MARSCHNER REVIEW

Nutrient acquisition strategies in agroforestry systems

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Abstract

Background Disentangling nutrient acquisition strategies between trees and crops is central to understanding positive nutrient interactions in agroforestry systems for improved low-input agriculture. However, as plants are responsive to a complex soil matrix at multiple scales, generalizable diagnostics across diverse agroforests remains challenging. *Scope* We synthesize research at various scales of the tree-crop interface that are cumulatively hypothesized to underpin nutrient acquisition strategies in agroforestry systems. These scales span the whole root system to fine-scale sites of acquisition actively engaged in biological and chemical interactions with soil. We target vertical and horizontal dimensions of acquisition patterns; localized root-soil dynamics including biological associations; root-scale plasticity for higher acquisition; and nutrient additions via biological nitrogen fixation and deep soil nutrient uplift. We consolidate methodological advances and the effects of environmental change on well-established nutrient interactions.

Conclusions Root distribution patterns remain one of the most universal indicators of nutrient acquisition strategies in a range of agroforestry systems, while root functional traits are emerging as an effective root-scale indicator of nutrient acquisition strategy. We validate that in agroforestry systems crop root functional traits reveal bivariate trade-offs similar to, but weaker than, crops in monoculture, with mechanistic links to nutrient acquisition strategies. While interspecific root overlap may be associated with nutrient competition, clear cases of enhanced chemically and microbially meditated processes result in species- and management-specific nutrient facilitation. We argue for agroforestry science to use distinct and standardized nutrient acquisition indicators and processes at multiple scales to generate more nuanced, while also generalizable, diagnostics of tree-crop interactions. And extensive research is needed on how agroforestry practices stabilize key nutrient acquisition patterns in the face of environmental change.

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Introduction

Over the past two decades, there has been a considerable expansion in research on alternative agricultural systems (Altieri 1999; Wezel and Soldat 2009; Tomich et al. 2011). Applications of agroecological principles to the design of agroecosystems have gained momentum as a contemporary lens to critique, evaluate, and manage

environmental and socio- economic issues surrounding agricultural landscapes (Méndez et al. 2013; Isaac et al. 2018). Notably, the integration of trees to cropping systems, or agroforestry, addresses many of the most pressing issues of our time, including food security, biodiversity loss, and climate change (Jose 2009; Somarriba et al. 2012; Tscharntke et al. 2012). Based on the well-described hypothesis that increasing biodiversity is associated with greater ecosystem function (i.e., productivity, efficient nutrient cycling, positive trophic interactions) (Cadotte et al. 2011; Cardinale et al. 2012), biologically complex agroforestry systems often reveal greater ecosystem functioning and a reduced reliance on chemical inputs (Drinkwater and Snapp 2007; Malézieux et al. 2009; Martin and Isaac 2015). Such benefits have been observed from farm to landscape levels of integration, and across temperate and tropical agroecosystems. While these benefits are a key target in future food production landscapes, such success requires well developed diagnostics of the plant-soil continuum.

Disentangling nutrient acquisition strategies and nutrient transfer processes is fundamental to encourage positive nutrient interactions in agroforestry systems for improved low-input agriculture (Hinsinger et al. 2011; Isaac and Kimaro 2011). Cannell et al.'s (1996) paper "*The central agroforestry hypothesis: the trees must acquire resources that the crop would not otherwise acquire*" has guided such principles in agroforestry design for optimal belowground interactions for over two decades. The optimization of tree and crop root interactions for balanced and non-competitive nutrient uptake has been the basis of innumerable studies in agroforestry systems around the world. Although there are multiple agroforestry system typologies (e.g. agrisilvicultural, silvopastoral and agrosilvopastoral), in tree-crop systems in particular, this work has resulted in clear advances, notably, identifying the drivers of soil phosphorus (P) sharing (see Hinsinger et al. 2011), quantifying the transfer rates of fixed nitrogen (N) (see Nygren et al. 2012), and sequencing the critical role of mycorrhizal fungi (see Carvalho et al. 2010). As the agroforestry literature on the role of enzymatic and microbial meditated processes advanced, so too has the root ecology literature. Major advances have been made in understanding root structure and function (Erktan et al. 2018), notably the repositioning of the importance of root order and functional classification frameworks (McCormack et al. 2015), the rapidly expanding knowledge on the role of roots in driving

critical microbial processes in the rhizosphere (de Vries et al. 2012), and the evolving literature on root trait trade-offs and consequences for predicting root acquisition strategies based on morphological and chemical characteristics (Weemstra et al. 2016).

Distinctive structural and functional characteristics of tree root systems, relative to crop roots, remains a cornerstone of agroforestry. However, roots can be highly responsive to environments employing concomitant, and at times opposing, strategies for nutrient acquisition. Plants acquire nutrients that are heterogeneously distributed in time and space, and within a diverse and complex soil matrix (Hodge 2004, 2006; de Kroon et al. 2009). Roots must also navigate obstructions to root growth and interact with plant neighbours and soil biota (Cahill et al. 2010; Bardgett et al. 2014). Thus, building on the work of others, we emphasize the importance of genotype × environment interactions [genetic control - i.e. intrinsic species/genotype nutrient acquisition strategies, and tree-crop response to environment and management - i.e. plasticity in nutrient acquisition within species/genotype] in determining the realized nutrient acquisition of trees and crops and resulting effects on crop nutrition and productivity across diverse agroforests.

