Theme: Radiata Site Productivity

Task No: F60107
Milestone Number: 1.07.7

Report No. FFR- RSP-003

Tree Species Effect on Soil Carbon – A Review

Authors:
L G Garrett, P W Clinton, M R Davis, H S Jones

Research Provider:
Scion

Date: June 2011

Leadership in forest and environment management, innovation and research

TABLE OF CONTENTS

EXECUTIVE SUMMARY

Forest soils contain about 30% of the terrestrial carbon pool and have a great capacity to store C. The utilisation and management of the soil C sink can contribute to off-setting greenhouse gas emissions, in addition to enhancing productivity and environmental benefits. Understanding the effects of different tree species on soil C dynamics is important for the management and enhancement of soil C sequestration in production forests. This review summarises our current understanding of the effects of tree species on soil organic carbon (SOC) dynamics, and factors contributing to differences in SOC sequestration. Forest soils are important to the cycling and long-term storage of C and nutrients. Tree species can influence soil C through differences in canopy structure, which influences soil environmental conditions, and through quantity and quality of organic matter inputs from above-ground and below-ground sources, which then influence the soil communities that decompose the organic matter. Studies have identified tree species as a factor in determining SOC stocks. However, very few studies in the international literature provide a direct comparison of tree species effects. Information on the effect of tree species on SOC dynamics in production forest systems, particularly in New Zealand, is very limited. Based on the limited number of studies, there appears to be potential to select tree species based on their litter input characteristics and differences in litter quality to increase SOC sequestration. There is a need for further research into the effects of tree species on soil C in order to better understand and manage soil C sequestration within production forests in New Zealand. Scion is installing new trials within the Protecting and Enhancing the Environment through Forestry (PEEF) programme that will allow further investigation of the effect of tree species on SOC dynamics.

INTRODUCTION

Forest soils are important for carbon (C) storage, and contain about 30% of the terrestrial C [1]. Soil C has received recent research attention in New Zealand (and globally) because of climate change mitigation strategies. New Zealand is obligated under the Kyoto Protocol and the United Nations Framework Convention on Climate Change to report on C stocks and changes in five pools, including soil, consistent with the Intergovernmental Panel on Climate Change Good Practice Guidance for Land Use, Land-Use Change and Forestry [2]. Knowledge of the factors controlling soil C storage and dynamics is essential for understanding the changing global C cycle, as a small change in the soil C stock can result in large turnover of soil C and subsequent release of respired CO_2 to the atmosphere [1, 3]. The benefits of enhanced soil C sequestration go beyond off-setting greenhouse gas emissions because SOC, as a major component of soil organic matter, has a key role in the long-term cycling of plant nutrients essential for sustaining forest productivity [4]. Moreover, soil organic matter is central to environmental quality as it influences soil structure, aeration, water storage and infiltration, and resistance to soil erosion and compaction.

Soil C stocks and dynamics in a forest are dependent on a number of factors including abiotic conditions (climate, topography, and soil type), tree species, and land management [1]. Soil C is generally greatest in the top 30 cm of soil profiles [4], but is also present at greater depths [5, 6] and is made up of organic and inorganic C sources. The latter are inherited from the soil parent material (e.g. limestone), or forms as calcium carbonate in semi-arid and arid soils, and is negligible in most New Zealand soils, whereas soil organic C (SOC) is influenced by organic biomass inputs and losses through decomposition. The formation and dynamics of SOC involve a range of complex biological, chemical, and physical properties and processes, and can be changed by the factors that influence SOC development and stability [4].

Managed planted forests in New Zealand cover 1.74 million hectares and are dominated by *Pinus radiata* (90% of the planted forest area), followed by Douglas-fir *(Pseudotsuga menziesii)* (6%) and other minor species (cypress species, eucalyptus species, and other softwoods and hardwoods) [7]. Forested landscapes comprise an important part of national soil C stocks, and the effects of different tree species on SOC dynamics are of interest to New Zealand. Although radiata pine dominates the planted forest estate, alternative species are becoming increasingly important, and it is likely that a wider range of species may be planted in response to global climate change. However there is very limited information on the effects of tree species in New Zealand on SOC. New trials are being installed within the current PEEF programme that will allow further study of the effect of tree species on SOC dynamics.

