

EFFECTS OF SPECIES MIXTURES ON FINE ROOT PRODUCTION IN A YOUNG
BOREAL FOREST

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Major Advisor

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ABSTRACT

1. Fine roots (< 2 mm) play a key role in terrestrial ecosystem processes. Species diversity loss has been recognized as one of the primary global change drivers that can have profound negative effects on ecosystem functionality and services to humanity. However, our understanding of the effects of plant diversity on fine root production remains limited.
2. We investigated the effects of species diversity on fine root production in a boreal forest that had grown naturally for eight years, following stand-replacing fire, by comparing the generation of fine-roots in single-species stands (*Populus tremuloides* Michx. (Populus) and *Pinus banksiana* Lamb. (Pinus)], and their mixtures (Populus+Pinus).
3. We hypothesized that: (i) fine root production is higher in mixed stands, (ii) across a given growing season, the effects of diversity on fine root production would be the greatest in August in a boreal forest, and (iii) fine root production in a mixed stand is strongly influenced by the dominant species.
4. We found no evidence of positive diversity effects on fine root production in a young natural boreal forest. Moreover, fine root production was not altered during sampling dates between May to October; however, the effects of tree species diversity on fine root production was positive in August. Rather, fine root production differed significantly

with the composition of overstory tree species, with *Populus* stands having the highest root production.

5. Our results suggested that mixtures of two shade-tolerant tree species at an early stage of development did not benefit fine root production, except during the mid-growth season. Further, our results supported the mass ratio hypothesis for species compositional effects on the belowground processes that we investigated.

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INTRODUCTION

The roots of mature trees are widely distributed, with horizontal roots that extend through the soil for distances of approximately 10 m from the tree trunk ([Smart et al. 2006](#)). These woody roots provide anchorage, transport, and storage functions, and serve as perennial outposts in a vast volume of soil that enable trees to address key ecological challenges: the rapid acquisition of growth-limiting water and nutrients. The acquisition of essential resources from highly heterogeneous soil volumes is achieved via small absorbing roots and their mycorrhizal associates ([Pregitzer 2002](#)). These small absorbing roots with typical diameters of less than 2 mm are called fine roots.

Biodiversity refers to the immense variety of all living things; the different plants, animals, microorganisms, the genetic information they contain, and the ecosystems that they form. Biodiversity is typically explored at three levels - genetic diversity, species diversity, and ecosystem diversity. According to the Encyclopedia of Earth, species diversity is a measurement of an ecosystem's species richness and species evenness. If an ecosystem has reduced species diversity, it may not function properly or efficiently. Biodiversity effects on ecosystem functionality in forests have attracted increasing attention over the last three decades ([Meinen et al. 2009b](#)); however, most studies have focused on the aboveground components of forest ecosystems. An improved elucidation of the relationships between diversity and productivity (DPR) belowground is essential, as belowground ecosystem processes contribute significantly to overall terrestrial productivity ([de Kroon et al. 2012](#)).

Fine roots play a critical role in the biogeochemical cycles of terrestrial ecosystems, and are vital for understanding forest ecosystem functionality and services. Previous studies have, for the most part, reported that higher plant species diversity functions to increase aboveground

productivity ([Zhang et al. 2012](#); [Liang et al. 2016](#)). In agriculture, fine root length might serve as an important indicator, which indirectly implies that the majority of mixed stands exhibit higher production than monocultured stands ([Tilman et al. 2001](#)). However, the effects of plant diversity on fine root production remain inconsistent, and experimental studies are rare in natural forests. Moreover, seasonal changes in aboveground plant production have been well described, whereas belowground plant production, particularly as relates to fine roots, has been poorly described to date ([Baddeley & Watson 2004](#)). Previous studies have shown that forest production is impacted by seasonal temperature changes ([Steele et al. 1997](#); [Yuan & Chen 2010](#)), where seasonal variabilities in temperature and precipitation culminate in optimal functional ranges for plants and soil organisms ([Han et al. 2016](#)).

Several mechanisms may be explained through increased fine root production under higher stand complexity in forests. First, in mature stands, high productivity and biomass demand elevated water and nutrient uptake from fine roots, leading to intense root interactions ([de Kroon 2007](#); [de Kroon et al. 2012](#)). In contrast, young stands with low root biomass ([Yuan et al. 2012](#)) may underutilize soil space and other resources (water and nutrients) with little resource competition and interspecific root interactions in species mixtures ([de Kroon et al. 2012](#)). Lastly, positive diversity effects on fine root productivity have been attributed to increased demands for foraging-limited nutrients, through the distribution of roots to vertical nutrient-rich layers ([Mommer et al. 2010](#); [Brassard et al. 2013](#)).

