Forest Ecology

The effect of trees on soils

July, 2018

Ormungandr Melchizedek

BSc(Hons) Plantsmanship, P.G. Dip. Forestry (Ecology & Management), Professional Tree Inspector, TechArborA,

Awen Tree Consultancy

Arboricultural, Ecological & Horticultural Services

www.awentreeconsultancy.org

All plants are interdependent organisms which influence their growing environment in a similar manner depending on their adaptations, specialisations, needs, size and range of biotic interactions (Cesarz, et al., 2013). The significant difference between trees and other plants is that trees impact their rhizosphere over far longer periods, often over centuries and millennia (Loehle, 1988; Ulrich, 1992). Few plant species other than trees can achieve life spans of between 5,000 and 10,000 years and all of those are comprised of clonal colonies (Ally, 2008; Mackenthun, 2016; IUCN, 2018; USDAFS, 2018). When we consider how trees effect soils we must understand that their effects can occur over a range of timescales, that climate, geology and topography are very variable factors, and that different genera of trees have different needs, demands and impacts on their rhizosphere (Binkley and Giardina, 1998; Nisbet, 2005).

As some of the largest and longest lived organisms on our planet trees are the biological backbone of many terrestrial ecosystems. Trees are both ecosystem engineers and an ecosystems themselves, and some species are vital for their landscape scale ecosystem as keystone species (Munzbergova and Ward, 2002; MacKenzie, 2010; RMTRR, 2018). Trees provide us with much of our atmospheric oxygen and diverse ecosystem services such as reducing the runoff of storm water and removing airborne pollution. In our megacities these services equate to half a trillion dollars a year (Endreny et al., 2017). However, as this essay focuses on the effects of trees on soils the following discussion looks at how trees impact soil biodiversity, nutrient levels and soil processes. Also, how they reduce soil loss, facilitate infiltration and otherwise modify the soil to their needs.

Soil covers most of our planet and is the result of the biotic and abiotic weathering of organic matter (OM) and bedrock parent material. It is made up of organic and inorganic matter, atmospheric gasses, living organisms and water. Soil structure is open, comprising of aggregates of organic and inorganic matter with cracks between the aggregates and pores within the aggregates that are filled with atmospheric gases or water (Lukac and Godbold, 2011). Soil plays a major role in the nutrient and biotic cycles of our planet and provides vital ecosystem services (Smith, et al., 2015). The combinations of the above constituents, topographic circumstances and climate variations over ages (pedogenesis) have created a highly diverse range of edaphic conditions. These conditions are always changing as a result of disturbance, climate change, land use change and natural succession (Harris, et al, 1996). All soils are teaming, to varying degrees (depending largely on the levels of organic matter) with an extreme diversity of microscopic flora and fauna. Soil born organisms such as archaea, bacteria, actinomycetes, algae, protozoa, fungi and mesofauna live in symbiosis with trees, other plants and animals (Wall, 2012; Walters, 2014).

The majority of microscopic organisms are found in the top three feet of soil where the feeder roots of trees seek moisture and nutrients. Some of these soil biota are extremely helpful to plants and play a crucial role in nutrient cycling, the sequestration of carbon and in promoting plant growth (Berendsen, et al., 2012; Averill, et al., 2014; George, et al., 2017; Suz, et al., 2017). These organisms, particularly mycorrhizae and nitrogen fixing bacteria like *Frankia* sp. and *Rhizobium* sp., form direct interactions with their host trees in mutualistic interactions. Mycorrhizae form their mutualisms through mycelial bridges and nitrogen fixing bacteria through root nodules, both of these interactions are initiated by the trees (Walters, 2014).

Plants that are known to be non-mycorrhizal are uncommon (FDACS, 2018). Most angiosperm trees and the majority of other plants form mutualisms with arbuscular mycorrhizal fungi (AMF). Some tree species, mostly gymnosperms, form mutualisms with ectomycorrhizal fungi (EMF), and fewer trees form mutualisms with ericaceous mycorrhizal fungi (ERM) (Kendrick, 2000; Walters, 2014). Some EMF can break down the bones of animals and the majority also access the nutrients deposited by animal activity (Walters, 2014). In all cases nutrients are exchanged between the organisms, the mycorrhizae gain photosynthates in the form of carbohydrates and the plants gain a vastly increased and highly efficient water and nutrient acquisition network comprised of hyphae. These tree-soil biota interactions directly impact the health of the soil (Kendrick, 2000; Suz, et al., 2017).