Most New Zealand research relates to afforestation studies involving *P. radiata* [8, 9]. Information from comparisons of tree species at one site is particularly limited [10]. Different tree species are known to influence SOC dynamics, stocks and the vertical distribution of SOC in the soil profile due to differences in organic C inputs to the soil and associated soil communities that decompose soil organic matter [11]. Studies of the influence of tree species on SOC have been included in reviews of species influences on general soil properties or forest management influences on SOC [3, 12-17], but there have been no reviews focussed on the influence of tree species on SOC stocks.

Understanding how different tree species affect the size and dynamics of the SOC pool is important in predicting how SOC will respond to land use or tree species change. This will improve the utilisation and management of the soil C pool to contribute towards off-setting greenhouse gas emissions, in addition to enhanced productivity and environmental benefits. The objective of this review is to consider the impact of tree species on the processes involved in forest SOC dynamics and resulting SOC stocks. We review New Zealand-based studies and circumstances where possible. However, we also use results of international studies because few relevant studies have been undertaken in New Zealand.

TREE SPECIES AND SOIL CARBON

The soil C pool in forested ecosystems represents the balance between organic matter inputs from live biomass production, and decomposition and loss from the soil. This equilibrium is controlled by various external factors including climate, topography, soil type, tree species, natural disturbances, land management activities [1, 3] and past land use [13, 14, 18] interacting over time. An understanding of the factors controlling SOC dynamics in forest soils is important for understanding and seeking to enhance SOC sequestration. For example, mineral soil type (particularly clay content) can have a significant role in determining SOC stocks. Clay-rich soils (>33% clay) have a greater capacity to accumulate SOC than soils with a lower clay content (<33% clay) [13]. Tree species influence SOC in a number of ways and a range of complex biological, chemical, and physical properties and processes are involved. For example, different forested ecosystems vary in their canopy characteristics and can have a considerable impact on water yield, soil environments, or microclimates [17, 19-21], which can in turn influence soil microbial communities and SOC decomposition [16]. Unravelling how tree species impact on SOC requires an understanding of the SOC sources and dynamics.

Soil Carbon Sources and Dynamics

Soil organic C sequestration occurs when the inputs of organic C are greater than the release of C through decomposition and respiration. Differences in SOC stocks under different tree species may relate to differences in the quantity and quality of organic matter inputs to the mineral soil either via the forest floor or directly to the soil through root turnover.

Above-ground

The quantity and quality of litter fall, including additions of branches and coarse woody debris which can be a long-term source of C and nutrients to the soil, varies with tree species [22, 23]. One study specifically established to look at the effects of site and species on forest floor dynamics was established in 1964-65 in Denmark [24]. Thirty years after these trials were established on seven sites, Verterdal and Rauland-Rasmussen [24] compared build-up of forest floor organic matter for seven species (*Fagus sylvatica, Quercus robur, Picea abies, Picea sitchensis, Pseudotsuga menziesii, Abies grandis, Pinus contorta*) along a soil fertility gradient. The results suggested that species choice was important in determining C storage and immobilisation of nutrients in the forest floor. There was a nearly four-fold difference in the forest floor mass between species, ranging from less than 5 t/ha for *Q. robur* to nearly 20 t/ha for *P. contorta*. They also found that forest floor C stocks under the same species were different among sites, with a decrease in forest floor C stocks with increasing mineral soil nutrient status. Tree species effects on forest floor C stocks can be rapid [3], and the forest litter chemistry (quality) and conditions created by the litter of different tree species have the most direct influence on decomposition rates [16, 24].