Seasonal fine root length patterns are important toward predicting fine root dynamics and carbon cycling in forest ecosystems ([Gill & Jackson 2000](#); [Fukuzawa et al. 2013](#)), which represent seasonal variations in the availability of water and nutrients ([Coners & Leuschner 2005](#); [Mainiero & Kazda 2006](#); [Valverde-Barrantes et al. 2015](#)). Fine root production generally increases during

spring and attains its highest level in late spring to mid-summer, and then decreases in the autumn ([Brassard et al. 2009](#)). Soil temperature was observed to follow air temperature (increasing from spring to summer) to reach a maximum at the beginning of August, which contributed to the acceleration of the fine root turnover rate ([Montagnoli et al. 2012](#)). [Steinaker & Wilson \(2008\)](#). This demonstrated that fine root production was enhanced over the growing season, as soil temperature increased and soil water decreased. Positive impacts on belowground fine root productivity were observed in species-rich stands, through their increased propagation through the soil volume ([Goldberg et al. 1999](#); [Hodge 2004](#)). In mixed stands, the growth/length of fine roots was also accelerated ([de Kroon 2007](#)), where fine root biomass was reported to be higher in species mixtures, in contrast to corresponding monocultures ([Schmid 2002](#); [Meinen et al. 2009b](#); [Brassard et al. 2010](#)). Other studies revealed no significant effect ([Bauhus et al. 2000](#); [Leuschner et al. 2001](#); [Meinen et al. 2009b](#); [Meinen et al. 2009a](#)), or even negative effects of species diversity on fine root biomass ([Bolte & Villanueva 2005](#)). Most of these experiments were conducted on grasslands, mature stands, or plantations.

The associations between species and diversity may be discussed by classifying stand components as three parts: dominant, subordinant, and transients. The dominant species of forests are presented as relatively significant, which make major contributions to overall plant biomass. Subordinant species occupy relatively small domains in stands and have high fidelity associations with particular vegetation types. Transients comprise a heterogeneous assortment of species with low abundance and persistence. A high proportion are juveniles of species that occur as dominants, or subordinates in neighbouring ecosystems, which is referred to as the mass ratio hypothesis ([Grime 1998](#)). The properties of ecosystems may be seriously impacted by the characteristics of dominant plants, which has been established through numerous experiments.

Various ecosystem properties were found to be strongly correlated with the functional characteristics of the dominant contributors to the biomass (([Hooper & Vitousek 1997](#); [Wardle et al. 1997](#)).

Objectives

We examined the effects of diversity on fine root productivity, measured as the generation of fine root length per month in eight-year-old single species-dominated, and mixed stands of natural boreal forests. The aim was to investigate whether fine root production increased in the mixed stands, in contrast to the monocultured stands. Further, our research elucidated the impacts of sampling date variations on fine root production. Our sample stands were selected as three overstorey types [single-species stands dominated by *Populus tremuloides Michx.* (Populus) and *Pinus banksiana Lamb.* (Pinus), to mixtures (Populus+Pinus)]. Pinus had a relative advantage in the mixed stands, which occupied 67% of the total. Moreover, we measured whether the dominant species in mixed stands impacted fine root production. As relates to my data analysis, we established nine plots with three replicates for each plant composition type.

Hypothesis

Here, I specifically tested whether, (i) fine root production was higher in mixed stands, (ii) the effects of diversity on fine-root production was highest in August, and (iii) fine root production in mixed stands was strongly influenced by the dominant species.

MATERIALS AND METHODS

STUDY AREA

This study was conducted in the central boreal forest of Canada, which is located north of Lake Superior and west of Lake Nipigon, ca. 100 km north of Thunder Bay, Ontario, Canada

(49°230 N–49°360 N, 89°310 W–89°440 W). The study area falls within the Moist Mid-Boreal (MBX) eco-climatic region, and is characterized by warm summers and cold, snowy winters (Ecoregions Working Group 1989). The mean annual temperature and precipitation, from 1981 to 2010 were 1.9 °C and 824 mm, respectively, at the closest climatic station of Cameron Falls (Environment Canada 2016). The soils of the upland sites are relatively deep glacial tills of the Brunisolic order (Soil Classification Working Group et al. 1998). The study area has an extensive history of stand-replacing fire, with an average fire return interval of approximately 100 years over the last century ([Senici et al. 2010](#)). The dominant overstory tree species includes jack pine (*Pinus banksiana* Lamb.), and trembling aspen (*Populus tremuloides* Michx.). Common understorey shrub species in the area include mountain maple (*Acer spicatum* Lam.), alder (*Alnus* spp.), and beaked hazel (*Corylus cornuta* Marsh.).

