



Water acquisition, sharing and redistribution by roots: applications to agroforestry systems

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Abstract

Aims In the face of problems caused by ‘intensive agriculture’ dominated by large areas of monocultures, mixed intercropping mimicking natural ecosystems has been reported to constitute a viable solution to increase and stabilize productivity. When designing such systems, root niche separation was thought to be a prerequisite to optimize production.

Methods This paper reviews the beneficial and adverse effects of trees and crops on water acquisition and redistribution in agroforestry ecosystems using the concepts of competition and facilitation between plants in link with root functional traits.

Results The results of the review showed that the reality was more complex leading agroforestry practitioners to adopt management practices to induce a separation in root activities thus avoid competition, particularly for water. Water uptake by plant roots is triggered by the water potential difference between the soil and the atmosphere when leaf stomata are open and depends largely on the root exploration capacity of the plant. Thus, root water uptake

dynamics are strongly related to root-length densities and root surface areas. In addition, plants with deep roots are able to lift up or redistribute water to the upper layers through a process known as hydraulic lift, potentially acting as “bioirrigators” to adjacent plants. The redistributed water could be of importance not only in regulating plant water status, e.g. by enhancing transpiration, but also in increasing the survival and growth of associated crops in mixed systems.

Conclusions Even though some more work is still needed to assess the volume of water transferred to neighbors, hydraulic lift could constitute an ecological viable mechanism to buffer against droughts and ensure productivity in regions with erratic rainfall. Giving the difficulty in measuring the above-mentioned aspects in the field, modeling of some of the most relevant parameters to quantify them might inform the design of future empirical studies.

Keywords Ecosystem services · Hydraulic lift · Mixed cropping · Productivity · Sustainability

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Introduction

In the face of the world current challenges to sustain good living conditions including increasing population numbers, a changing climate or the degrading agro-ecosystems associated with a declining agricultural productivity, there is a need for approaches that could ensure food security. Indeed, ‘intensive agriculture’ is dominated by large areas of high-yielding monocultures, i.e. cultures using a single

species, that are resource-consuming and have led to many environmental problems that intercropping could help to address (Brooker et al. 2015; Machado 2009). For instance, agroforestry or the combination of trees with agricultural crops or pasture, was listed among the climate smart technologies (Dinesh et al. 2017). This is due, in large part, to the fact that intercropping has the potential to promote an efficient use of two limiting factors for plant growth, i.e. water and nutrients, by an improved acquisition of these resources through complementary root distributions, water sharing mechanisms such as hydraulic redistribution (HR), common mycorrhizal networks, and/or reduced runoff leading to increased water infiltration (Bayala and Wallace 2015; Brooker et al. 2015; Mao et al. 2012; Prieto et al. 2012b). To take advantage and promote the use of these mechanisms in agricultural systems there is a need for a careful design of the species mixtures used (Altieri et al. 2015; Dupraz et al. 1997; Malézieux et al. 2009; Ong and Leakey 1999; van Noordwijk and Ong 1999). In agroforestry systems, annual crops are typically shallow-rooted while perennial plants include trees that have root systems extending deeper in the soil giving foundation to the safety-net hypothesis (Rowe et al. 1999; van Noordwijk and van de Geijn 1996; van Noordwijk et al. 2015). The safety-net hypothesis, i.e. intercepting mobile nutrients leaching from crop root zones, is also complementary to the nutrient pump hypothesis which refers to the taking-up of nutrients, generally relatively immobile, from deep soil layers, their incorporation in aboveground plant tissues (i.e. leaves) and their transfer to upper soil layers through leaf shedding and decomposition (Ong and Leakey 1999; van Noordwijk and Ong 1999; Jobbagy and Jackson 2004). However, these mechanisms can be far more complex and dynamic (Akinnifesi et al. 2004; Brooksbank et al. 2011a; Schroth 1998; van Noordwijk et al. 2015) and depend on seasonal shifts of water availability and nutrient extraction from different soil depths (Bargués Tobella et al. 2017).