Forest floor C stocks are commonly observed to be greater under pine species than under deciduous tree species [3]. This can be attributed to the slower decay of conifer litter as a result of conifers having more recalcitrant chemical components (lignin) in the litter that are difficult to decompose [25], and a more nutrient-poor litter [17]. The varying quality of litter from different species has been discussed by Royer-Tardif and Bradley [26]. In their example, jack pine (*Pinus banksiana*) is considered to have poor litter quality relative to aspen (*Populus tremuloides*) (Table 1). Under jack pine there is a build up of litter with no humus horizon, and the litter is characterised by a lower pH, and higher C:N and fungi:bacteria ratios than litter under aspen. These different types of litter are known as mor and mull litter respectively.

Table 1: Litter quality under jack Pine and aspen from Royer-Tardif and Bradley [26].

	Jack Pine	Aspen
Humus type	mor	mull
F horizon depth (cm)	3-4.5	2
H horizon depth (cm)	0	3
Fungal:Bacteria	large	low
pH	4.0	5.0
C:N	30	20
Litter quality	low	good

F = fragmented litter
H = humus

The incorporation of organic C into the mineral soil can be via physical mixing caused by soil fauna [16] or via the translocation of organic matter or organic compounds (dissolved organic C, or water soluble organic C), or both [27]. Increased activity of soil fauna stimulates the transfer of organic matter to deeper soil layers where it may become stabilised (e.g., in earthworm casts) [28]. Effects of tree species on soil faunal activity [17] could be related to the litter quality and decomposition environment created by the litter. For example, with broadleaf tree species there is more biological activity than with conifer tree species, therefore more fragmentation and humification of the fragmented litter material, resulting in thinner F horizons and thicker H horizons [29].

Below-ground

Carbon inputs to the mineral soil from below-ground sources can be significant and come from dead roots and root exudates [30, 31]. Roots make a significant contribution to the live biomass of trees, with estimated root:shoot ratios varying between 18% and 32% among forested biomes (boreal, temperate and tropical forests) [30]. In temperate forests root:shoot ratios were estimated to average 18% for coniferous species and 23% for deciduous species [30]. This compares well with the estimated value for *P. radiata* of 20% [32]. Rooting depth distributions vary with forest type; for example, boreal forests can have 80–90% of their roots in the top 30 cm of soil, whereas temperate coniferous forests and temperate deciduous forests have only 52% and 65% respectively of their roots in the upper 30 cm of soil [30]. This effect may, to some extent, be due to physical barriers to growth rather than being related to tree species — permafrost restricts rooting depth in some boreal forests, while water-logging and poor aeration, and physical resistance to root penetration can also restrict rooting depth [30]. Rooting depths can be substantial where barriers are absent; for example *P. radiata* roots can extend to depths of 5 m or more [32] indicating that there is potential for C sequestration in deeper soil horizons with deep-rooting tree species.

Root size distribution differs with tree age [32] and tree species, particularly in fine root (≤2 mm diameter) distribution and turnover [33]. Fine roots are a significant C pool that varies (by amount and depth range) with tree species. Their small diameter, fast turnover rate, and rapid decomposition (in comparison to woody biomass), means that fine roots are disproportionally important in below-ground C inputs to the mineral soil [31]. Higher fine root production in broadleaf tree species (compared to coniferous species) was significantly correlated with higher SOC stocks.[34]. Tree species with fine root microflora associations (N-fixing tree species) have shown a larger effect on forest soil than other species due to nitrogen inputs which result in higher SOC stocks [35]. The increase in SOC from N-fixing tree species results from the greater accumulation of new SOC and reduced decomposition of old SOC [35-37].

Soil Communities

Microbial biomass is generally accepted to make up less than 5% of the SOC, and the activity of this biomass controls the decomposition of soil organic matter inputs [38]. The cycling of microbial biomass may play a key role in developing and increasing soil organic matter [38]. Tree species are an important factor influencing the soil microbial biomass and composition through differences in the quality of organic matter inputs, which alters the processing of the soil organic matter by soil communities [4, 24, 39]. Microbial composition has been shown to differ between conifer and broadleaved species [40]. Litter quality differences have resulted in differences in the soil community involved in soil organic matter decomposition [24].