SAMPLING DESIGN

To test the effects of mixed species on fine-root production in the young boreal forest, nine plots were selected as three overstorey types [single-species stands dominated by *Populus tremuloides* Michx. (*Populus*) and dominated by *Pinus banksiana* Lamb. (*Pinus*), to mixtures (*Populus*+*Pinus*)], where each stand type was repeated in triplicate. According to the definitions for single- and mixed-species stands in the forest resource inventory, the standards for stand selection were that single species-dominated stands contain a stand basal area of a single species that is over 80%, while for mixed-species stands, none of the component species had a more than 80% stand basal area ([Ma et al. 2017](#)). Two minirhizotron tubes (6.4 cm wide x 108 cm long) were randomly installed in each plot on June 2017. Holes were drilled at 45° with diameters that accommodated the insertion of the minirhizotron tubes in the sample plots. Further, experimental data was extracted using Rootsnap software, and the assumption of the normality and

homogeneity of the data was confirmed prior to carrying out the statistical analysis. The results of the statistical analysis were obtained when the data aligned with the test standards.

DATA COLLECTION

Images were collected from the nine plots by using a CI-600 in situ root imager that was precisely positioned relative to the minirhizotron tube, which facilitated repeated observations, from May to October in 2018. Subsequently, Rootsnap software was employed to measure the lengths of the fine roots, which could be seen in the images, while marking their status (live or dead). Finally, the data was presented in Excel tables.

Based on the minirhizotron observations from Padilla et al. (2015) root length production and loss were recorded on the sampling date.

The observed fine root (L_o) is the assumption of live roots and dead roots. The calculation of the annual fine root length ($\text{m m}^{-2} \text{a}^{-1}$) in one composition is as follows: $Total L_o / Total area$.

The calculation of fine root production ($\text{cm m}^{-2} \text{month}^{-1}$) for each month is as follows: $(L_{o2} - (L_{o1} - (L_{g2} - L_{g1}))) / (Time2 - Time1)$, in which L_{o2} and L_{o1} are presented as total observable root lengths at the end of $Time2$ and the beginning of $Time1$ of the sampling date. The distinction between L_{g2} and L_{g1} is the length of roots that has disappeared within the same period, which contained dead and decomposed roots ([Padilla et al. 2015](#)). In northern forests, where frozen and snow-packed soils hinder sampling, fine root production during the winter months was assumed to be negligible ([Konôpka et al. 2005](#)). The annual fine root production was the sum of production for each month, from May to October.

Species mixture effects on fine root productivity were calculated as the ratio (R_o) of the observed productivity value ($P_{observed}$) to the expected value ($P_{expected}$, the weighted average

monoculture yield of the component species) of annual fine root production, or biomass in mixtures ([Loreau & Hector 2001](#)).

R_o = Fine-root production in mixed species/Expected fine-root production.

Expected fine-root production = $\sum (P_i \times m_i)$,

where P_i is the observed fine root production in pure stands, and m_i is the proportion of basal area for species i in mixed stands.

STATISTICAL ANALYSIS

The effects of overstory type (T) and sampling date (D) on fine root production (RLP) were tested using a linear mixed effect model (1) with *lme4* package (Bates et al. 2014) in R:

$$RLP = \beta_0 + \beta_1 \cdot T + \beta_2 \cdot D + \beta_3 \cdot T \times D + \pi_{plot} + \varepsilon \quad (1)$$

where β is the coefficient to be estimated; π_{plot} is the random effect factor of the plot, accounting for autocorrelation between observations within each plot; ε is sampling error.

Moreover, we also utilized the linear mixed effect model (2) to test the effects of the sampling date (D) on R_o :

$$R_o = \beta_0 + \beta_1 \cdot D + \pi_{plot} + \varepsilon \quad (2)$$

where β is the coefficient to be estimated; π_{plot} is the random effect factor of plot, accounting for autocorrelation between observations within each plot; ε is sampling error. Through the Shapiro-Wilk test, our data met the normality and homogeneity standards; therefore, no log transfer was required. R (version 3.5.3, R Development Core Team, Vienna, Austria) was implied to analyze the data.

RESULTS

Based on Table 1, we found a significant difference between the fine root lengths of the coniferous and broadleaf stands ($P < 0.05$), as well as between the mixed and broadleaf stands ($P < 0.05$) over one year. Also, we found an insignificant difference between the mixed and coniferous stands ($P > 0.05$) over one year. Figure 1 reveals that the annual fine root production in the broadleaf forest was highest ($> 6 \text{ m m}^{-2} \text{ a}^{-1}$), whereas the annual fine root production in the conifer stand was lowest ($< 4 \text{ m m}^{-2} \text{ a}^{-1}$). The annual fine root production in the mixed forest was from between $4 \text{ m m}^{-2} \text{ a}^{-1}$ and $6 \text{ m m}^{-2} \text{ a}^{-1}$, which ranked second among the three different forest stand types.

