhizosphere during their lifespan, without additional P becoming available. The graphs show estimated net gain of P from soil per unit root length. Net P gain is the P taken up minus the P invested in the root tissue. P uptake per meter of root was estimated by assuming that the root can take up all 'available P' within the rhizosphere, where the rhizosphere was defined as all soil within distance d = 1 mm from the root surface: P uptake = V_{soil} * P_{soil} * BD where V_{soil} is the volume (in mL) of the rhizosphere soil per m of root; P_{soil} is the concentration of available P (in µg g^{-1}); BD is bulk density (in g mL^{-1}). P investment was estimated as the root tissue P content per m root length minus the fraction that is resorbed into the plant during senescence: P invested = (1-rf) * V_r * SD_r * P_r where rf is the resorption fraction, V_r is the volume of root (mL) per m root length (calculated from the root diameter and length), SD_r is the specific density of the root (g mL^{-1}) and P_r is the mass-based P concentration of the root (in µg g^{-1}). Soil bulk density was assumed 1.4 g cm^{-3}. Root traits that are constant in the model were assigned values very close to global means reported in Guerrero-Ramirez et al. (2021): P_r 1000 µg g^{-1}, SD_r 0.2 g g^{-1}

Concluding remarks

Plant internal recycling of P has significant implications for ecosystem P cycling and productivity. There are significant gaps in our understanding of P resorption and how it relates to tissue lifespans and other traits, and this is particularly the case for roots. As shown in this paper, roots represent a large part of the plant, have fast turnover, and high P concentrations, yet their role in re-use of P upon senescence is largely unknown. There is a need for detailed studies into the physiology of P resorption, from the biochemical to the whole-plant level. Along with data on biomass allocation and biomass turnover, this information will substantially improve models that may help understand and predict the role of P in vegetation responses to issues such as climate change and nitrogen deposition.

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Data availability Data for leaf and root traits were retrieved from public databases. Leaf data were obtained from TRY (https://www.try-db.org/), using unrestricted data only. Root data were obtained from GRooT (https://groot-database.github.io/GRooT/).

Declarations

Competing interests The author has no relevant financial or non-financial interests to disclose.

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