SOC Stabilisation and Protection

The processes of organic C decomposition can take from days to centuries [4, 10]. The quality of organic inputs from different tree species influences residence time, chemical stablisation, and protection of SOC [41, 42]. For example, Laganaière et al. [41] found tree species differences in the light fraction SOC, the uncomplexed SOC, and silt and clay SOC pools. The whole SOC pool was greater under black spruce than under aspen (46.3 vs 34.7 tC/ha, respectively). However, a higher proportion of the SOC stock under aspen was chemically protected within silt and clay C pools. The higher SOC stocks under black spruce were caused by the poor quality litter of the black spruce and an increase in the uncomplexed organic matter compared to aspen, but was also due to environmental constraints to decomposition found in these forests.

It is known that the litter from different tree species can influence the acidity of the soil [43], and in more acid soils greater C complexation with aluminium can occur, leading to SOC "protection" [44, 45]. Moreover, the turnover time of SOC increases with increased soil depth, as subsoil SOC is chemically and physically stabilised [46]. These effects can persist long after conversion into another land use [18, 44, 45], and have important implications for SOC stocks.

Soil Carbon Stocks

Tree species differ in their organic C inputs (quantity and quality) to the soil and in their effects on soil processes, C stability, and depth distribution in the soil. Therefore the resulting SOC stocks would be expected to be different with different tree species [1]. Soil organic carbon stocks have been observed to vary with forest biome, with boreal forests containing more SOC stocks than temperate forests [1]. In addition differences between tree groups (e.g. coniferous and broadleaf) have been observed and considered important in determining SOC stocks, but there is no consensus on the specific effects of coniferous or broadleaf tree species on SOC. For example, Schulp et al. [29] found higher SOC stocks (0–20 cm soil depth) under coniferous forests (76.44 tC/ha) than under broadleaved forests (67.45 tC/ha) (approximately 60 years of age). This trend was also reported by Laganière et al. [41], with higher SOC stocks under black spruce (46.3 tC/ha) than under aspen (34.7 tC/ha) (0–15 cm soil depth). However, the opposite has also been observed. Wang et al. [34] found SOC stocks in the top soil (0–10 cm) under *Pinus massoniana* were lower than (29.2 tC/ha) under broadleaf tree species (*Castanopsis hystrix, Michelia macclurei, and Mytilaria laosensis*) (32.6–34.9 tC/ha), but at greater depths (10–30 cm) SOC stocks were similar. A review by Jandl et al. [3], noted that the effects of tree species on SOC stocks were variable.

There are considerably more studies on the effect of afforestation, as opposed to long-term plantations, on SOC stocks, and these studies may offer greater comparisons of the effect of tree species. Some meta-analyses and reviews of SOC stock assessments with afforestation have been undertaken that show tree species is an important factor in determining SOC stocks [12-14]. In the upper soil (<10 or <30 cm), amounts of SOC increased with afforestation under hardwoods and softwoods, yet changed little under eucalypts and decreased under radiata pine[14]. In a meta analysis pine plantations were observed to reduce SOC stocks by 12–15% with no effect from planting deciduous species[12]. A more recent meta-analysis suggested that when the forest floor

layer (surface organic layer) was considered in the SOC stocks, pine species would have the potential to sequester SOC with a 12% increase with afforestation compared to agricultural soil [13]. The same meta-analysis found broadleaf (excluding *Eucalyptus*) tree species had a greater capacity to accumulate SOC than coniferous trees (excluding *Pinus*) (25% and 2% increase with afforestation, respectively) and *Eucalyptus* increased SOC stocks by approximately 12% with afforestation. [13]

More specific tree species effects on SOC are observed with N-fixing tree species which have a larger effect on soil C than other species and have higher SOC stocks [35, 37, 47]. For example, an afforestation study in Australia found that an N-fixing tree species (*Acacia mearnsii*) accumulated SOC with mean rates that varied from 0.8 to 1.6 tC/ha/year more than a non-N-fixing tree species (*E. melliodora*) [47].