Table 1. Effects of species composition on annual fine root production by Tukey's HSD test.

Species	P
Coniferous – Broadleaf	0.004*
Mixed – Broadleaf	0.045*
Mixed – Coniferous	0.142

* represents $P < 0.05$.

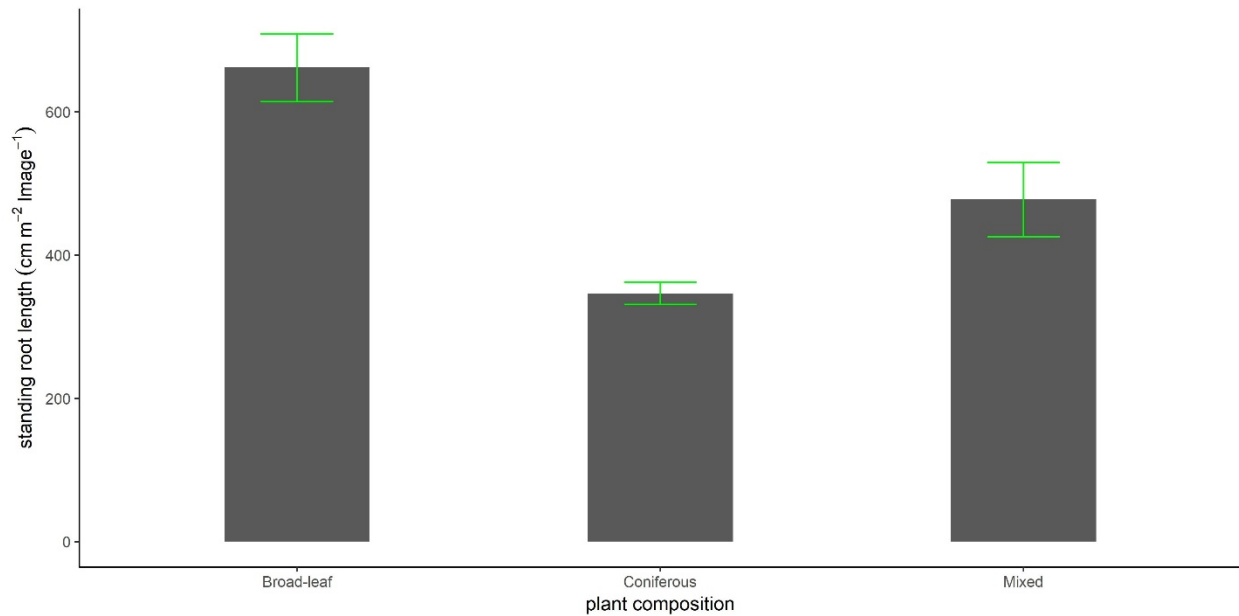


Fig 1. Annual root length (mm) of different species composition

Table 2 shows that the forest stand type had a significant effect on fine root production ($P < 0.05$), and the sampling month of the forest stand had no significant influence on fine root production ($P > 0.05$). There was no interactive influence between the sampling month and forest type on fine root production ($P > 0.05$).

Table 2 Effects of plant composition on fine root production within different sampling months.

Source	d.f.	MS	P
Type	2	11.65	0.045 *
Month	4	5.06	0.557
Type : Month	8	14.42	0.401
Residuals	25	41.25	

List represents the source of variation (Source), degree of freedom (d.f.), mean sum of squares (MS), and significance (P). * represents $P < 0.05$.

Table 3 indicates a marginal difference in the fine root production between the coniferous stand and broadleaf stands ($P = 0.0583$). No significant differences were observed between the

other two stand groups. The fine root production of the broadleaf stands underwent a dramatic change from June to October. It was observed to decrease from June to August, while it increased from August to September (Fig. 2). The fine root production in both the mixed and conifer stands represented a slight change, in contrast to the fine root production of the broadleaf stands on the sampling dates (Fig.2). As shown in Fig. 2, we observed that the fine root production in the broadleaf stands peaked in October. However, fine root production in the mixed stand peaked in July, whereas it peaked in August for the conifer stand. As revealed in the results of Table 2, seasonal variations had negligible significance for fine root production.

Table 3 Effects of stand type on fine root production.