This complexity has prompted an increased interest of the scientific community in agroforestry systems that started with more descriptive work and then moved to more complex studies trying to understand the mechanisms behind resource sharing between intercropped plants and the quantification of these processes for plant growth (Black et al. 2015; van Noordwijk et al. 2004). The fast development of different tools and approaches in this field have helped researchers to investigate plant root distributions and structure in these systems for a better understanding of the interactions and processes involved

belowground (Cardinael et al. 2015; Ong et al. 2014; Tracy et al. 2015). Despite these advances, root research in mixed tree-crop agroforestry systems remains challenging because of the difficulty in finding the relevant spatial and temporal scales for the high heterogeneity of soil conditions in these systems. Besides spatial differentiation of root systems between plant species, some functional traits linked to resource acquisition, including selective root placement (SRP), root length density (RLD) or specific root length (SRL), are increasingly being used to evaluate the competitiveness of plant species (e.g. acquisitive fast-growing versus conservative slow-growing strategies) for the different resources in mixed systems (Bardgett et al. 2014; Prieto et al. 2015; Ravenek et al. 2016; Reich 2014). However, to date there is no consensus on which are the most relevant traits that confer a true advantage in belowground plant competition (Ravenek et al. 2016).

Putting more efforts in these under-researched areas will be pivotal for designing the best mixtures of tree and crop species for agroforestry practices that provide beneficial outputs both for the communities and the environment (Altieri et al. 2015; Gutoa et al. 2012; Malézieux et al. 2009). Based on the key concepts of interspecific competition and facilitation between plants in link with root functional traits, this paper reviews the beneficial and adverse effects of trees and crops on water acquisition and redistribution in agroforestry ecosystems.

Water acquisition by roots

Sampling patterns to measure soil water contents in agroforestry systems vary according to the studied agroforestry practice (transect, random, etc.) but taking soil water content measurements at various distances from the plant and at different soil depths and comparing situations with agroforestry practice against monoculture practices (control) has been the most common approach (Bayala and Wallace 2015; Ong et al. 2014; Fig. 1). Measurement methods have also undergone a tremendous development from gravimetry measurements based on soil weighing to automated and remotely controlled measurements using wireless networks that allow a continuous monitoring of the soil water status (Bogena et al. 2007; Tracy et al. 2015). Even though the relationship between tree cover and water supply is not straightforward, the tree components in agroforestry practices are in general expected to reduce runoff and thus increase soil water infiltration favoring the uptake