New Zealand Afforestation Research

Paired site studies of afforestation of grassland in New Zealand indicate that SOC stocks (0–30 cm soil depth) under *P. radiata* 10 years old and older are on average 8.5 t/C/ha lower than under grassland. In contrast, limited data for other species suggest there may be a slight gain (1.6 tC/ha) under plantations ten years of age or older. However, the variation in the data was high and the authors concluded that the evidence for the difference between *P. radiata* and other species being real was weak [9].

In the only direct comparison of the influence of tree species on SOC in New Zealand, Huang et al. [10], measured SOC mass in the soil total, light and heavy fractions (separated by density fractionation) in the first 10 years after afforestation of grassland with *Eucalyptus nitens*, *Pinus radiata* and *Cupressus macrocarpa*. Although there were differences between species in individual soil layers, cumulatively, for the full 0–30 cm depth, there was no significant effect of sampling year or tree species on SOC in the whole soil up to age 10. Analysis of separate fractions suggested that C mass in the soil heavy fraction remained stable, but the C mass in the light fraction decreased at year 5 under the three species. Soil $\delta^{13}C$ analysis showed that the decrease in the light fraction may have been due to reduced C inputs from grassland species. After the initial reduction, the recovery of SOC in the light fraction depended on tree species. At year 10, an increase of 33% in light fraction SOC was observed at the 0–30 cm depth under *E. nitens*, compared to that under the original grassland (year 0). Planting *P. radiata* restored light fraction SOC to the original level under grassland, whereas planting *C. macrocarpa* led to a decrease of 33%. The authors concluded that the increase of light fraction SOC between years 5 and 10 was most likely due to C input from tree residues. Most of the increased C was derived from root turnover under pine and from both root and leaf turnover under *E. nitens*, as indicated by plant C biomarkers such as lignin-derived phenols and suberin- and cutin-derived compounds in the 0–5 cm soil layer [10].

From the international afforestation studies, broadleaf tree species typically had higher SOC stocks than coniferous species, and N-fixing tree species sequester more SOC than other tree species. However, predicting how tree species affect SOC stocks in planted forests beyond the first rotation is an area in which further work is required.

Looking Ahead

The selection of tree species in the management of planted forests involving afforestation and reforestation has important implications on the SOC pool and dynamics. Selecting for a tree species that promotes greater SOC sequestration and higher SOC stocks has the potential to greatly alter the SOC pool [13, 16]. For example, selecting for tree species or genotypes with larger root systems and higher fine root turnover could greatly increase the inputs and retention of C to the SOC pool. Moreover, SOC stocks and SOC residence times may be increased by selecting for tree species with higher litter quality and greater litter incorporation into the soil. However, a lot of uncertainty about the effects of tree species on SOC stocks remains. Consequently, more targeted, long-term research is needed to better understand the mechanisms by which tree species effect SOC sequestration and SOC stocks, especially across sites with diverse characteristics and management practices.

SUMMARY AND CONCLUSIONS

Tree species affect forest SOC via differences in the quantity and quality of organic C inputs to the soil and receiving soil communities, which in turn affect SOC sequestration and stability. Variation in the organic C inputs associated with different tree species changes the soil microbial community structure and function, which influences decomposition, respiration and SOC residence time.

Broad forest types (e.g. broadleaf forests), rather than individual species were often referred to in the literature when discussing effects on SOC. This may be because considerable uncertainty remains regarding the potential response of SOC dynamics to individual tree species. Typically broadleaf tree species have higher SOC stocks than coniferous species, and N-fixing tree species sequester more SOC than other tree species.