	Estimated	Error	Value	P
Coniferous – Broadleaf	-1.802	0.612	-2.943	0.058
Mixed – Broadleaf	-1.144	0.612	-1.868	0.228
Mixed - Coniferous	0.658	0.612	1.075	0.562

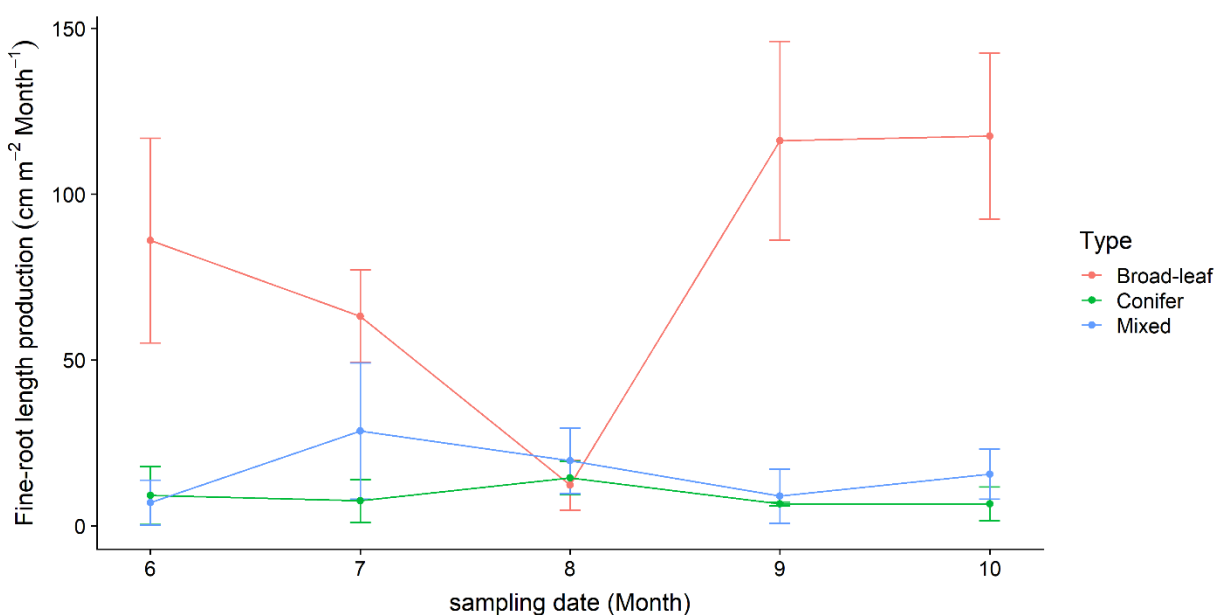


Fig 2. Effects of plant composition on fineroot production following different sampling months.

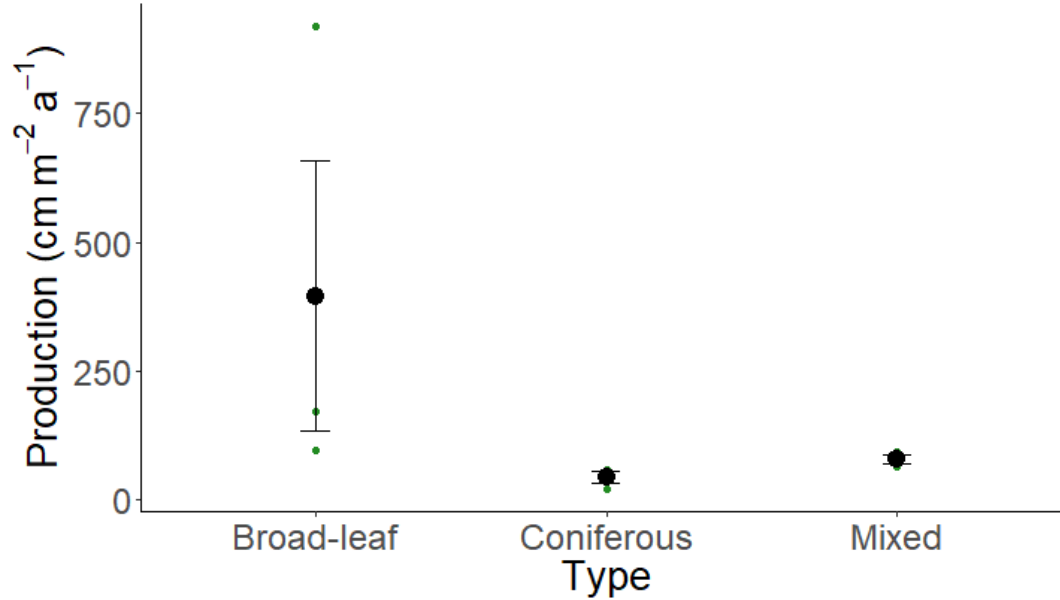


Fig 3. Annual root production of different forest compositions. Black points are the average value of fine root production for each plant composition, green points are the three replicates for each plant type. Error bars represent 1 SEM (n = 3).