The communities of fungal networks which interlink most plants in any established ecosystem provide countless niches for other soil born organisms which both predate upon and thrive alongside them. As such the relationship between plants and mycorrhizae is considered amongst the most important forms of biological interactions on the planet as they underpin the majority of terrestrial ecosystems (Lonsdale, et al., 2008; Koelling, 2017). Mycorrhizae tend to increase the resistance of the host trees to drought, water stress and disease, they help trees to become more vigorous and expand their root systems. This feedback loop increases the diversity of tree-soil biotic interactions which benefit soil health. Many microorganisms, including fungi and bacteria, produce cellular debris and polysaccharides which maintain and develop soil crumb structure, and facilitate the ingress of moisture and atmosphere (Morel et al., 1991; Marschner and Rengel, 2007; Bücking, et al., 2012). Mycorrhizae increase the weathering of the bedrock and act positively on the aggregation of crumb structure, impermanently binding macro-aggregates (Walters, 2014). Without trees being present in the soil the biotic activity of mycorrhizae and other soil organisms would be greatly lessened. Indeed, mycorrhizae and nitrogen fixing bacteria cannot thrive without their host plants, many of which are trees (Walters, 2014).

In expanding their root systems trees engineer soil health. Through increasing their roots trees develop soil biota populations and communities. They adapt their rhizosphere to their needs though root exudates, and while making soil nutrients more available (increasing decomposition rates, and altering soil pH) also attract additional beneficial microorganisms when under stress, both directly and indirectly suppressing soil pathogens (Berendsen, et al., 2012; Joly, et al., 2017). Mesofauna, many of which function as vectors for microbial inoculation, feed on diverse micro-organisms and OM. These tiny invertebrates are also important for the health of many soil ecosystem functions such as decomposition and the carbon cycle. They thrive of the litterfall, deadwood and rhizodeposition of trees (Seeber, et al., 2012; George, et al., 2017). As trees can live for centuries or more they have the capacity to become biotic libraries as hosts for soil biota. However, it is not just mutualist organisms that trees have to contend with over their life spans. Many soil microorganism symbioses with trees do not promote plant growth or improve their immune response. These are the parasites and commensalists. The former can involve stealth pathogenesis, for example the cambium killer *Armillaria mellea* (Honey Fungus) which overcomes and consumes healthy trees, quickly turning an otherwise healthy tree into coarse woody debris (CWD) (Lonsdale, 2009).

As with all things trees succumb to the ravages of time. Over the seasons bark, leaves and branches are dropped to the forest floor as OM. All the OM that comprises a tree over the course of its lifetime is fed back into the soil within which it grew, litterfall being the main source of nutrient return (Osman, 2013). Trees shed branches (cladoptosis) for many reasons. In so doing they relocate the energy that would otherwise be lost (Kozlowski et al., 1991). They also lose branches in high winds and ultimately (through senescence, disease and/or exposed location) fall or are consumed in place by decomposers. This woody matter, deadwood or CWD is vital for biodiversity as it provides a wide range of microhabitats. CWD is also an important slow release store of nutrients and it plays a key role in forest biogeochemical cycles (Lonsdale, et al., 2008). Macronutrients such as nitrogen, potassium, phosphorus and calcium, essential micronutrients such as magnesium and sulphur, and other elements such as carbon are locked up within the CWD (Poznanovic, et al., 2014). Saprobes, insects, worms and bacteria slowly consume and digest the CWD and the nutrients and elements move into the food-cycle. The soil fauna utilise the consumed amino acids and proteins in their bodies or otherwise excrete or deposit them through their own senescence into the soil where they become available to the feeder roots of trees and other plants (Lukac and Godbold, 2011; Kendrick, 2000).