These findings suggest that tree species selection in forest management could have substantial consequences for SOC stocks and therefore the soil C pool contributing towards off-setting greenhouse gas emissions, productivity and environmental benefits. The selection of tree species or genotypes with larger root systems and higher fine root turnover could greatly increase the inputs and retention of C to the SOC pool. Moreover, SOC stocks and SOC residence times may be increased by selecting for tree species with higher litter quality and greater litter incorporation into the soil.

With increasing focus on managing SOC sinks in forests, a greater understanding of the effects of tree species on SOC sequestration is needed, with specifically designed trials for tree species comparisons on SOC stocks. New trials being installed in the current PEEF programme will allow further study of the effect of tree species on SOC dynamics.

ACKNOWLEDGEMENTS

REFERENCES

1. Lal, R., *Forest soils and carbon sequestration.* Forest Ecology and Management, *220* (1-3), pp. 242-258. (2005).

2. IPCC, *Intergovernmental Panel on Climate Change. Good Practice Guidance for Land Use, Land-use Change and Forestry*: The Intergovernmental Panel on Climate Change (IPCC), Japan. (2003).

3. Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkkinen, K., and Byrne, K.A., *How strongly can forest management influence soil carbon sequestration?* Geoderma, *137* (3-4), pp. 253-268. (2007).

4. Condron, L.M., Starks, C., O'Callaghan, M., Clinton, P.W., and Huang, Z., *The role of microbial communities in the formation and decomposition of soil organic matter.* In G.R. Dixon and E.L. Tilston (Eds.), In Soil microbiology and Sustainable Crop Production: Springer Science publication. (2010).

5. Canary, J.D., Harrison, R.B., Compton, J.E., and Chappell, H.N., *Additional carbon sequestration following repeated urea fertilization of second-growth Douglas-fir stands in western Washington.* Forest Ecology and Management, *138* (1-3), pp. 225-232. (2000).

6. Oliver, G.R., Beets, P.N., Garrett, L.G., Pearce, S.H., Kimberly, M.O., Ford-Robertson, J.B., and Robertson, K.A., *Variation in soil carbon in pine plantations and implications for monitoring soil carbon stocks in relation to land-use change and forest site management in New Zealand.* Forest Ecology and Management, *203* (1-3), pp. 283-295. (2004).

7. MAF, *A National Exotic Forest Description as at 1.April 2009*: Ministry of Agriculture and Forestry, Wellington. 64 pp. (2010).

8. Davis, M.R., and Condron, L.M., *Impact of grassland afforestation on soil carbon in New Zealand: A review of paired-site studies.* Australian Journal of Soil Research, *40* (4), pp. 675-690. (2002).

9. Baisden, W.T., Beets, P.N., Davis, M., Wilde, R.H., Arnold, G., and Trotter, C.M., *Changes in New Zealand's soil carbon stocks following afforestation of pastures.* Palmerston North: Landcare Research New Zealand Ltd and New Zealand Forest Research Institute Ltd. (2006).

10. Huang, Z., Davis, M.R., Condron, L.M., and Clinton, P.W., *Soil carbon pools, plant biomarkers and mean carbon residence time after afforestation of grassland with three tree species.* Soil Biology and Biochemistry, *43* (6), pp. 1341-1349. (2011).

11. Binkley, D. (Eds.), *The influence of tree species on forest soils: Processes and patterns.* The influence of tree species on forest soils: Processes and patterns. Agronomy Society of New Zealand Special Publication #10, Lincoln University Press, Canterbury, New Zealand. (1995).

12. Guo, L.B., and Gifford, R.M., *Soil carbon stocks and land use change: A meta analysis.* Global Change Biology, *8* (4), pp. 345-360. (2002).

13. Laganière, J., Angers, D.A., and Parè, D., *Carbon accumulation in agricultural soils after afforestation: a meta-analysis.* 439-453. Blackwell Publishing Ltd. (2010).