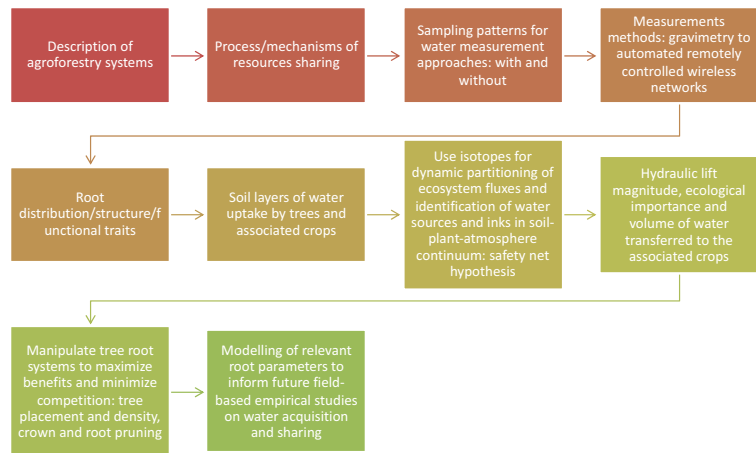
of water from deep soil layers by plant roots and a potential recycling of this water in upper soil layers through water redistribution (discussed in more detail in the next section). Kuyah et al. (2016) reviewed the roles of trees on agroforestry farms in semi-arid sub-Saharan Africa and found that, in most cases, trees had beneficial effects on associated crops by enhancing soil water availability in 58% of the studies considered in their review. These correspond to situations in which a strategic placement of trees in the landscape at an optimal density induces desired positive effects on local hydrology (Brooksbank et al. 2011b; Siriri et al. 2010, 2012). For example, it has been reported that a moderate tree cover could enhance groundwater recharge (Ilstedt et al. 2016) because of increased infiltrability and higher preferential flow due to the channels left by decayed roots and an increased faunal activity (Bargués Tobella et al. 2014; Ghestem et al. 2011). In the same site, it was found that trees obtained 90% of their water from upper soil layers during the rainy season and switched to taking up 50% of their water from groundwater during the dry season (Bargués Tobella et al. 2017; Roupsard et al. 1999). That could partly explain why some tree species in drylands can flower and fruit during the dry season, but this remains an assumption that needs to be verified in future studies. Thus, this source of blue water (water from rivers, lakes and groundwater) being recycled as green water (rainwater absorbed by the plants) may be playing an important role in the overall performance of the agroecosystems in these areas. Furthermore, it has been found that an increase of tree cover beyond the optimum to maintain a stable groundwater recharge, decreased infiltration and recharge but remained at higher levels than in scenarios without any trees (Ilstedt et al. 2016). In addition, tree roots help aggregate soil particles increasing soil stability and reducing runoff and increasing water infiltration. This effect is due to tree root exudates that could explain approximately 20%–75% of the variation on the anti-erodibility of soils (AES) according to Wang et al. (2017). Exudates and decayed roots are also a source of carbon to the soil which, together with root mass densities, were reported to influence the formation of soil aggregates and increase their stability (Kalhor et al. 2017; Le Bissonnais et al. 2018).

The roots of plants have several functions such as anchorage, storage (carbohydrates), resource acquisition (water and nutrients), and communication (cytokinins, gibberellins and other growth regulators) but most of the controlling factors of these functions are still not fully known (Hopmans and Bristow 2002; Ryan et al. 2016).

Information on the root distribution of tree species is mostly concentrated on the total root mass, that generally includes both fine (< 2 mm) and coarse roots (> 2 mm) while it is the finest part of the root systems (i.e. the finest roots and lower root orders) that are most dynamic and most actively involved in water and nutrient uptake and hence of greater interest in agroforestry (van Noordwijk and van de Geijn 1996; Wajja-Musukwe et al. 2008). Water uptake by the roots is triggered by a demand of this resource from the leaves creating a tension that propagates down to the roots and induces an inflow (or outflow in the case of redistribution) of water from the rhizosphere following paths of low soil hydraulic resistance (Lobet et al. 2014; McElrone et al. 2013; Steudle 2001). Thus, root uptake dynamics are usually related to root-length densities and root surface area (Lobet et al. 2014; van Noordwijk 1993), even if we do not account for the fact that uptake is also controlled by root age and other mechanisms taking place within the roots and in their surrounding rhizosphere (mucilage exuded by roots, the gradient in soil water potential around the roots, changes in hydraulic conductivities along the roots, etc., Carminati et al. 2016; Hopmans and Bristow 2002).

In agroforestry systems crops take up water mostly from the upper soil whereas trees may display a more opportunistic strategy obtaining most of its water from the upper soil during the wet season and switching to water stored deeper in the soil, e.g. groundwater, during the dry season when upper soil layers are dry (Bargués Tobella et al. 2017). Many studies have revealed that the root distribution of most tree species in agroforestry systems overlaps in the upper soil layers with the shallower root systems of associated annual plants (Schroth 1995; Smith et al. 1999). This root distribution allows accumulating a high proportion of their fine roots in upper soil layers and gives the plant access to intermittent soil moisture and soil nutrients in topsoil layers while the primary root grows deeper to facilitate extracting soil water from deeper wetter layers (Dhyani et al. 1990). Such accumulation of fine roots in the upper soil layers may generate a competition between the tree and associated annual crops for water (and nutrients) since root placement is a strategy for competitiveness (Ravenek et al. 2016). Despite this, selecting tree and crop species and provenances according to root-related criteria with deeper roots for agroforestry systems (Schroth 1995) is rarely done (Rowe et al. 1999; Smith et al. 1999) but a few studies have found separate niches for tree and crop absorptive root systems in response to agricultural practices with tree roots developing below the