CWD is not rich in nitrogen but it does act as a host for free-living bacteria which fix atmospheric nitrogen in the soil (Barford, et al., 2001). Large branches and fallen trees act as dams on slopes, allowing organic matter to accumulate and thereby slow down soil erosion. Standing CWD can function as a habitat for birds and mammals, and can also provide a rooting habitat for other plants e.g. functioning as a nursery environment for young trees, figure 1 (Tedersoo et al. 2003; Poznanovic, et al., 2014). Larger pieces of CWD also shade the soil from higher temperatures and create damp micro-niches for flora and fauna, almost half of which is dependent on the biomass input of CWD (Puplett, 2018). This, alongside the shade from the crown and the facilitation of water infiltration into the soil via the root system, increases dampness, slows down decomposition and shifts the soil towards being a greater carbon sink through a reduced soil respiration rate (Lukac and Godbold, 2011).

Bacteria thrive alongside trees as decomposers of OM, locking up nutrients in their cells. These organisms are predated upon by nematodes which also consume root hairs (sloughed of plant matter comprising diverse organic chemicals (rhizodeposition)) and fungal hyphae. As well as being an important food source for microorganisms rhizodeposition is also closely associated with carbon sequestration (Luyssaert, ae al., 2008; Hütsch et al., 2002; Lukac and Godbold, 2011). As trees are among the largest organisms they are central to the carbon cycle, fixing carbon into organic matter through photosynthesis, 40% of dry matter being comprised of carbon (Lambers, et al., 2008). All autotrophs, including trees, metabolize carbon into carbohydrates, proteins and fats which are very attractive to herbivores, mesofauna and saprobic fungi. These organisms are vital to the process of decomposition which transfers some of the carbon in the CWD into the soil (carbon sequestration) (Lukac and Godbold, 2011).

Figure 1: A fallen tree (Coarse Woody Debris (CWD)) across the river-formed ravine of Puck's Glen in Argyll Forest Park, Scotland. The rotting CWD provides a habitat for various plants including mosses, ferns and functions as a nursery environment for young trees. Species present on the trunk include *Vaccinium myrtillus*, *Asplenium* sp. *Blechnum* sp., *Betula* sp., *Abies* sp. and *Chamaecyparis lawsoniana*. The CWD will be teaming with bacteria, saprobes and mesofauna. When it inevitably collapses it will dam the stream, thereby creating new niches and continuing to add its slowly releasing nutrient store to the existing soil environment. Image by author, June 2018.

The root systems of trees bring the soil micro biome to life providing diverse niches for the succession of soil born microorganisms, and in so doing they facilitate the decomposition and mineralisation of their ecosystem (Suz, et al., 2014). The roots of trees and their mycorrhizal extensions modify the soil though facilitating the formation of cracks and pores in the soil crumb structure (decompaction) which has a stabilising influence on the soil environment e.g. improved drainage (Morel et al., 1991; Harris, et al., 1996; Leifheit, et al., 2014). The rhizodeposition of root exudates from roots also play a part in the formation of aggregates through their sticky mucilages which bind soil particles and provide a food source for micro organisms. Root exudates can also have neighbourhood effects on the local community of plants, promoting or retarding (allelopathy) the germination of species (Marschner and Rengel, 2007; Coder, K.D., 2011). Further to this, roots reduce soil erosion and uptake the dominant portion of water and nutrients in the local rhizosphere (Lukac and Godbold, 2011). Trees generally uptake a large percentage of available water from the soil and transpire almost all of it through their leaves. This has consequences for the local plant community, particularly during periods of water stress (Lambers, et al., 2008).

Trees intercept rain in their canopy and moisture from atmospheric humidity, much of which is evaporated back into the atmosphere. Water from the canopy does reach the soil as throughfall and stemflow, delivering with it a store of particles that were brought by the wind, both nutrients and pollution (Nisbet, 2005). The impact of this on understory trees and other plants is very variable and depends on the habitat and their adaptations (Park and Cameron, 2008). Over a life cycle trees have the capacity to deplete their rhizosphere of nutrients, in particular phosphorus and nitrogen, locking them up (limitation) in their organic matter (Menge, et al., 2012). As the lifetime of a tree increases it adapts its soil environment to its needs, altering the pH of the soil. Angiosperm trees generally increase soil pH and gymnosperms reduce it. This is due to the calcium levels in broadleaf litter being higher than that of conifers (Reich, et al., 2005).