Figure 1 depicts key belowground indicators (root system distribution patterns and individual root functional traits) and processes (nutrient interception and chemical/biological rhizosphere dynamics) at the tree-crop interface in agroforestry systems. Cumulatively, we know that the tree component of an agroforestry system can unlock nutrient advantages by i) reductions in losses via a safety net (see Bergeron et al. 2011; Kumar and Jose 2018), 2) additions of 'new' nutrients via N_2 fixation and uplift of deep soil nutrients (see Nygren et al. 2012; Pierret et al. 2016) and, 3) changes in morphological and chemical processes at the rhizosphere scale via root plasticity and activity (see Munroe et al. 2015; Borden et al. 2019). Tree roots stratified below the crop root zone capture unused nutrients that move down the soil profile. This spatially stratified action in the soil profile is based on the niche partitioning hypothesis to maximize closed nutrient cycles in agroforestry systems (Ong and Leakey 1999), typically for very mobile nutrients such as nitrate (NO_3^-) moving in soils via mass flow. Associated with the safety net process is nutrient pumping - the acquisition of both mobile and weathered minerals deeper in the soil profile (Lehmann 2003), the translocation of nutrients to litter tissue, the deposition of litter on the soil surface via litterfall, and the addition of nutrients to the top soil via
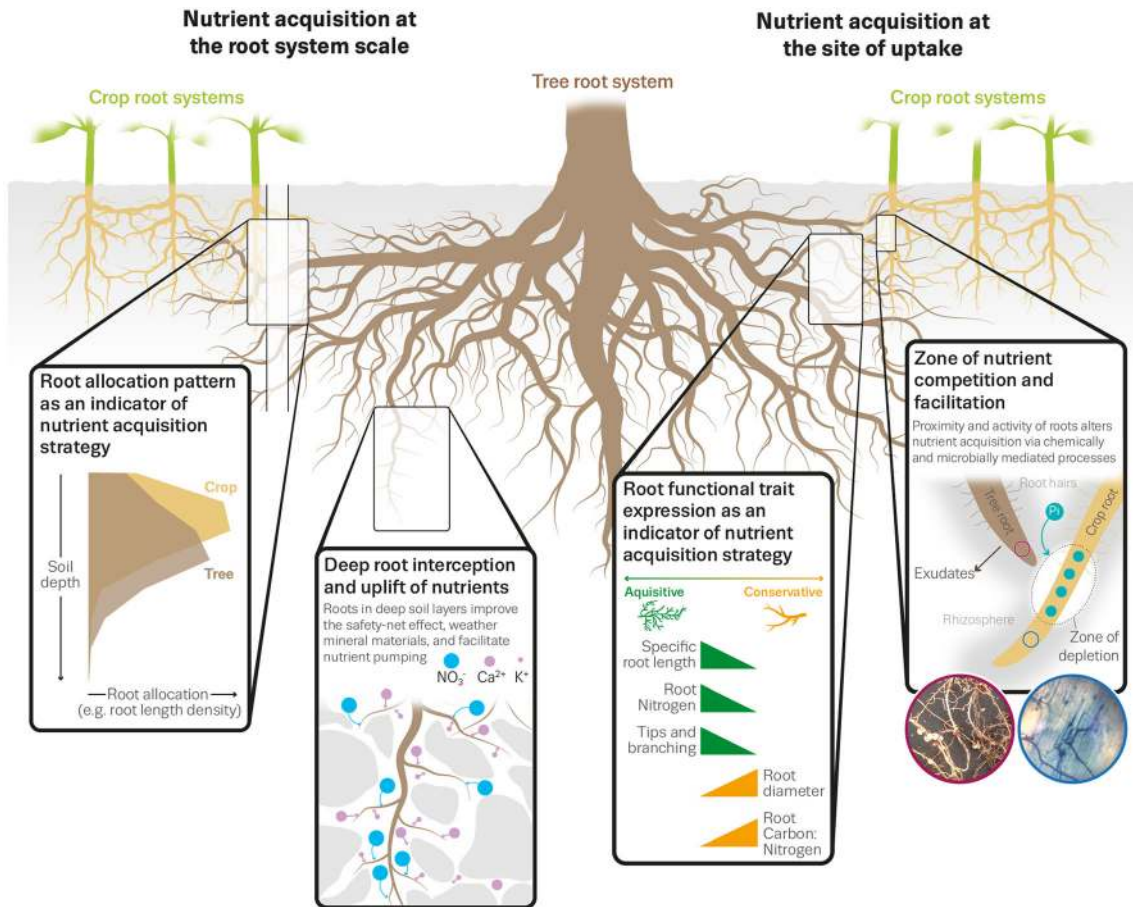
Fig. 1 Nutrient acquisition in agroforestry systems. Indicators (tree and crop root distribution and fine root functional traits) and processes (deep soil nutrient capture and rhizosphere chemical and microbial processes) are shown. The two boxes on the left depict nutrient acquisition strategies at the whole root system scale and the two boxes on the right depict nutrient acquisition strategies at the sites of uptake

decomposition processes (Mafongoya et al. 1998). Overall positive effects from nutrient pumping is, arguably, conditioned on the biomass-ratio hypothesis (Grime 1998); ecosystem processes such as decomposition are largely dependent on the most dominant species in the community, often the tree component. Within the zone of tree and crop root interactions, fine lateral roots are characterized by a range of nutrient acquisitive traits and conservative traits, thus forming a dominant axis of nutrient acquisition strategies among and across species (Weemstra et al. 2016; Isaac et al. 2017). Finally, this zone of interspecific interaction is also characterized by an array of chemically and microbially mediated mechanisms (Kurppa et al. 2010; Hinsinger et al. 2011) that result in site-specific nutrient competition or facilitation.

This assemblage of indicators and processes, with well-established theoretical underpinnings, have

contributed to our understanding of nutrient dynamics in agroforestry systems world-wide, yet has also encouraged highly variable scales of analysis resulting in a need for agroforestry science to define base operating scales. To do this, we present nutrient acquisition strategies at different spatial scales that are relevant to component trees and crops. These scales of belowground measurements organize into three categories, standardized to specific units within an agroforestry system: the whole root system (total belowground biomass and distribution), the lateral roots (growth and morphology of nutrient acquiring organs), and the site of uptake (zone of nutrient movement from the soil environment into absorptive roots). The expression of these measured plant compartments is driven by soil, neighbour and soil × neighbour effects, all operating in highly heterogenous environments. More recently, research has begun

to focus not only on soil and neighbour effects but also on climatic effects.

This review draws on various literatures to describe classic and contemporary views and findings on nutrient acquisition in agroforestry systems. We synthesize research at various scales of the tree-crop interface that are cumulatively hypothesized to underpin acquisition strategies in agroforestry systems. These scales span the whole root system to fine-scale sites of acquisition actively engaged in biological and chemical interactions with soil. We chart: 1) vertical and horizontal root system scale patterns at the tree-crop interface, 2) localized root-soil dynamics including biological associations, 3) lateral root scale plasticity for higher acquisition, and 4) new nutrient addition via biological N fixation and deep soil nutrient uplift. We also consolidate methodological advances as well as the effects of environmental change on well-established tree crop nutrient interactions.

Nutrient acquisition at the tree-crop interface: the whole root system to fine-scale sites of uptake

Vertical and horizontal nutrient acquisition patterns among component species

Building upon early syntheses by Huxley (1985) on the importance of investigating the tree-crop interface, arguably the most widely studied belowground aspects of agroforestry systems are the vertical root distributions of trees and crops (Livesley et al. 2000; Dawson et al. 2001; Jose et al. 2001; Moreno et al. 2005; Mulia and Dupraz 2006; Isaac et al. 2014a; Borden et al. 2017, 2019; Kumar and Jose 2018), with the implicit assumption that nutrient acquisition strategies can be evaluated based on patterns of roots with depth. Although the location of roots does not necessarily indicate root activity (Vanlauwe et al. 2002), in general, the vertical distribution of plant roots typically shows a higher density of roots nearer the soil surface and decreases with depth, matching the general distribution of soil nutrients (Jobbágy and Jackson 2004). With that said, root system architecture can vary widely across species (Das and Chaturvedi 2008; Borden et al. 2017). In a tropical hedgerow agroforestry system with N isotope applications with soil depth, uptake of ^{15}N declined significantly with depth for the shallower rooted N_2-fixing tree (Gliricidia sepium), whereas consistent uptake of ^{15}N occurred from all depths to 65 cm for the deeper-rooted

tree species (Peltophorum dasyrrachis) (Rowe et al. 2001). These interspecific differences in structure and function of trees can have differential impacts on belowground interactions with crops. For example, Bouttier et al. (2014) reported reduced fine root length densities and yield of hay next to shallow-rooted poplar hybrids compared to when hay was intercropped with deeper-rooted oak trees (Quercus rubra). Thus, a primary management strategy for optimal nutrient interactions continues to be the selection of tree species with complementary root distributions to that of crops, which typically means deeper rooted trees (Fig. 1).