Fig. 1 Current knowledge on water acquisition and sharing and their potential applications in agroforestry systems



crop rooting depth (Akinnifesi et al. 1999; Dupraz et al. 2005; Howard et al. 1997; Rowe et al. 1999; Ruhigwa et al. 1992; Singh 1994). A good option may therefore be to manipulate tree root systems to maximize benefit while minimizing competition with crop species (Bayala et al. 2013; Cardinael et al. 2015; Hou et al. 2003; Siriri et al. 2013), which implies reducing niche overlap by limiting tree root growth in the crop rooting zone (Bayala et al. 2013; Namirembe 1999). Tree pruning has been demonstrated to reduce root growth in shallow layers but requires tedious work and labor and is not a desirable practice for carbon sequestration and nutrient cycling (Schroth 1995; Smith et al. 1999; Wajja-Musukwe et al. 2008). Another possibility would be to manipulate the tree crown because roots do not act as simple pumps and their activity is regulated by the demand in the aboveground parts of the plant (Jeschke and Hartung 2000; Jones et al. 1998). For instance, Kizito et al. (2012) showed that a partial coppice of the canopy of *Guiera senegalensis* reduced daytime sap-flow rates, i.e. plant transpiration. Plant water uptake is determined by a combination of soil water availability and potential transpiration by the canopy (Hoad et al. 2001). There is emerging evidence pointing to crown pruning as an effective tool to manipulate tree root dynamics of shallow-rooted tree species (Bayala et al. 2002, 2004; Bazié et al. 2012; Jackson et al. 2000; Jones et al. 1998; Siriri et al. 2013). All these studies revealed a decrease in tree root densities in shallow soil because of the forced reduction of the tree aboveground demand. Indeed, Jones et al. (1998) observed a marked reduction in root length densities of *Prosopis juliflora* trees 60 days after pruning, a reduction that was more pronounced in

upper soil layers. This reduced competition from tree roots in shallow soil layers allowed for a better development of crop roots and associated sorghum plants developed higher root densities under pruned *P. juliflora* trees even though this occurred only in the uppermost shallow layers (10–20 cm depth). Another effect of tree crown pruning is that a reduction or removal of the tree crown will lead to an increase in soil temperature and a reduction of soil water in the upper soil layers around the tree (Bayala et al. 2004) that will affect fine root growth and development since fine roots are highly sensitive to changes in soil temperature and moisture. Because root functioning is also under the control of aboveground parts of the plant (Friend et al. 1990; Hoad et al. 2001; Jeschke and Hartung 2000; Steudle 2000), crown reduction will also lead to a decrease in water and nutrient demand and consequently a reduction of fine roots in shallow soil layers. Water and to some extent nutrients are the most limiting factors in semi-arid areas. If, because of crown pruning, less water and nutrients are taken up by trees from the topsoil layer, this means greater availability of these resources for the associated crops, at least in the short term. Consequently, this may lead to more space for crop roots and thus higher crop root density and ultimately to better crop production under pruned trees (Bayala et al. 2004). A decrease in the production of tree fine roots in upper soil layers and their increase in deeper soil layers may not only reduce tree/crop competition and improve crop production but also help improve the benefits of the “safety-net” hypothesis described by Cadisch et al. (1997), Rowe et al. (1999) and Vanlauwe et al. (2002). This hypothesis postulates that deep rooting trees can utilize more efficiently leached

nutrients beyond the range of crop roots when the demand for these nutrients is high (Cadisch et al. 1997; Gathumbi et al. 2002; Lehmann et al. 1998a, b; Suprayogo et al. 2002). A high safety-net efficiency requires a minimal tree RLD to a certain depth, a minimal level of activity of tree roots present in the soil layers considered, and a minimal demand by the tree for the nutrient considered (Cadisch et al. 1997; Vanlauwe et al. 2002).