In conclusion, the interactions between trees and their soil environment are highly complex and variable. Each tree is a complex adaptive ecosystem which provides food and habitat for diverse flora and fauna (Kozlowski, et al, 1997). All trees increase local biodiversity as they age, while simultaneously depleting the nutrient reserves in the soil (Lambers, et al., 2008). Trees augment the soil though CWD, rhizodeposition, biotic interactions and alter the soil pH through the level of leaf litter calcium depositions (Reich, et al., 2005). Their roots facilitate the ingress of water, stabilise their rhizosphere and play a major role in terrestrial nutrient cycling. Trees modify their environment to their needs, facilitate the ingress of the atmosphere into the soil, drive up biodiversity and sequester carbon (Barford, et al., 2001; Lukac and Godbold, 2011). Trees also act as propagation vectors for fungal decomposers and a host of other organisms that co-exist alongside them and within them (Walters, 2014). The trophic cascade which results from the presence of tress through biotic interactions with active mycorrhizae and bacteria in the rhizosphere is not limited to the soil and includes larger organisms such as worms, herbivores and other associates (Khaitov, et al., 2015). Trees are ecosystem engineers and therefore impact diverse soil related factors including nutrient availability, soil biota diversity, biological ecosystem resilience, ecosystem services and the biodiversity of tree dominated plant communities. Trees facilitate healthy soil ecosystems and the response of woodland or forest ecosystems to invasive species, pollution, climate change, the impacts of the timber industry (afforestation & biomass production) and habitat restoration (Harris, et al., 1996; Prescott and Vesterdal, 2013). However, we are far from a complete picture. There remain many gaps in our knowledge regarding the nature, diversity and function of tree-soil biotic interactions and the biogeochemical cycles of the soil (Smith, et al., 2015).

References

Ally, D., 2008. The Cost of longevity: Loss of sexual function in natural clones of *Populus tremuloides*." PhD, University of British Columbia, Vancouver.

Averill, C., Turner, B.L., and Finzi, A.C., 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature*, 505, 543–545.

Barford, C.C., Wofsy, S.C. Goulden, M.L., Munger, J.W., Pyle, E.H., Urbanski, S.P., Hutyra, L., Saleska, S.R., Fitzjarrald, D., and Moore, K., 2001. Factors Controlling Long- and Short-Term Sequestration of Atmospheric CO2 in a Mid-latitude Forest. *Science*. 294 (5547), 1688–1691.

Berendsen, R.L., Pieterse, C.M.J., and Bakker, P.A.H.M., 2012. The rhizosphere microbiome and plant health. *Trends in Plant Science*, 17 8, 478-486.

Binkley, D., and Giardina, C., 1998. Why do tree species affect soils? The Warp and Woof of tree-soil interactions. Biogeochemistry 42, 89-106.

Bücking, H., Liepold, E. and Ambilwade, P., 2012. The Role of the Mycorrhizal Symbiosis in Nutrient Uptake of Plants and the Regulatory Mechanisms Underlying These Transport Processes. Plant Science, Intech.

Cesarz, S., Fender, A-C., Beyer, F., Valtanen, K., Pfeiffer, B., Gansert, D., Hertel, D., Polle, A., Daniel, R., Leuschner, C., and Scheu, S., 2013. Roots from beech (Fagus sylvatica L.) and ash (Fraxinus excelsior L.) differentially affect soil microorganisms and carbon dynamics Soil Biol. Biochem., 61, 23-32.

Coder, K.D., 2011. Black Walnut Allelopathy – Tree Chemical Warfare. Warnell School of Forestry and Natural Resources, Alleopathy Series, WSFNR11-10.

Endreny, T., Santagata, R., Perna, A., Stefano, C.D., Rallo, R.F. and Ulgiati, S. 2017. Implementing and managing urban forests: a much needed conservation strategy to increase ecosystem services and urban wellbeing. *Ecological Modelling*, 360, 328-335.