As depicted in Fig. 3, fine root production in the coniferous stand was relative to the mixed stand. Moreover, the figure shows a significant difference between the broadleaf stand and the two other stands.

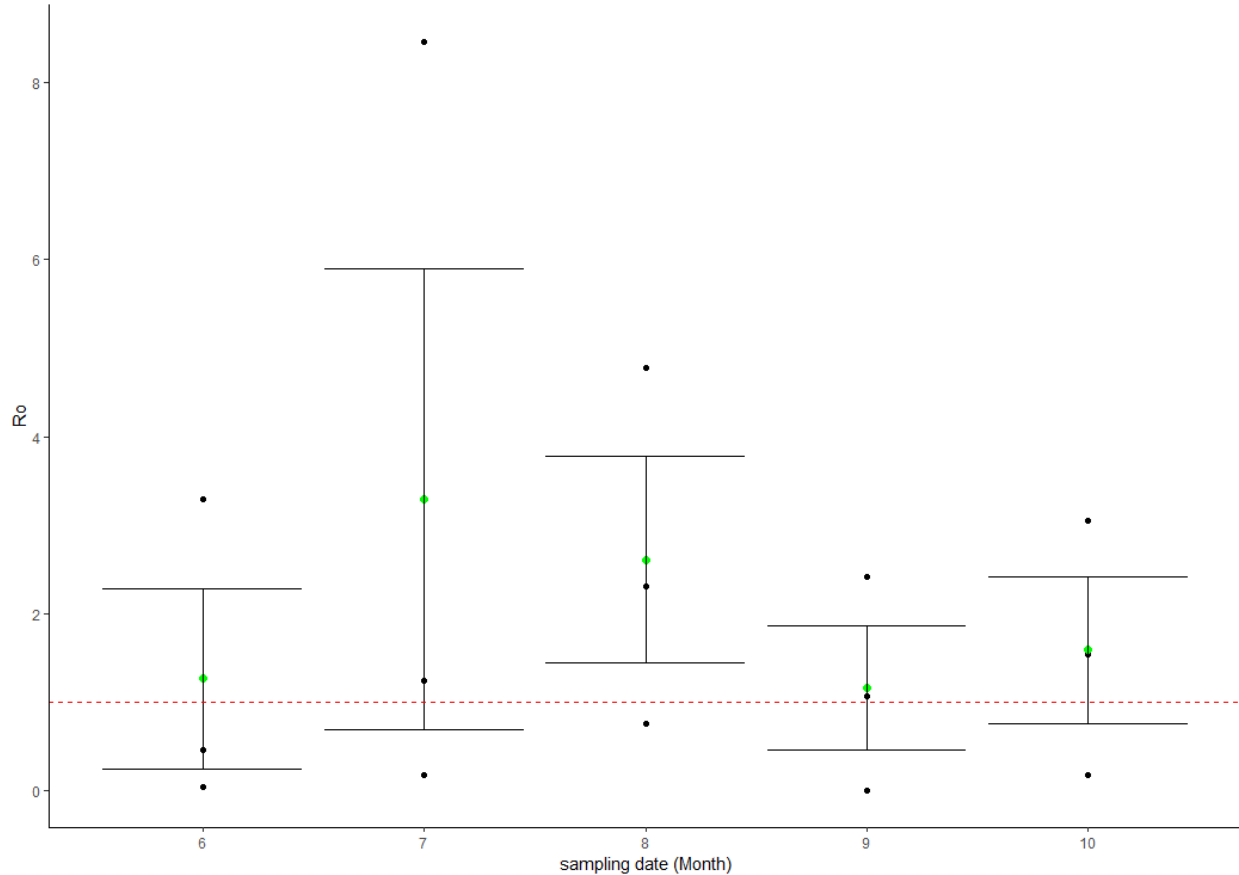


Fig 4. Diversity effect (R_o) on fine root production at different sampling dates. Green points are the average value of fine root production for each plant composition, black points are the three replicates for each plant type. Error bars represent 1 SEM ($n = 3$). Dotted line is presented as $y = 1$.

Fig. 4 reveals the effects of diversity on fine root production following seasonal variations. In Fig. 4, R_o was higher than 1 in August, which means that the diversity effect was positive. However, Fig. 4 presents R_o as being less than 1 on the other sampling dates, which means that the diversity effect was negative. These results were consistent with our hypothesis that the effects of diversity on fine root production was highest in August.