Interspecific interactions, however, can also exert strong control on the expression of root system architecture (Callaway et al. 1991, 2003). Studies in agroforestry systems reveal that the spatial distribution of roots can be modified when grown in mixture with other species (Mulia and Dupraz 2006; Isaac et al. 2014a; Cardinael et al. 2015; Kumar and Jose 2018; Borden et al. 2019). For example, there is evidence of trees (e.g. walnut (Juglans regia × nigra cv. NG23), oak (Quercus ilex)) rooting more deeply when next to annuals (e.g. wheat, grasses) (Moreno et al. 2005; Mulia and Dupraz 2006). Similar plastic responses have been observed for tree crop roots (e.g., cocoa (Theobroma cacao) adjusting root distribution in response to fast-growing pioneer shade tree species, Terminalia ivorensis (Isaac et al. 2014a; Borden et al. 2019). In their review of tree-crop root interactions, Kumar and Jose (2018) note the importance of tree density in determining the plastic response of roots in agroforestry, with closer spaced trees and tree crops resulting in stronger plastic response. Evidence of this density-dependent root response resulted in complementarity in soil phosphorus (P) acquisition found via root uptake partitioning of ^{32}P labelling in coconut-dicot tree agroforestry (Gowda and Kumar 2008), while potential resource complementarity via root segregation between neighbouring cocoa and and fast growing timber species (Isaac et al. 2014a) and cocoa and the N_2-fixing shade tree species, Gliricidia sepium (Schwendenmann et al. 2010) have been confirmed with natural abundance of stable isotopes (δ^{18}O and δ^2H). In a Eucalyptus grandis and Acacia mangium mixture, Laclau et al. (2013) report vertical stratification of fine roots, relative to the corresponding monoculture stands, with a neutral effect on performance. However, more work needs to directly link the range of complementary root plasticity to crop yield in agroforests.

Nutrient acquisition in the horizontal dimension is strongly controlled by the spatial arrangement of trees and crops – e.g. root growth in tree rows vs. crop rows (Thevathasan and Gordon 1997; Jose and Gillespie 1998; McGrath et al. 2001; Mora and Beer 2013). The horizontal extent of the tree-crop interface and its impact on nutrient acquisition varies by species and ontogeny, or tree size. However, the simultaneous effects of belowground competition along with directed nutrient inputs from tree litter are challenging to tease apart. For example, in temperate tree-based intercropping (TBI) systems, variable soil organic carbon (C) and soil N patterns from tree litter inputs were observed as far as ~10 m from tree row (Bambrick et al. 2010). In shelterbelt systems, contributions from fixed N from a leguminous shrub (*Caragana arborescens*) declined from 40% to 20% of crop N with increasing distance (4 m to 20 m) from shrub row (Issah et al. 2015). Yet these important nutrient contributions overlap with a concentrated zone of competition; for example, in a TBI system, decline in some crop yields were observed within 2 m from the tree row (Thevathasan et al. 2012). Thus, belowground, divergent effects on nutrient acquisition of component species are likely occuring with distance from trees. In TBI systems, shifts in legume crop N acquisition strategies with distance from tree have been detected, with a smaller root and shoot biomass but a higher rate of N_2 fixation near the tree row (Isaac et al. 2014b). On a similar spatial gradient, variation in maize rooting densities have been observed, with lower crop root length but higher tree root length closer to trees, suggesting stronger competition with increasing proximity (Livesley et al. 2000). In contrast, no spatial effect, nor observed changes in tree fine root length densities, were detected in N uptake with distance from hedgerows (*Peltophorum dasyrrachis* and *Gliricidia sepium*) (Rowe et al. 2001). Ultimately, the realized horizontal nutrient acquisition patterns in agroforestry systems are highly dependent on root densities with distance from trees, which will be strongly controlled for by tree age and species.

Active management practices of tree and crop root distribution can reduce belowground competition at the tree-crop interface. Physical trenching or barriers may be used to modify nutrient acquisition patterns with depth and horizontal distance from the tree. For example, root barriers established in a temperate TBI system led to lower crop uptake of N from fertilizer, presumably due to reduced competition from trees for mineralized N in soil (Jose et al. 2000). However, modification of the available soil volume for trees was suggested to increase black walnut (*Juglans nigra*) rooting density in the smaller soil volume and subsequently increased the allelopathic juglone in the tree rows (Jose and Gillespie 1998), with potential impacts on other species in non-excluded areas. Pruning has also been shown to modify the depth at which trees in agroforestry systems acquire nutrients (Rowe et al. 2006), and is now being included in important process-based agroforestry models that estimate root architecture in 3-dimensions (Dupraz et al. 2019) However, we note that active suppression of direct competition between tree and crop roots may also be circumventing other important sources of complementarity and facilitation within common rooting zones that are a function of root-root interactions.

Acquisition of deep soil nutrients

The importance of deep soil nutrient capture to agroforestry systems has long been recognized; Robertson (1994) modelled the importance of deep N uptake and redistribution to crops in an *Acacia senegal-Sorghum bicolor* system, Sanchez (1995) lists deep nutrient capture as a key pathway for new N, Hartemink et al. (1996) measure NO_3^- uptake from deep subsoils. Deep soil nutrient acquisition is arguably most important in environments where i) the risk of nutrient leaching is high, ii) highly weathered tropical soil orders, such as Ferralsols, are present, or iii) nutrient sources unavailable to crop roots are located in unweathered material. Indeed, while there remain substantial gaps in knowledge on deep root-soil interactions, such as rock weathering and nutrient acquisition below ~1 m to 3 m in the soil profile, recent research suggests that these processes are key for improving geochemical cycling in agroforestry systems (Pierret et al. 2016), and that these processes are highly related to soil water dynamics in the soil profile (Wu et al. 2016). For instance, Bergeron et al. (2011) demonstrate an active NO_3^- safety-net role of poplar roots in a TBI system to a depth of 1 m. Studies that descend beyond 3 m are limited, but in other managed tree ecosystems, such as eucalyptus plantations, deep root research shows active tree roots 10 m or deeper (Laclau et al. 2001, 2013). Bordron et al. (2019) found specific root uptake potential (nutrient uptake per length of root) of *Eucalyptus grandis* was highest at 50 cm depth for NO_3^- (^{15}N) and at 3 m depth for potassium (K^+) (using Rb^+ as an analogue) and calcium (Ca^{2+}) (using Sr^{2+} as an analogue) indicating

strong nutrient acquisition by depth patterns. These depths for nutrient acquisition are not uncommon in agroforestry systems; shade tree roots have been clearly identified to grow to depths greater than 1 m in coffee (*Coffea arabica*) agroforestry systems (Padovan et al. 2015) and down to 3 m in cocoa agroforestry systems (Abou Rajab et al. 2018). Nutrients can be taken up by deep tree roots and deposited via litterfall in shallower soils, consequently becoming accessible to crops, i.e., nutrient pumping effect. The effects of nutrient pumping on soil nutrient profiles have been observed for cations, in particular Ca^{2+} and K^+ (Jobbágy and Jackson 2004). In general, but in agroforestry specifically, the mechanisms and importance of these deep soil processes deserve more research.