14. Paul, K.I., Polglase, P.J., Nyakuengama, J.G., and Khanna, P.K., *Change in soil carbon following afforestation.* Forest Ecology and Management, *168* (1-3), pp. 241-257. (2002).

15. Post, W.M., and Kwon, K.C., *Soil carbon sequestration and land-use change: Processes and potential.* Global Change Biology, *6* (3), pp. 317-327. (2000).

16. Prescott, C., *Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils?* Biogeochemistry, *101* (1), pp. 133-149. (2010).

17. Augusto, L., Ranger, J., Binkley, D., and Rothe, A., *Impact of several common tree species of European temperate forests on soil fertility.* Ann. For. Sci., *59* (3), pp. 233-253. (2002).

18. Beets, P.N., Oliver, G.R., and Clinton, P.W., *Soil carbon protection in podocarp/hardwood forest, and effects of conversion to pasture and exotic pine forest.* Environmental Pollution, *116*, pp. S63-S73. (2002).

19. Beets, P.N., and Oliver, G.R., *Water use by managed stands of Pinus radiata, indigenous podocarp/hardwood forests, and imporved pasture in the central North Island of New Zealand.* New Zealand Journal of Forestry Science, *32* (2), pp. 306-323. (2007).

20. Chapin, F.S., *Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change.* Annals of Botany, *91*, pp. 455-463. (2003).

21. Prescott, C.E., *The influence of the forest canopy on nutrient cycling.* Tree Physiology, *22* (15-16), pp. 1193-1200. (2002).

22. Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., and Cummins, K.W., *Ecology of coarse woody debris in temperate ecosystems.* Advances in Ecological Research, *15*, pp. 133-302. (1986).

23. Binkley, D., and Giardina, C., *Why do Tree Species Affect Soils? The Warp and Woof of Tree-soil Interactions.* Biogeochemistry, *42* (1), pp. 89-106. (1998).

24. Vesterdal, L., and Raulund-Rasmussen, K., *Forest floor chemistry under seven tree species along a soil fertility gradient.* Canadian Journal of Forest Research, *28* (11), pp. 1636-1647. (1998).

25. Berg, B., *Litter decomposition and organic matter turnover in northern forest soils.* Forest Ecology and Management, *133* (1-2), pp. 13-22. (2000).

26. Royer-Tardif, S., and Bradley, R., *Forest floor properties across sharp compositional boundaries separating trembling aspen and jack pine stands in the southern boreal forest.* Plant and Soil, pp. 1-12. (2011).

27. Sollins, P., Homann, P., and Caldwell, B.A., *Stabilization and destabilization of soil organic matter: mechanisms and controls.* Geoderma, *74* (1-2), pp. 65-105. (1996).

28. Lorenz, K., Lal, R., and Donald, L.S., *The Depth Distribution of Soil Organic Carbon in Relation to Land Use and Management and the Potential of Carbon Sequestration in Subsoil Horizons.* In Advances in Agronomy (Vol. 88, pp. 35-66): Academic Press. (2005).

29. Schulp, C.J.E., Nabuurs, G.-J., Verburg, P.H., and de Waal, R.W., *Effect of tree species on carbon stocks in forest floor and mineral soil and implications for soil carbon inventories.* Forest Ecology and Management, *256* (3), pp. 482-490. (2008).

30. Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., and Schulze, E.D., *A global analysis of root distributions for terrestrial biomes.* Oecologia, *108*, pp. 389-411. (1996).

31.   Jackson, R.B., Mooney, H.A., and Schulze, E.-D., *A global budget for fine root biomass, surface area, and nutrient contents.* Proceedings of the National Academy of Sciences, *94* (14), pp. 7362-7366. (1997).

32.   Beets, P.N., Pearce, S.H., Oliver, G.R., and Clinton, P.W., *Root/shoot ratios for deriving below-ground biomass of Pinus radiata stands.* New Zealand Journal of Forestry Science, *37* (2), pp. 267-288 (2007).