DISCUSSION

Species effects on fine root production

Compared with the conifer stands, there was an overyielding belowground pattern in the mixed stands, whereas the fine root production in pure broadleaf stands was far higher than the

mixed stands in our experiments. Our data did not match our first hypothesis that fine root production was higher in the mixed stands. Our results indicated that a single mechanism could not be responsible for the increased effects of diversity on fine root production in the young natural boreal forest. Our experiments were based on an eight-year-old sampling site, where stand age may have played a critical role in the effects of diversity related to low root biomass and productivity in the young stands ([Yuan et al. 2012](#)), with the underutilization of soil spaces with little root interactivity. The increased effects of diversity with stand development might have resulted from multiple processes: increased horizontal and vertical soil volume filling, increased forest floor depth/volume, and forage-limiting soil nutrients. Each of these elements may have resulted in the more complete utilization of soil space and nutrients, while benefiting from enhanced soil nutrient inputs and retention ([Ma et al. 2017](#)). Young species possess more shallow belowground roots, which limits the elevation of nutrient levels in the soil and interactive effects between different tree species. Horizontal and vertical volume filling is lower in young mixed forests, which translates to an insignificant variation in species diversity.

Seasonal diversity effects

Since R_o was more than 1 in August, but less than 1 on the other sampling dates, this was consistent with our second hypothesis that the diversity effect results in August were the highest (Fig. 4). Our results indicated that the effects of diversity on fine root production peaked only during the summer months. Our results indicated that the effects of diversity on fine root production might result from temporal complementarity. The phenological complementary aboveground could result in the augmentation of fine root productivity. Plant communities with contrasting growth strategies and different fine root traits might absorb nutrients and water more efficiently ([Xiang et al. 2015](#)). Soil moisture was a crucial factor for quantifying water content

with variable sampling dates. Generally, changes in the soil water content responded to altered soil temperature and precipitation.

The fine root production in the mixed stands was relative to that in the coniferous stands, but far different to fine root production in broadleaf and mixed stands, where coniferous species were dominant, in contrast to broadleaf species. This was consistent with our third hypothesis that fine root production in mixed stands was strongly influenced by dominant species, which also provided strong evidence for the characteristics of dominant species having a significant impact on the properties of ecosystems. Since the age of our sampling stands was eight years, further research is required to quantify whether subordinates might have an influence on fine root production.

Minirhizotron technology issues

Minirhizotrons can provide detailed information on fine root production. However, the manual processing of minirhizotron images is time-consuming, which limits the number and scope of experiments that can reasonably be analyzed ([Zeng et al. 2008](#)). During the data analysis process, images provided by minirhizotrons are two-dimensional, which restricts the full observation and functionality of fine roots. According to the operation of my experiments, I used Rootsnap to deal with the images that were provided by the minirhizotrons. I observed some obvious fine root folding in the images, which interfered with the measurement of their length.

CONCLUSION

In conclusion, our analysis revealed that mixed forest stands had no significant difference, in terms of accelerating fine root production. Our analysis demonstrated that the response in a young nature boreal forest was not as obvious as in grasslands or mature forests. The positive effects of diversity on fine root production in August provided evidence for the increased effects of diversity on fine root productivity associated with seasonal variations. Our results warrants further research tht should include a broad range of stand ages in various ecosystems to explore the potential effects of diversity on productivity.

LITERATURE CITED

- Baddeley, J.A. & Watson, C.A. (2004). Seasonal patterns of fine-root production and mortality in *Prunus avium* in Scotland. *Canadian journal of forest research*, 34, 1534-1537.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.
- Bauhus, J., Khanna, P. & Menden, N. (2000). Aboveground and belowground interactions in mixed plantations of *Eucalyptus globulus* and *Acacia mearnsii*. *Canadian Journal of Forest Research*, 30, 1886-1894.
- Bolte, A. & Villanueva, I. (2005). Interspecific competition impacts on the morphology and distribution of fine roots in European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.). *European Journal of Forest Research*, 125, 15-26.
- Brassard, B.W., Chen, H.Y.H. & Bergeron, Y. (2009). Influence of Environmental Variability on Root Dynamics in Northern Forests. *Critical Reviews in Plant Sciences*, 28, 179-197.
- Brassard, B.W., Chen, H.Y.H., Bergeron, Y. & Paré, D. (2010). Differences in fine root productivity between mixed- and single- species stands. *Functional Ecology*, 25, 238-246.
- Brassard, B.W., Chen, H.Y.H., Cavard, X., Laganière, J., Reich, P.B., Bergeron, Y. *et al.* (2013). Tree species diversity increases fine root productivity through increased soil volume filling. *Journal of Ecology*, 101, 210-219.
- Coners, H. & Leuschner, C. (2005). In situ measurement of fine root water absorption in three temperate tree species—Temporal variability and control by soil and atmospheric factors. *Basic and Applied Ecology*, 6, 395-405.
- de Kroon, H. (2007). How do roots interact? *Science*, 318, 1562-1563.
- de Kroon, H., Hendriks, M., van Ruijven, J., Ravenek, J., Padilla, F.M., Jongejans, E. *et al.* (2012). Root responses to nutrients and soil biota: drivers of species coexistence and ecosystem productivity. *Journal of Ecology*, 100, 6-15.
- Fukuzawa, K., Shibata, H., Takagi, K., Satoh, F., Koike, T. & Sasa, K. (2013). Temporal variation in fine-root biomass, production and mortality in a cool temperate forest covered with dense understory vegetation in northern Japan. *Forest Ecology and Management*, 310, 700-710.