Crops can also have deep roots. Indeed, a relatively large proportion of nutrients can be acquired by crops from the larger volume of subsurface soils with lower nutrient concentrations compared to the narrower topsoil layer with higher nutrient concentrations (Lehmann 2003; Pierret et al. 2016). While perennial crops are more likely to be deeply rooted, some annual crops such as maize and winter wheat are known to have roots below 1 m (Livesley et al. 2000). Indeed, maize has been shown to acquire large amounts of ^{15}N from 65 cm, despite low root length density at this soil depth (Rowe et al. 2001).

Active root strategies: linking root growth and placement to soil nutrient status

Root systems are considered modular in nature (Hodge 2006; de Kroon et al. 2009; McNickle et al. 2009) and root system architecture is a product of modifications within individual root systems in response to fine-scale variation in soil, the nutrient status of the plant, and intrinsic constraints of the genotype. Relatively higher density of roots in a given soil volume has long been understood as a plants' response to capitalize on localized, elevated soil resources (Hutchings and de Kroon 1994; Pritchard 1998). This process is attributable to complex and integrated sensing and signalling mechanisms that respond to the soil environment given internal resource demands (Forde and Lorenzo 2001), and availability and mobility of those resources in soil (Hodge 2004). For example, due to the slow rate of diffusion of PO_4^- in soil solution, acquisition of P from soil is increased through changes in non-patterned (i.e., environmentally triggered) fine root branching and root hair growth (López-Bucio et al. 2003; Lambers et al. 2006).

Evidence of active foraging by root systems in agroforests shows preferential rooting into soil with elevated nutrients, whether from natural variation in soil nutrients or localized fertilization (McGrath et al. 2001; van Kanten et al. 2005; Borden and Isaac 2019; Borden et al. 2019). In a coffee-*Erythrina poeppigiana* agroforestry system, Mora and Beer (2013) observed that the scale of spatial patterns of coffee root length density across a plot was associated with P, zinc (Zn), and exchangeable bases. In cocoa agroforestry systems, Borden et al. (2019) found expected high densities of cocoa fine roots in the uppermost mineral soil, which followed the vertical patterns in soil nutrient availability, but also found important soil nutrient variation that occurred laterally within the scale of individual root systems. In that study, cocoa fine root densities were spatially related to heterogeneously distributed, non-manipulated levels of nutrient ions in soil: available NO_3^- and ammonium (NH_4^+), and exchangeable K^+ and Ca^{2+} (Borden et al. 2019). Interestingly, lateral root foraging patterns of cocoa in response to soil nutrient availability or in response to nutrient additions has also been found to vary between monoculture and agroforestry systems, suggesting differential nutrient demands across management treatments play a role in controlling the foraging strategies of crops in agroforestry (Borden and Isaac 2019; Borden et al. 2019).

Numerous studies that manipulate soil conditions and neighbour interactions under controlled conditions show dramatic plasticity of root growth and placement in response to soil nutrients and competitors within localized patches (Mahall and Callaway 1992; Cahill et al. 2010; Borden and Isaac 2019). In particular, root placement can be modified by the growth and activity of neighbour roots in soil (Malamy 2005; Cahill et al. 2010). Root-root interactions include resource-driven mechanisms, such as roots sensing where neighbour roots have depleted soil nutrients (zones of depletion, Fig. 1), and/or the release of root-detectable compounds (Hinsinger et al. 2005). A neighbour can deplete resources in the area immediately surrounding the root, which may discourage root growth and proliferation by another plant root into that same area, but inhibitory or allelopathic chemicals can be released from roots and also suppress root elongation or initiation of neighbouring roots (Mahall and Callaway 1992; Callaway et al. 2003). In agroforests, McGrath et al. (2001) reported that roots of *Theobroma grandiflorium* cultivated on P-depleted soils in the Amazon preferentially grew in P-fertilized soil and that root growth and

morphology was important for competing with neighbouring palm tree (*Bactris gasipaes*) roots. Root competition and avoidance between crop and tree roots at such localized scales can be challenging to assess under field conditions without manipulations of soil nutrients and/or when the overall densities of roots are already very high (McGrath et al. 2001) or are insufficient to cause a response among component species (Borden et al. 2019). We certainly require further research to elucidate the drivers of overlap vs. segregation of tree and crop roots observed in agroforestry systems along soil resource gradients.

Root-soil and root-root interactions: nutrient release and transfer

While niche partitioning in agroforestry systems can improve overall resource acquisition efficiencies, there will often be large spatial overlap of trees and crop root systems. Yet, in these cases, spatial and temporal overlap in roots may not signal simple competition between plants (see Schroth 1999). What occurs are a whole suite of possibilities for complementarity or facilitation with root-root and root-soil interactions. Spatial proximity among active roots can lead to advantages related to the promotion of nutrient availability in soil. Roots can actively alter the chemistry in the rhizosphere to increase nutrient concentration in soil (Fig. 1), for example via exudation of H^+/OH^-, organic acids, or enzymes such as phosphatase to promote P availability in soil solution (George et al. 2002; Hinsinger et al. 2011). Root exudates are a key C and nutrient source in soils and are highly variable within a root system (Phillips et al. 2008). Exudates contribute substantially to benefits in the root-soil interface (Danjon et al. 2013), and such contributions in agroforestry systems are often derived from the tree component. For instance, in maize-tree agroforestry systems on Ferralsols, organic anion exudation and acid phosphatase activity of tree roots mobilized P in the rhizosphere (Radersma and Grierson 2004). In coffee systems on mixed alluvial soils, significantly higher NO_3^- concentrations were detected in agroforestry rhizospheric soils as compared to monocultures (Munroe et al. 2015). In an *Acacia senegal*-wheat (*Triticum turgidum durum*) agroforestry system, rhizospheric soil exhibited low pH and higher inorganic P in the presence of the tree root (Isaac et al. 2012). Furthermore, there is emerging evidence of complex multi-trophic interactions occurring in the rhizosphere

that can mediate root-root interactions (Mommer et al. 2016). Resource uptake and delivery of root-based organic inputs are occurring throughout the root systems (Upson and Burgess 2013), which likely contributes to complex interactions with soil microbial communities in time and space (Mommer et al. 2016). The importance of multi-trophic dimensions in rhizosphere processes in agroforests is little understood but likely immense.

Leguminous tree roots with nodule development via soil bacteria (Fig. 1) and subsequent biological N fixation, can substantively contribute to N sources for crop uptake in agroforestry (Nygren et al. 2012; Munroe and Isaac 2014; Kaba et al. 2019). Numerous studies have estimated N_2-fixation rates and quantified broad N inputs in agroforestry systems (Beer et al. 1998; Nygren et al. 2000; Isaac et al. 2011). Annually, N_2 fixation may add from tens to hundreds of kilograms of N per hectare to an agroforestry system (see Nygren et al. (2012) and Munroe and Isaac (2014) for reviews on this topic), indicating that the amount of N fixed by N_2-fixing trees in agroforestry systems is quite variable and highly affected by climate, soil characteristics, mycorrhizal status, and by management factors, such as nutrient inputs, pruning frequency/intensity, and tree physiology.