Thus, pruning has been shown to reduce root biomass and this was ascribed to translocation of carbohydrates from roots to shoots to maintain their growth and the functional equilibrium between the two compartments (Govindrajan et al. 1996; Hoad et al. 2001; Namirembe 1999). Nevertheless, the impact of pruning is variable and depends on the species considered (Akinnifesi et al. 1999; Jones et al. 1998; Odhiambo et al. 2001; Schroth and Lehmann 1995), on management practices (Govindrajan et al. 1996; Namirembe 1999) and on environmental conditions (Vanlauwe et al. 2002; Vogt et al. 1998). The distribution of plant roots within soil layers is also a dynamic process disagreeing with Jones et al. (1998) and Smith et al. (1999) who found that tree roots dominated agroforestry plots all year-round. Indeed, Odhiambo et al. (2001) reported that tree roots were only the most abundant about half of the cropping period. In some circumstances, pruning induces no effect on tree roots and may even increase root production (van Noordwijk and Purnomosidhi 1995). In any case, the effect of tree pruning and root reductions on well-established trees is transient and needs to be repeated in subsequent periods since root growth and production will recover as the tree crown regains its size (Bayala et al. 2004; Namirembe 1999; Odhiambo et al. 2001).

Water sharing and redistribution by roots

In addition to improving soil conditions for enhanced water infiltration and storage, trees reduce solar radiation underneath leading to lower evapotranspiration and greater soil water contents under their canopies. Another process leading to increased soil water content in the upper rooting zone under trees is the process of hydraulic lift (HL) or water redistribution by roots, which is defined as the passive

movement of water through the roots of trees, from deeper and wetter soil layers to shallower and drier horizons, along a gradient of soil water potential (Richards and Caldwell 1987). The HL process usually occurs during the night when plant transpiration is low or null (Prieto et al. 2010b; Hultine et al. 2003) and the water potential gradient is established between wetter and drier soil layers, but has been reported to occur during the day under particular soil conditions, e.g. along water potential gradients created by variations in soil salinity (Hao et al. 2009). Although the direction of water movement is typically upward, towards drier, shallow soil layers, measurements of sap flow in taproots and lateral roots of trees have demonstrated that roots can also redistribute water downward or laterally from moist surface soils to drier regions of soil (Burgess et al. 1998; Hultine et al. 2003; Nadezhkina et al. 2006). This bidirectional movement of water was termed “hydraulic redistribution (HR, Burgess et al. 1998). The process of HL is generally found in species with dimorphic root systems with access to water from both shallow and deep soil layers (Scholz et al. 2008). Hydraulic lift has been shown to be ubiquitous as long as conditions favors its occurrence and has been reported in a large number of species from various climates including Mediterranean ecosystems, cool temperate regions and seasonally dry tropical and subtropical habitats (Horton and Hart 1998; Jackson et al. 2000; Neumann and Cardon 2012; Prieto et al. 2012b). One important aspect is that HL has also been described in many woody species widely used in agroforestry systems such as *Azadirachta indica*, *Acacia tortilis*, *Eucalyptus kochii* subsp. *borealis*, *Guiera senegalensis*, *Parkia biglobosa*, *Piliostigma reticulatum*, *Vitellaria paradoxa* (Bayala et al. 2008; Brooksbank et al. 2011a; Kizito et al. 2006, 2012; Ludwig et al. 2003; Smith et al. 1997).