FDACS (Florida Department of Agriculture and Consumer Services), 2018. Mycorrhizae. [Online] www.freshfromflorida.com Accessed 24th May, 2018.

George, P.B., Keith, A.M., Creer, S., Barrett, G.L., Lebron, I., Emmett, B.A., Robinson, D.A., Jones, D.L., 2017. Evaluation of mesofauna communities as soil quality indicators in a national-level monitoring programme. *Soil Biology and Biochemistry*, 115, 537–546.

Harris, J.A., Birch, P., and Palmer, J., 1996. Land Restoration and Reclamation. Longman Ltd., Essex.

Hütsch, B.W., Augustin, J. And Merbach, W., 2002. Plant rhizodeposition - an important source for carbon turnover in soils. *Journal of Plant Nutrition and Soil Science*, 165, 397-407.

IUCN, 2018. *Posidonia oceanica*. [Online] www.iucnredlist.org Accessed 24th May 2018.

Joly, F.-X., Milcu, A., Scherer-Lorenzen, M., Jean, L.-K., Bussotti, F., Dawud, S.M., Müller, S., Pollastrini, M., Raulund-Rasmussen, K., Vesterdal, L., Hättenschwiler, S., 2017. Tree species diversity affects decomposition through modified micro-environmental conditions across European forests. *New Phytologist*, 214, 1281-129.

Kendrick, B., 2000. The Fifth Kingdom. 3rd Ed. Focus Publishing, Massachusetts.

Khaitov, B., Patino-Ruiz, J.D., Pina, T., Schausberger, P., 2015. Interrelated effects of mycorrhiza and free-living nitrogen fixers cascade up to aboveground herbivores. *Ecology and Evolution*, 5(17), 3756-3768.

Koelling, C., (Ed), 2017. Plant Science – A Technological Perspective. Academic Pages.

Kozlowski, T., Kramer, P., and Pallardy, S., 1991. The Physiological Ecology of Woody Plants. *Academic Press*, UK.

Kozlowski, T.T., and Pallardy, S.G., 1997. Physiology of Woody Plants (2nd Ed.). Academic Press, California.

Lambers, H., Chapin III, F.S., and Pons, T.L., 2008. Plant Physiological Ecology, 2nd (Ed). Springer, New York.

Leifheit, E.F, Veresoglou, S.D., Lehmann, A., Morris, K.E. and Rillig M.C., 2014. Multiple factors influence the role of arbuscular mycorrhizal fungi in soil aggregation—a meta-analysis. *Plant and Soil*, Vol. 374 (1–2), 523–537.

Loehle, C., 1988. Tree life history strategies: the role of defenses. *Canadian Journal of Forest Research*, Vol. 18 (2), 209-222.

Lonsdale, D., Pautasso, M., and Holdenrieder, O., 2008. Wood-decaying fungi in the forest: conservation needs and management options. *European Journal of Forest Research*, 127, 1-22.

Lonsdale, D., 2009. Principles of Tree Hazard Assessment and Management. Research for Amenity Trees No.7. Forestry Commission, Stonehouse.

Lukac, M., and Godbold, D.L., 2011. Soil Ecology in Northern Forests. A Belowground View of a Changing World. Cambridge University Press, Cambridge.

Luyssaert, S., Schulze, E.D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais. P. and Grace, J., 2008. Old-growth forests as global carbon sinks. *Nature*, 455 (7210), 213–215.

Mackenthun, G.L., 2016. The world's oldest living tree discovered in Sweden? A critical review. *New Journal of Botany*, 5 (3), 200-204.

MacKenzie, N.A, 2010. Ecology, conservation and management of Aspen. A Literature Review. Scottish Native Woods (Aberfeldy).

Marschner, P. and Rengel, Z., Eds., 2007. Nutrient Cycling in Terrestrial Ecosystems. *Springer-Verlag*, Berlin Heidelberg.

Menge, D.N.L, Hedin, L., and Pacala, S.W., 2012. Nitrogen and Phosphorus Limitation over Long-Term Ecosystem Development in Terrestrial Ecosystems. PLoS One, 7(8), e42045.