Fixed N is delivered to crops in agroforestry through two pathways: indirect via decomposition and mineralization of organic compounds (leaf litter, dead roots and nodules), and direct via root exudates, root transfer, and common mycorrhizal networks. Nygren et al. (2013) speculated that the higher density and overlap of roots in surface soils for both cocoa and leguminous shade tree *Inga edulis* led to facilitative transfer of N derived from root nodules. Kurppa et al. (2010) used soil isotopic enrichment to investigate the transfer of N from leguminous shade trees, *Gliricidia sepium* and *Inga edulis*, to cocoa saplings under semi-controlled conditions in the field and found all transfer of fixed-N was attributed to belowground transfer. In *Caragana arborescens* shelterbelt systems, Issah et al. (2015) report 40% of annual crop N uptake was derived from fixed N using ^{15}N isotopic dilution. Leguminous tree and grass systems have shown a range of N transfer rates via root-root interactions. Rao and Giller (1993) showed a ~3% contribution between *Leucaena diversifolia* and the grass *Cenchrus ciliaris*, while in a greenhouse study, Jalonen et al. (2009) showed the grass *Dichantium aristatum* absorbed 22% of N exuded from roots of the leguminous tree *Gliricidia sepium* with ~4–14% of grass N derived from leguminous tree root exudates.

While the study of N_2 fixation and N transfer within tropical agroforestry has predominately drawn upon methodologies originally developed for temperate agriculture, the unique spatial arrangement and morphological characteristics of crops and N_2-fixing trees within agroforestry systems present unique challenges for conceptualizing, as well as (sampling and) measuring, the fate of fixed N. Importantly, field studies using natural abundance techniques have shown clear spatial variability in the magnitude of the contribution of fixed N to N acquisition in agroforestry systems (Issah et al. 2015; Meylan et al. 2017). Notable though, while the potential for N_2-fixing trees and shrubs to enhance soil fertility within agroforestry systems is clear, the transfer of fixed-N to associated crops, however, does not always occur.

Mycorrhizal [arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF)] fungi associations represent an active nutrient acquisition strategy of roots as well as a mechanism for direct nutrient transfer between species within agroforestry systems. Trees and tree-based intercropping systems are known to act as reservoirs for abundant and diverse mycelial networks for crops (Ingleby et al. 2007; Bainard et al. 2011). Arbuscular mycorrhizal fungi form symbiotic associations with over 80% of all terrestrial plants (Sanders 2003), including most tropical trees and crop plants such as coffee and cocoa (Kähkölä et al. 2012). Within an agroforestry context, AMF and EMF contribute to the direct transfer of N as well as other indirect processes including enlarging soil volumes for nutrient access, soil microsite exploration, and a suite of changes to P absorption kinetics and solubilization (Carvalho et al. 2010). While numerous studies have suggested the involvement of mycorrhizal mediated transfer (Rao and Giller 1993; Nygren and Leblanc 2009; Isaac et al. 2012), experimentation is limited in quantifying contributions of common mycorrhizal networks to direct transfer of nutrients. For instance, Jalonen et al. (2009) showed nutrient flows through common mycorrhizal networks between plants in agroforestry systems using stable isotopes in a greenhouse experiment. However, when the proportion of N transferred by fungi has been detected, it has been small. Despite the difficulty in studying direct transfer by common mycorrhizal networks, and the relatively small role they likely play, recent research suggests that AMF can transfer substantial N to their host plant from organic material (Leigh et al. 2009). This has significant implications on the ability of crops to acquire N from decomposing litter

of N_2-fixing plants. For instance, Kähkölä et al. (2012) found that AMF inoculation of cocoa saplings improved N uptake from *Inga edulis* leaf litter by 0.5% and root litter by 5%. Therefore, overall contributions of AMF to N dynamics in agroforestry systems may be more important than, solely, direct transfer via common mycorrhizal networks.

Root-scale plasticity for higher nutrient acquisition

At the scale of individual lateral roots, a plant increases its capacity to absorb soil resources by increasing the amount of absorptive root surface area and/or the uptake capacity of root surface area. This expression of root plasticity, and thus measurable root trait variation, is in part due to the integration of signals from the rooting environment (Miner et al. 2005). Documenting systematic responses of traits to environmental conditions has long been a main theme of community ecology (e.g. Chapin et al. 1993) and more recently agroecosystems (Martin and Isaac 2015; Wood et al. 2015). Root functional traits have been used as indicators of competitive ability among species in agroforestry, for example relatively high specific root length in maize was speculated to provide a competitive advantage in nutrient acquisition compared to intercropped trees (Livesley et al. 2000). However, despite the key role root trait variation plays in resource acquisition potential (Cahill et al. 2010; Bardgett et al. 2014), and other ecosystem functions such as soil stability (Rillig et al. 2015; Le Bissonnais et al. 2018), there are very few analyses and applications of functional traits at the root scale in agroforestry systems (Martin and Isaac 2015). Evidence from community ecology (Larson and Funk 2016; Roumet et al. 2016; Weemstra et al. 2016) and agroforestry systems (Isaac et al. 2017; Borden and Isaac 2019; Martin et al. 2019) supports the hypothesis that certain root functional traits covarying along a dominant axis of resource acquiring to resource conserving traits (Fig. 1). At one end of this spectrum, distinct root morphological and chemical trait expression [i.e. high specific root length, specific root area, specific root tip density (or branching intensity), root N concentration] indicate resource acquisition while at the other end of the spectrum, large root diameter and high root C:N can indicate resource conservation (Prieto et al. 2015; Fort et al. 2016; Weemstra et al. 2016). In some cases, these trait trade-offs have been linked to established metrics of plant performance in agroforestry systems [e.g. yield

(Gagliardi et al. 2015) and N_2 fixation rates (Martin et al. 2019)].

Understanding how plants respond to multiple signals from highly heterogeneous soil environments is arguably more challenging. Root functional traits have been used to empirically describe root response to a range of regional and localized soil chemical resources including macro- and micro-nutrients, soil moisture regimes, and soil pH, as well as multiple physical properties including soil structure, texture, and aggregation (reviewed by McCormack et al. 2015; Weemstra et al. 2016). In both temperate and tropical agroforestry systems, root functional trait expression tends toward the acquisitive end of the acquisition to conservation axis when a crop is in close proximity to a shade tree; specifically, studies have found decreased root diameter and increased specific root length in wheat (Duan et al. 2017), lower root tissue density in cocoa (Borden et al. 2019), and higher root tip abundance in coffee (Isaac et al. 2017). More acquisitive trait values commonly reported in species mixtures may indicate higher belowground competition but also higher nutrient cycling, although there are exceptions (Abou Rajab et al. 2018). Notably, variation in acquisitive root traits of coffee across different climatic regions have largely been explained by whether the individual plant is in an agroforestry system or not (Isaac et al. 2017). Similar patterns are observed at the farm or agroforest scale for cocoa (Borden and Isaac 2019). Futhermore, individual cocoa plants in agroforestry systems expressed large variation in specific root length, root diameter, and root tissue density, which were coupled to availability of specific nutrients in localized soil scales (Borden et al. 2019).