The ecological or agroecological relevance of HR both to the plant engaged in HR and for neighboring plants has been widely reported by many authors (see reviews by Burgess 2011; Caldwell et al. 1998; Liste and White 2008; Neumann and Cardon 2012; Prieto et al. 2012b). For the plant, HR can improve plant transpiration rates and plant water status (Dawson and Pate 1996); reported estimates of the total volume of water lifted range from 5% to 30% of the total plant transpiration suggesting that hydraulic redistribution

could postpone the development of water stress and mitigate the impact of soil drying in the surface horizons (Caldwell et al. 1998; Emerman and Dawson 1996; Oliveira et al. 2005; Warren et al. 2005, 2007). Hydraulic lift has other side benefits such as higher fine root survival (Bauerle et al. 2008), a limited root embolism during the day by refilling xylem conduits at night (Domec et al. 2004, 2006; Prieto and Ryel 2014) or improved soil nutrient recycling that could benefit both the woody species and associated crops (Aanderud and Richards 2009; Armas et al. 2012; Cardon and Gage 2006; Cardon et al. 2013; Prieto et al. 2012a). For neighboring plants, water that is redistributed to shallow soil layers can also be taken up by plants living in close association to plants engaged in HL enhancing their transpiration and ultimately increasing their survival and biomass production (Bogie et al. 2018; Izumi et al. 2018; Lee et al. 2018; Prieto et al. 2011). Nevertheless, the net effects that species engaged in HR have on their neighbors is still unclear (Prieto et al. 2012b). There are reports of positive, neutral or even negative effects depending on ecosystem type, plant life form or whether donor and receiver species shared common ecto- and endomycorrhizal networks. We need to note here that common mycorrhizal networks are strongly involved in water and nutrient sharing between plant species (Allen 2007; Montesinos-Navarro et al. 2019) and play an important role in the transfer of lifted water between species and within individuals of the same species (Querejeta et al. 2003, 2012; Egerton-Warburton et al. 2007; Prieto et al. 2016; Warren et al. 2008). However, our knowledge on the importance of mycorrhizal pathways in agroforestry systems is still very limited (de Carvalho et al. 2010) and will not be discussed in this review but opens up new areas of research to differentiate between root-only- and root-mycorrhizal-based transfer of HL water (Fig. 2). Several studies have shown that HL enhances water availability to plants (McMichael and Lascano 2010; Hirota et al. 2004; Prieto et al. 2011; Shen et al. 2011; Smart et al. 2005; Wan et al. 2000), thereby promoting microbial processes and decomposition processes which release nutrients from organic matter and soil minerals (Aanderud and Richards 2009; Armas et al. 2012; Austin et al. 2004; Cardon et al. 2013; Matimati et al. 2014; Munoz et al. 2008; Prieto et al. 2012a; Smith et al. 1999; Yoder and Nowak 1999) that could also benefit the growth and survival of plant neighbors. The process of HL may therefore contribute significantly towards meeting the

water, and or nutrient supplies needed to support growth and grain filling in associated crops in agroforestry systems with limited water availability (Bogie et al. 2018; Izumi et al. 2018). The potential application and exploitation of HL to improve water availability to crops or seedlings/saplings in forestry and ecological restoration has been already suggested (Burgess 2011; Liste and White 2008) but, to date, real-world experimental tests in agroforestry systems are still limited but show promising results. For example, Kizito et al. (2012) estimated that, in two species commonly used in agroforestry (*Guiera senegalensis* and *Piliostigma reticulatum*), HL alone could account for up to 35–47 mm of water annually, which represents between 8% and 10% of the mean annual precipitation (450 mm) in the Sahel. Under similar environmental conditions, Vadez et al. (2013) showed that pearl millet (*Penisetum glaucum*) yield could increase by up to 3.5–4.7 g per plant for each additional mm of water provided, which means that, in regular planting densities of 10,000 plants ha⁻¹, the additional water provided through HL could result in substantial yield increases of 35–47 kg ha⁻¹ mm⁻¹. Experimental evidence of such increases in plant crop biomass when grown in association with species engaged in HL was reported in a subsequent study by Bogie et al. (2018). These authors used an enriched deuterium (²H) water tracer to demonstrate that the associated pearl millet crop took up water that had been lifted by the shrubs. They concluded that, along with other potential beneficial factors of growing crops in association with the shrubs (shade or lower temperatures), HL contributed largely to the 900% increase in pearl millet biomass from below 200 kg ha⁻¹ in the control. In addition to the extra water provided by HL, crops could also benefit from other side benefits of improved soil moisture conditions such as a faster nutrient recycling and uptake under plants engaged in HL (Sun et al. 2014). Also, competition for water between crops and associated species has been observed in agroforestry systems when tree root systems had no access to groundwater (Rao et al. 1998; Dupraz et al. 2005) and a requirement for species selection is that facilitative species have deep roots and access to deep water, or they will probably otherwise outcompete crops for a limited water supply (Barron-Gafford et al. 2017; Van Noordwijk and Ong 1999). Thus, the relative importance of complementarity for water via HR or competition may therefore depend on particular soil conditions such as soil moisture content, as well as other factors known to shape inter-plant interactions (Bayala