Morel, J.L, Habib, L., Plantureux, S., and Guckert, A., 1991. Influence of maize root mucilage on soil aggregate stability. *Plant and Soil*, 136, 111–119.

Munzbergova, Z. and Ward, D., 2002. Acacia Trees as Keystone Species in Negev Desert Ecosystems. *Journal of Vegetation Science,* 13 (2), 227-236.

Nisbet, T., 2005. Water Use by Trees. Forestry Commission, Information Note FCIN065.

Osman, K.T., 2013. Nutrient Dynamics in Forest Soil. In: Forest Soils. Springer, Cham.

Park, A., and Cameron, J.L., 2008. The influence of canopy traits on throughfall and stemflow in five tropical trees growing in a Panamanian plantation. Forest Ecology and Management, 255, 5–6, 1915-1925.

Prescott C.E. and Vesterdal L., 2013. Tree species effects on soils in temperate and boreal forests: emerging themes and research needs. *Forest Ecology and Management*, 1-3.

Poznanovic, S.K., Lilleskov, E.A., and Webster, C.R., 2014. Sharing rotting wood in the shade: ectomycorrhizal communities of co-occurring birch and hemlock seedlings.Mycorrhiza, 25(2), 153-164.

Puplett, D., 2018. Ecological Features of the Caledonian Forest - Dead Wood. [Online] www.treesforlife.org.uk/forest/dead-wood/ Accessed June 10th 2018.

Reich, P.B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M. et al., 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. *Ecology Letters*, 8, 811–818.

RMTRR (Rocky Mountain Tree-Ring Research), 2018. OLDLIST, A Database Of Old Trees. [Online] www.rmtrr.org/oldlist.htm Accessed 26th May 2018.

Seeber, J., Rief, A., Richter, A., Traugott, M., and Bahn, M., 2012. Drought-induced reduction in uptake of recently photosynthesized carbon by springtails and mites in alpine grassland. *Soil Biology & Biochemistry*, 55, 37–39

Smith, P., Cotrufo, M., Rumpel, C., Paustian, K., Kuikman, P., Elliott, J., Mcdowell, R., Griffiths, R., Asakawa, S., Bustamante, M., House, J., Sobocká, J., Harper, R., Pan, G., West, P., Gerber, J., Clark, J., Adhya, T., Scholes, R., Scholes, M., 2015. Biogeochemical cycles and biodiversity as key drivers of ecosystem services provided by soils. *Soil*, 1 (2), pp.665-685.

Suz, L.M., Barsoum, N., Benham, S., Dietrich, H.P., Fetzer, K.D., Fischer, R., García, P., Gehrman, J., Kristöfel, F., Manninger, M., Neagu, S., Nicolas, M., Oldenburger, J., Raspe, S., Sánchez, G., Schröck, H.W., Schubert, A., Verheyen, K., Verstraeten, A., Bidartondo M.I, 2014. Environmental drivers of ectomycorrhizal communities in Europe's temperate oak forests. *Molecular Ecology*, 23, 5628–5644.

Suz, L.M., Kallow, S., Reed, K., Bidartondo, M.I. and Barsoum, N., 2017. Pine mycorrhizal communities in pure and mixed pine-oak forests: Abiotic environment trumps neighbouring oak host effects. *Forest Ecology and Management*, 406, 370-380.

Tedersoo, L., Kõljalg, U., Hallenberg, N., Larsson, K.H., 2003. Fine scale distribution of ectomycorrhizal fungi and roots across substrate layers including coarse woody debris in a mixed forest. *New Phytologist*, 159, 153–165.

Ulrich, G., 1992. Forest ecosystem theory based on material balance. *Ecological Modelling*, 63, pp. 163-183

USDAFS (United States Department of Agriculture Forestry Service), 2018. Pando - (I Spread). [Online] www.fs.usda.gov Accessed 24th May 2018

Wall, D. (Ed), 2012. Soil Ecology and Ecosystem Services. Oxford University Press, UK.

Walters, D., 2014. Lectures on mycorrhizal fungi, N fixing bacteria and plant-microbe chemical signalling. Module No. C290-4Z/001, Plant Biotic Interactions, Scottish Agricultural College, Kings Buildings, 2014.