Trait-based research at the root scale provides a more nuanced assessment of how variation in root functional traits within a species – or intraspecific trait variability – influence key ecosystem functions. From our research on tree-crops in Central America and West Africa agroforestry systems, we show that while mean trait values of crop species may indicate an overall strategy for soil resources acquisition, there can be large range of variability among individual plants of the same species (Fig. 2). Trait variation and key trait trade-offs that define an individual plant's strategy within a root system can have implications for nutrient acquisition in agroforestry. Here we present five root functional traits [three acquisitive (higher specific root length, root N, specific root tip abundance) and two conservative traits (higher root diameter and C to N ratio)] among over 180

individual plants across two dominant tree-crops (cocoa and coffee) in two prevailing management scenarios (monoculture and agroforestry). Patterns of hypothesized bivariate relationships between root trait trade-offs hold across tree crop species in monoculture and agroforestry scenarios, regardless if the crop is in mixture with an N_2-fixing species or a timber species. However, at the species scale, coffee and cocoa in agroforestry systems express weaker root trait trade-offs as compared to in monoculture, suggesting that changes in an individual plant's allocation to root acquisitive traits do not necessarily mean a trade-off in conservative trait values associated with root longevity. For instance, higher specific root length of coffee in an agroforestry system does not have the same relationship with the C to N ratio in root tissue as it would in monoculture. Similarly, higher root N in cocoa in an agroforestry system is nearly completely decoupled with expected changes in root diameter, while a trade-off is observed for crop roots in monoculture. Both of these examples illustrate the role of functional traits as indicators of nutrient acquisition and long term plant-soil feedbacks in these mature agroforestry systems.

Advances in nutrient acquisition detection methodology

In-field studies on nutrient acquisition in agroforestry systems require methods that effectively measure nutrient acquisition at appropriate scales. What has yet to be addressed, to the best of our knowledge, is reconciling the scale at which measurements are made that are appropriate for the nutrient uptake pattern of interest. Here we consolidate established methods and build upon emerging approaches in direct and indirect in-situ sampling (Table 1). To overcome complications arising from multiple nutrients of interest with different availabilities and mobilities in soil, using more than one method will likely be the most effective to understand overall plant strategies belowground and also to discern the underlying mechanisms which drive competitive and/or complementary interactions in agroforests. In order to capture multi-scalar and comparable data on belowground process, we suggest this methodological consolidation as a type of methods standardization for agroforestry systems science.

Fig. 2 Bivariate relationships between acquisitive root traits (x-axes) and conservative root traits (y-axes) measured on individual plants: coffee (n = 62) and cocoa (n = 120) grown in monoculture (M) or agroforestry (AF). Data modified from Isaac et al. 2017 and Borden 2018. We present r^2 and p-values with the sampling site and block as random effects
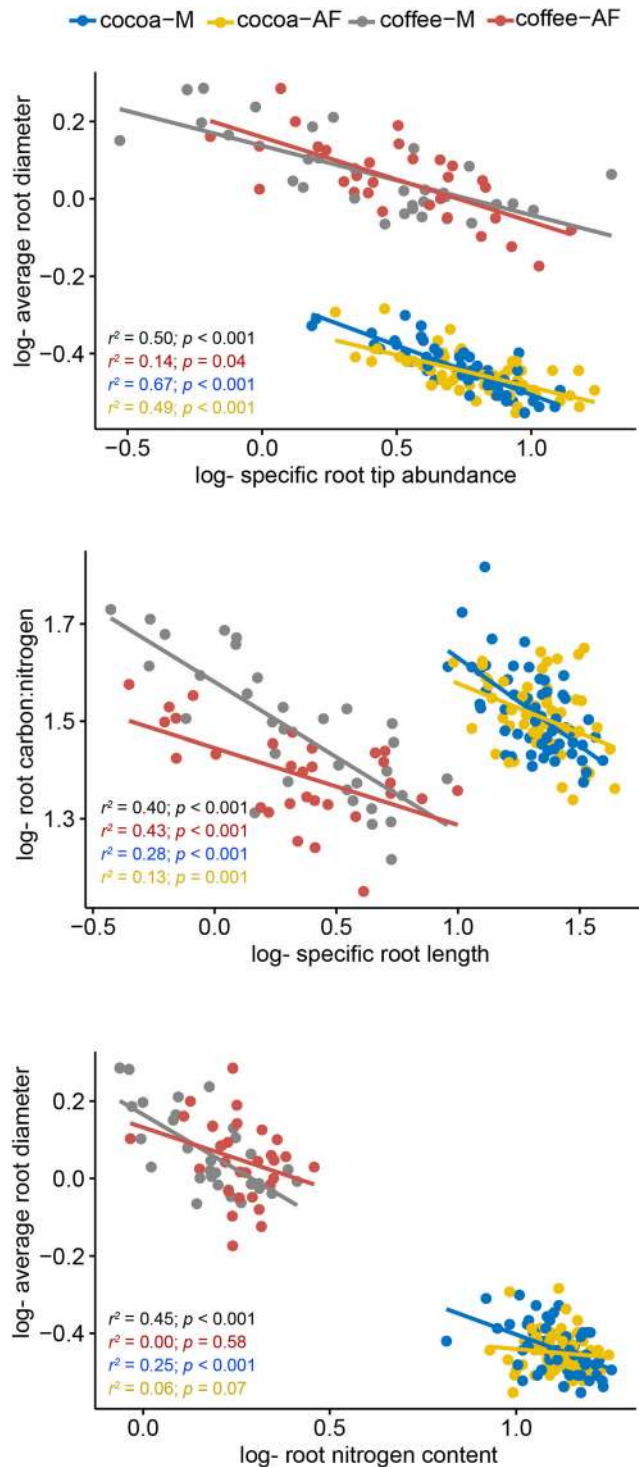
Sampling the tree-crop × soil environment

Soil nutrient availability has been observed to vary dramatically within agroforestry systems (Mora and

Beer 2013), where the spatial arrangement of trees and crops can invoke distinct zones of soil fertility (Rigal et al. 2019). As such, spatially-explicit sampling, that avoids pooling of soil and plant samples, has been a

Table 1 Methods to study nutrient acquisition in agroforestry systems. Four broad methods are categorized amongst three scales of analysis. Key nutrient acquisition processes are identified and associated examples are provided. Target nutrients per method are also identified

Scale of analysis	Physical sampling	Isotopes	Imaging		Modelling	Process of interest with examples from the literature
			Near-surface	Rhizotrons		
Vertical and horizontal nutrient acquisition patterns	Soil coring, soil profile sampling in monoliths	Natural abundance profile matching; estimate nutrient transfer rates	GPR (0.9–1.5 GHz) for coarse root structure and distribution; potential >1.5 GHz for fine root biomass	Manual or semi-automatic analysis of root production with depth	Nutrient uptake by depth intervals; Total plant uptake	- Vertical segregation of nutrient acquisition between tree and crop (Isaac et al. 2014a; Borden et al. 2017; Abou Rajab et al. 2018) - Horizontal extent of tree influence on nutrient acquisition (Isaac et al. 2014b) - Monitoring root dynamics (Mohamed et al. 2018)
Localized nutrient acquisition patterns	Ingrowth cores; localized fertilization	Isolate location of nutrient uptake with labelled fertilizer		Identify mycorrhizal fungi		- Spatially-explicit root-nutrient relationships on 2-dimensional plans (Mora and Beer 2013; Borden et al. 2019) - Root and mycorrhizal foraging for nutrients (McGrath et al. 2001; Jalonen et al. 2009; Borden and Isaac 2019)
Site of acquisition	Standardized root and soil sampling; functional delineation of absorptive roots			Root activity-soil status interactions		- Fine-scale nutrient-specific acquisition strategies (Bordron et al. 2019; Borden et al. 2019) - Overall acquisition strategy of plant roots (Duan et al. 2017; Isaac et al. 2017) - Effects on rhizosphere (Munroe et al. 2015)
	Target nutrients					
	Indicator of mobile (NO_3) and non-mobile (H_2PO_4, Ca^{2+}, K^+, Mg^{2+}) nutrient uptake	Stable isotopes ^{15}N and ^{18}O for N and H_2O, and rare elements Rb^+ and Sr^{2+} for K^+ and Ca^{2+}	All soil resources; Indicator of soil resource partitioning	Identification of uptake mechanisms	Soil nutrient pools and fluxes; mostly N	