et al. 2008; Hirota et al. 2004; Ludwig et al. 2003, 2004). These reported benefits for plant production and survival, however, may be thus largely dependent on the context and the species involved (Prieto et al. 2012b), which may be particularly true in mixed agroforestry systems where shading and micro-climatic effects could have an equally important influence on plant growth and survival (Prieto et al. 2011).

One interesting aspect of the use of HR in agroforestry systems is promoting positive plant interactions by an active management of agroforestry systems. One example of such management was provided by Sekiya et al. (2011) that grew a crop in association to deep-rooted forage plants in an agricultural field. To remove competition for water and promote the uplift of water from deep soil layers, they removed the shoots of deep-rooted plants forcing HL 24 h a day, which resulted in a better crop water status and greater biomass production. As these shoot-less plants were found to be effective bio-irrigators, the mechanism at play could be HL until root death and a capillary or “wick” effect afterwards (Leffler et al. 2005). This calls for a better understanding of the fundamentals of HL before we can apply effective bio-irrigation techniques such as total plant removal.

Although this example has not been replicated since, common agricultural practices in agroforestry systems that do not completely remove the canopy, such as tree pruning or shading, can be tested as effective mechanisms favoring the process of HL since reducing above-ground canopy transpiration can enhance the amount of water lifted to topsoil layers (Prieto et al. 2010a, b; Sekiya and Yano 2004). Furthermore, the remnants from cutting the shoots of deep-rooted forage plants can be recycled into forage for animals providing an additional benefit for such systems. Therefore, a directed selection of pairs of species in intercropped systems along with agricultural practices, may help overcome this problem and promote water sharing between the tree and neighboring crops and the use of HR as a bioirrigation system. However, our knowledge in the incorporation of species engaged in HL in agroforestry systems is still very limited and further efforts in applied research are still needed to assess which species would be better suited to be used as “bioirrigators”, in which context or environments, the magnitude of the volumes effectively transferred to the associated crops/plants and what crops would benefit more from this lifted water along with its impact on plant productivity (Fig. 2).