33.   Yuan, Z.Y., and Chen, H.Y.H., *Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: Literature review and meta-analyses.* Critical Reviews in Plant Sciences, *29* (4), pp. 204-221. (2010).

34.   Wang, H., Liu, S.-R., Mo, J.-M., Wang, J.-X., Makeschin, F., and Wolff, M., *Soil organic carbon stock and chemical composition in four plantations of indigenous tree species in subtropical China.* Ecological Research, *25* (6), pp. 1071-1079. (2010).

35.   Binkley, D., *How Nitrogen-fixing trees change soil carbon.* In D. Binkley and O. Menyailo (Eds.), In Tree Species Effects on Soils: Implications for Global Change NATO Science Series, Kluwer Academic Publishers, Dordrecht. . (2005).

36.   Kaye, J.P., Resh, S.C., Kaye, M.W., and Chimner, R.A., *Nutrient and carbon dynamics in a replacement series of Eucalyptus and Albizia trees.* Ecology, *81* (12), pp. 3267-3273. (2000).

37.   Resh, S.C., Binkley, D., and Parrotta, J.A., *Greater soil carbon sequestration under nitrogen-fixing trees compared with Eucalyptus species.* Ecosystems, *5* (3), pp. 217-231. (2002).

38.   Condron, L.M., Starks, C., O'Callaghan, M., Clinton, P.W., and Huang, Z., *The role of microbial communities in the formation and decomposition of soil organic matter.* In G.R. Dixon and E.L. Tilston (Eds.), In Soil microbiology and Sustainable Crop Production: Springer Science publication. (2009).

39.   Grandy, A.S., Strickland, M.S., Lauber, C.L., Bradford, M.A., and Fierer, N., *The influence of microbial communities, management, and soil texture on soil organic matter chemistry.* Geoderma, *150* (3-4), pp. 278-286. (2009).

40.   Ushio, M., Wagai, R., Balser, T.C., and Kitayama, K., *Variations in the soil microbial community composition of a tropical montane forest ecosystem: Does tree species matter?* Soil Biology and Biochemistry, *40* (10), pp. 2699-2702. (2008).

41.   Laganière, J., Angers, D.A., Pare, D., Yves, B., and Chen, H.Y.H., *Black Spruce Soils Accumulate More Uncomplexed Organic Matter than Aspen Soils.* Soil Science Society of America Journal, *75* (3), pp. 1125-1132. (2011).

42.   Hobbie, S., Ogdahl, M., Chorover, J., Chadwick, O., Oleksyn, J., Zytkowiak, R., and Reich, P., *Tree Species Effects on Soil Organic Matter Dynamics: The Role of Soil Cation Composition.* Ecosystems, *10* (6), pp. 999-1018. (2007).

43.   Ovington, J.D., and Madgwick, H.A.I., *AFFORESTATION AND SOIL REACTION.* European Journal of Soil Science, *8* (1), pp. 141-149. (1957).

44.   Beets, P.N., Oliver, G.R., and Clinton, P.W., *Soil carbon protection in podocarp/hardwood forest, and effects of conversion to pasture and exotic pine forest.* Environmental Pollution, *116* (SUPPL. 1), pp. S63-S73. (2002).

45. Meder, R., Beets, P.N., and Oliver, G.R., *Multivariate analysis of IR, NIR, and NMR spectra of soil samples from different land use conversions: native forest, pasture, and plantation forest.* New Zealand Journal of Forestry Science, *37* (2), pp. 289-305. (2007).

46. Lorenz, K., Lal, R., and Shipitalo, M.J., *Stabilized Soil Organic Carbon Pools in Subsoils under Forest Are Potential Sinks for Atmospheric CO$_2$.* Forest Science, *57* (1), pp. 19-25. (2011).

47. Kasel, S., Singh, S., Sanders, G.J., and Bennett, L.T., *Species-specific effects of native trees on soil organic carbon in biodiverse plantings across north-central Victoria, Australia.* Geoderma, *161* (1-2), pp. 95-106. (2011).