central methodological approach in agroforestry research given a need to understand the spatial effects of the component species (Lose et al. 2003; Borden et al. 2019). For methodologies focused on fine scale sites of acquisition, there have been recent improvements made to collection protocols, measurements, and categorization of roots drawing from functional ecology literature (Pérez-Harguindeguy et al. 2013; McCormack et al. 2015, 2017; Freschet and Roumet 2017; Iversen et al. 2017). Notably, these efforts include specifying and parameterizing root measurements by their functional role and their ecological significance (Mommer and Weemstra 2012; Bardgett et al. 2014; Faucon et al. 2017). For example, resource uptake rate and mycorrhizal associations of roots vary depending on the relative location within the root system (i.e., root order) (Rewald et al. 2011; Iversen 2014). Increasingly, emphasis is placed on measuring functionally-relevant root organs, instead of relying solely on the conventional, and more arbitrary, 2 mm cut off that divides coarse structural roots from more ephemeral fine roots responsible for nutrient uptake. This is achieved by classifying tree roots by root order, or more broadly differentiating absorptive fine roots (approximately the first three root orders, which are more strongly associated with resource uptake) from transport fine roots (higher order fine roots, which are more strongly associated with resource transport) (McCormack et al. 2015). While predictable patterns in root trait variation are emerging from ecology (Weemstra et al. 2016; Freschet and Roumet 2017), more work is needed within agroforestry systems to link tree and crop root form to function. This is especially true since intraspecific variation is of particular importance in cultivated systems (Martin and Isaac 2015; Damour et al. 2018), and the integration of trees is an important determinant in crop root functional trait expression (Isaac et al. 2017; Borden and Isaac 2019; Borden et al. 2019; Martin et al. 2019).

Imaging nutrient acquisition structures with non-destructive methods

Non-destructive methods are appealing given the challenges of studying nutrient uptake in situ, particularly for larger root systems of trees or when repeated measurements are desired. Furthermore, methods that estimate the structure of root systems can support work that uses root allocation patterns as indicators of nutrient acquisition. Root topological models have been used to describe the coarse root architecture of cocoa and *Inga edulis* shade tree root systems, revealing root distribution in 3-dimensions and estimating the location and extent of component species overlap of N_2-fixing tree and crop roots (Nygren et al. 2013). Near-surface geo-imaging technologies, such as ground-penetrating radar (GPR), have also proven effective at describing coarse root architecture when field conditions permit radar signal detections of roots (e.g., dryer, not too clayey soil) (Isaac and Anglaaere 2013). This imaging approach has effectively been used to describe intraspecific variability of the vertical distribution of coarse roots of tree crops across different edaphic and agroforestry management conditions (Isaac et al. 2014a) and interspecific variability among trees in tree-based intercropping (TBI) systems (Borden et al. 2017). An advantage in using these approaches is in the ability to more completely describe extensive, irregularly distributed tree root systems, although some additional physical sampling may be required for parameterizing topological models (Nygren et al. 2013), or calibrating geo-imagery data (Borden et al. 2017). However, to accurately gauge nutrient acuqisiton, which is carried out predominantly by absorptive fine roots, root structural metrics can be complemented by data on fine roots and/or nutrient uptake data (via isotopic analyses) to capture acquisition patterns in different spatial dimensions (Isaac et al. 2014a; Borden et al. 2017). While coarser resolution geo-imaging technology is typically limited to perennial root systems, the recent use of higher frequency (1.6 GHz) GPR detected annual crop roots (winter wheat and energy cane) (Liu et al. 2018) suggests potential for non-destructive, repeatable measurements of annual crop roots in agroforestry systems. In situ image analysis of fine root dynamics via photography or high-resolution scanners installed on minirhizotrons have also proven particularly useful, as recently demonstrated in a study across TBI systems in France (Mohamed et al. 2018).

Isolating sites and transfer of soil nutrient acquisition using isotopes

Stable isotope analyses have long been a relatively robust method to non-destructively isolate locations of soil nutrient acquisition and estimate rates of nutrient uptake. Stable isotopes ^{15}N and ^{18}O and rare elements Rb^+ (K^+ analogue) and Sr^{2+} (Ca^{2+} analogue) are effective in diagnosing key plant-soil interactions in agroforestry systems. The two most common isotopic

signatures used to assess root resource acquisition in soil profiles, $\delta^{15}N$ and $\delta^{18}O$, are linked to assessments of nutrient ($\delta^{15}N$) and water ($\delta^{18}O$) uptake. As described in previous sections, both the natural abundance and isotopic dilution methods are used to detect amounts of N_2 fixation and N transfer as well as water acquisition zones in agroforestry systems. Various plant tissues are sampled (^{15}N in leaves, ^{18}O and ^2H in stem water) and accompanied by a range of important conditions to be met for robust estimates. In all cases, the complexity of agroforestry systems can introduce many limitations. Reliable isotopic data to measure N transfer in agroforestry systems must prioritize minimizing: i) skewing of $\delta^{15}N$ signatures via fractionation with in the soil-plant systems, ii) using unrepresentative tissue samples, and iii) misrepresentation of donor plant $\delta^{15}N$ (Craine et al. 2015). Matching oxygen isotopic signatures in extracted stem water and soil water to identify active root zones in soil profiles is useful if two conditions are met: i) soil horizons must have distinct values of isotope ratios that are consistently different from each other and greater than what would normally occur in a plant, and ii) no fractionation of isotopes as the water molecules travel up the plant (Dawson et al. 2002; Link et al. 2015). The use of rare elements have been effectively used to determine zones of acquisition in soil profiles, especially in deep soils. Most notably, in a *Eucalyptus grandis* plantation, Bordron et al. (2019) used NO_3^{-}-^{15}N, Rb^+ and Sr^{2+} tracers at depths of 10, 50, 150 and 300 cm in a sandy Ferralsol soil and showed high levels of functional specialization of roots in deep soil layers for low mobility cations, as well as limited losses via leaching under high fertilization. If all key plant and soil conditions are met, isotopic analysis is an outstanding tool for agroforestry science to advance detection capabilities of nutrient acquisition patterns and quantify nutrient transfer rates.

Modelling the root-soil nutrient continuum

Nutrient uptake models for individual plants are becoming increasingly refined such that uptake rates can vary across the root system – see Dunbabin et al. (2013) for an in-depth synthesis of 3-dimensional root architectural models and functional-structural plant modelling. This has been a challenge for modelling nutrient uptake in agroforestry systems given component tree species with larger and long-lived root systems that may have large variation in root function, both in space and in time.