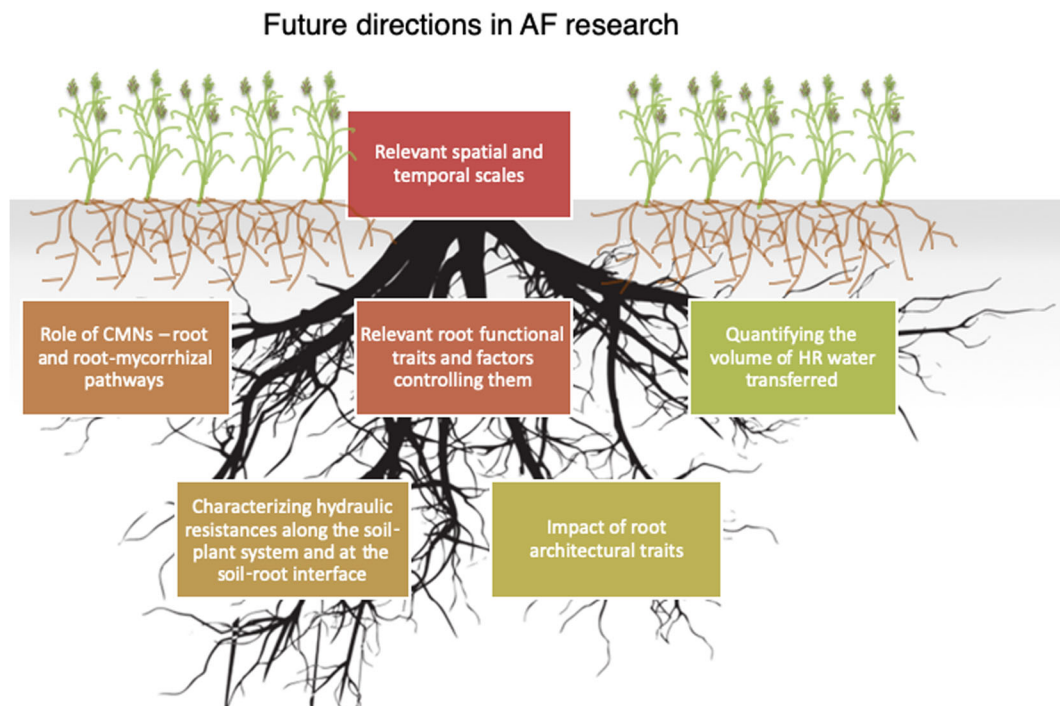


Fig. 2 Future investigation areas for water acquisition and sharing in agroforestry systems

Conclusion

This review provides an overview of our current knowledge on water acquisition and sharing mechanisms in agroforestry systems. Based on key concepts such as interspecific competition and facilitation through water transfer between plants, this paper reviews water acquisition and redistribution patterns and their potential application in agroforestry ecosystems. In promoting agroforestry as an ecologically adapted farming system for addressing environmental issues caused by intensive monoculture, the central assumption that underpinned the science and practice is that trees take up water from deep soil layers and recycle it in upper soil layers through water redistribution, thus making it available to nearby shallow rooted associated crops. Therefore, research actions have covered a range of topics including safety net hypothesis, root distribution, root functional traits, HL/redistribution and its ecological importance, hydraulically water lifted transfer between species, water source using isotopes, and modelling of relevant root parameters to inform future field-based empirical studies on water acquisition and sharing. In this sense, a better characterization of the hydraulic resistances of the soil-plant system, particularly at the soil-root interface in one hand and in another hand a better characterization of the soil system and hydraulic architectures are pivotal to improving our quantitative understanding of HL (Meunier et al. 2017). Despite clear advances, root research in mixed tree-crop agroforestry systems remains challenging because of the difficulty in finding the relevant spatial and temporal scales as well as a lack of consensus about the most relevant traits that confer a true advantage in below-ground plant competition. Other under-researched areas which equally deserve more attention to be able to design the best mixtures of tree and crop species for agroforestry practices that provide beneficial outputs both for the communities and the environment include (Fig. 2):

- Investigating and determining the controlling factors of the root functional traits;
- Clarifying and quantifying the role of common mycorrhizal networks in the mechanism of HL, including the proportion of water transferred through root-only- and root-mycorrhizal-based HL, and their importance and applications in agroforestry systems;

- Characterizing hydraulic resistances along the soil-plant system, particularly at the soil-root interface, and root hydraulic architectures to gain knowledge on the potential for water uptake and water transfer patterns in agroforestry systems;
- Quantifying the volume of water transferred to neighboring plants through HL and their species and environment, including soil type and dependence;
- Disentangling the advantages and potentially adverse effects of hydraulically redistributed water (e.g. in saline systems).

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