Some of the more commonly used process-based models that capture nutrient acquisition in agroforestry systems account for plant architecture and root distribution of the component species. Nutrient uptake modelled in WaNuLCAS (van Noordwijk and Lusiana 1998) is based on the total uptake potential of N at distinct soil depths. Uptake potential is derived from the summed crop and tree components capacity for uptake as indicated by their root length and nutrient concentration in soil, and the nutrient demands of the crop and tree components as indicated by plant biomass. More recent advancements in the Hi-sAFe model, parameterized for temperate agroforests with deciduous trees, account for vertical and horizontal N acquisition patterns of trees in agroforests through 3-dimensional voxels that can include some key nutrient acquisition parameters such as fine root lifespan and specific root length as well as fraction of colonized roots (Dupraz et al. 2019). These tree structure and acquisition patterns then impact the crop component, including inputs of additional N from senesced tree roots, although the belowground processes modelled (e.g. root architecture) are in need of field validation studies (Dupraz et al. 2019). These types of generalized process-based models are a mainstay in the agroforestry literature (see Luedeling et al. 2016), while species-specific models have lagged; for instance, in coffee agroforestry, given limited data for full parameterization of process-based models (van Oijen et al. 2010). Moreover, parameterization of models that integrate acquisition of nutrients other than N are lacking for agroferstry systems. Altogether, there is a need for spacially accurate representation of roots and associated mycorrhizae and nutrient uptake potential within individual root systems that are parameterized for mixed species agroecosystems.

Pressing research: effects of environmental change on nutrient acquisition strategies in agroforestry systems

Agroforestry practices are increasingly promoted as an adaptation strategy to climate change (Verchot et al. 2007; Schoeneberger et al. 2012; Mbow et al. 2014). To date, research on climate change effects in agroforestry systems has primarily focused on the water availability-plant growth axis, addressed with distinctive experimental designs to assess reduced rainfall and high evapotranspiration potential, tree-crop water

acquisition, and tree microclimates (Schwendenmann et al. 2010; Nasielski et al. 2015; Abdulai et al. 2018). Cumulatively, these processes can mitigate or accentuate climate change impacts on crop growth and yield in agroforestry systems. While this is certainly a critical realm of agroforestry research, there is also urgency to understanding how these processes interact with nutrient dynamics. On one hand, where regional climates are becoming wetter under higher precipitation, trees on farms that improve retention of soil nutrients are likely to be essential. On the other hand, in regions that are becoming drier and hotter, we can expect changes to ecosystem processes in agroforestry systems such as i) lower quality tree litter inputs, ii) greater constraints on nutrient mineralization and subsequent nutrient mobility, iii) reduced translocation of C to roots, and potentially iv) acute effects of tree growth on crop performance. Under suboptimal climatic conditions, including extreme weather events, tree-crop nutrient acquisition patterns will respond to multiple trade-offs in factors such as shade levels, litter inputs, microclimate regulation (humidity, wind), and hydraulic redistribution.

In general, there is a paucity of empirical work on the effects of climatic change on nutrient acquisition in agroforestry systems. We know that in coffee agroforests in India, rainfall and/or irrigation effects were notable in these studies; native timber trees (*Grevillea robusta*) shed higher amounts of litter in dry than in wet sites while mixtures of native shade trees provided similar amounts of higher quality litter (Nesper et al. 2018). However, as expected, rainfall and/or irrigation increased coffee yields (Boreux et al. 2016). Similarly, in coffee agroforests in Central America, the overall acquisition strategy of coffee roots was largely controlled by sites of distinct climates representing a range of mean annual precipitation and temperature (Isaac et al. 2017). In TBI systems, water availability controlled competition between *Juglans nigra* and maize for mineralized N (Jose et al. 2000), while fine root dynamics may be largely controlled by climate, as suggested by the differential root elongation rates of *J. nigra* (Mohamed et al. 2018). Under sub-optimal climatic conditions, we know that key microbial communities were more resilient in a temperate TBI system (Furze et al. 2017), a Mediterranean agroforestry system (Guillot et al. 2019), and a *Zanthoxylum bungeanum*-based intercropped system (Sun et al. 2016). Relationships between root trait expression and microbial communities involved in soil C and N dynamics were

reported under droughty conditions (De Vries et al. 2016), but much work is needed to elucidate the interactive function of microbial-plant nutrient acquisition patterns in agroforestry systems to achieve resilience under environmental change.

Conclusions

We synthesize research at various scales of the belowground tree-crop interface that are cumulatively hypothesized to underpin nutrient acquisition strategies and crop performance in agroforestry systems. Understanding the mechanisms related to nutrient acquisition that contribute to overall complementary, facilitative, and/or competitive interactions observed in agroforests requires thorough consideration of the multiple scales at which trees and crops interact with and acquire nutrients in soil. These scales span the whole root system, which dictate the magnitude and spatial extent of acquisition patterns, to fine-scale sites of acquisition, which are actively engaged in biological and chemical interactions with soil. In this context, plot or farm research can continue to rely on whole root systems scale of analysis (root biomass, distribution patterns, and isotope uptake patterns), which remain one of the most universal indicators of nutrient acquisition strategies in a range of agroforestry systems, to assess broad patterns in nutrient acquisition between trees and crops. In contrast, mechanistic diagnostics undoubtedly require analyses at the level of lateral roots or sites of nutrient uptake. For example, interspecific root overlap can be associated with nutrient competition, but clear cases of enhanced chemically and microbially meditated processes result in species- and management- specific nutrient facilitation. To capture these multi-scalar dimensions of nutrient acquisition, advancements in agroforestry research necessitate measuring and analyzing the mechanism and nutrient of interest at appropriate scales. To contribute to this effort, we consolidate established methods, build upon emerging approaches in direct and indirect in-situ sampling, and suggest standardizing the scale × method nexus.

The standardization of root functional traits in agroforestry research is a promising framework to capture the multi-scalar nature of nutrient acquisition processes in agroforestry systems. This framework addresses a common challenge in agroforestry research – constrained data from specific species within bounded

abiotic conditions – making it difficult to generate broad hypotheses or infer generalizable conclusions. Based on new multi-sited, multi-species root trait analyses, we demonstrate that in agroforestry systems, root functional traits and trait trade-offs reveal bivariate patterns similar to, but weaker than, crops in monoculture, with mechanistic links to nutrient acquisition strategies. Plant functional traits as diagnostic indicators in agroforestry systems remain a wide open and relatively unexplored line of inquiry. We argue for agroforestry science to use these distinct nutrient acquisition indicators at multiple scales to generate more nuanced, while also more generalizable, diagnostics of tree-crop interactions.

Throughout our review, we show that hypotheses on agroforestry belowground properties and processes are generated based on key ecological theories, but also on confirmed nutrient behaviour such as nutrient mobility and transfer. Agroforestry research is often grounded in providing applied information for on-farm management, however, agroforestry also has an important role in contributing to broader ecological literature, such as understanding the mechanisms that drive biodiversity-ecosystem function relationships. But most pressing, the extent and conditions in which agroforestry practices mediate impacts of climatic extremes on crop performance requires an understanding of how environmental change destabilizes established root-microbial nutrient acquisition strategies in diversified agroecosystems.

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