- Gill, R.A. & Jackson, R.B. (2000). Global patterns of root turnover for terrestrial ecosystems. *The New Phytologist*, 147, 13-31.
- Goldberg, D.E., Rajaniemi, T., Gurevitch, J. & Stewart-Oaten, A. (1999). Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, 80, 1118-1131.
- Grime, J. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, 86, 902-910.
- Han, S.H., Yun, S., Lee, J., Kim, S., Chang, H. & Son, Y. (2016). Estimating the production and mortality of fine roots using minirhizotrons in a *Pinus densiflora* forest in Gwangneung, Korea. *Journal of Forestry Research*, 27, 1029-1035.
- Hodge, A. (2004). The plastic plant: root responses to heterogeneous supplies of nutrients. *New phytologist*, 162, 9-24.
- Hooper, D.U. & Vitousek, P.M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*, 277, 1302-1305.
- Konôpka, B., Yuste, J.C., Janssens, I.A. & Ceulemans, R. (2005). Comparison of Fine Root Dynamics in Scots Pine and Pedunculate Oak in Sandy Soil. *Plant and Soil*, 276, 33-45.
- Leuschner, C., Hertel, D., Coners, H. & Buttner, V. (2001). Root competition between beech and oak: a hypothesis. *Oecologia*, 126, 276-284.
- Liang, J., Crowther, T.W., Picard, N., Wisser, S., Zhou, M., Alberti, G. *et al.* (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science*, 354.
- Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72.
- Ma, Z., Chen, H.Y.H. & Bellingham, P. (2017). Effects of species diversity on fine root productivity increase with stand development and associated mechanisms in a boreal forest. *Journal of Ecology*, 105, 237-245.
- Mainiero, R. & Kazda, M. (2006). Depth-related fine root dynamics of *Fagus sylvatica* during exceptional drought. *Forest Ecology and Management*, 237, 135-142.
- Meinen, C., Hertel, D. & Leuschner, C. (2009a). Biomass and morphology of fine roots in temperate broad-leaved forests differing in tree species diversity: is there evidence of below-ground overyielding? *Oecologia*, 161, 99-111.
- Meinen, C., Hertel, D. & Leuschner, C. (2009b). Root Growth and Recovery in Temperate Broad-Leaved Forest Stands Differing in Tree Species Diversity. *Ecosystems*, 12, 1103-1116.

- Mommer, L., Van Ruijven, J., De Caluwe, H., Smit-Tiekstra, A.E., Wagemaker, C.A.M., Joop Ouborg, N. *et al.* (2010). Unveiling below-ground species abundance in a biodiversity experiment: a test of vertical niche differentiation among grassland species. *Journal of Ecology*, 98, 1117-1127.
- Montagnoli, A., Terzaghi, M., Di Iorio, A., Scippa, G.S. & Chiatante, D. (2012). Fine-root seasonal pattern, production and turnover rate of European beech (*Fagus sylvatica*L.) stands in Italy Prealps: Possible implications of coppice conversion to high forest. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*, 146, 1012-1022.
- Padilla, F.M., Miranda, J.d.D., Armas, C. & Pugnaire, F.I. (2015). Effects of changes in rainfall amount and pattern on root dynamics in an arid shrubland. *Journal of Arid Environments*, 114, 49-53.
- Pregitzer, K.S. (2002). Fine roots of trees—a new perspective. *New Phytologist*, 154, 267-270.
- Ravenek, J.M., Bessler, H., Engels, C., Scherer-Lorenzen, M., Gessler, A., Gockele, A. *et al.* (2014). Long-term study of root biomass in a biodiversity experiment reveals shifts in diversity effects over time. *Oikos*, 123, 1528-1536.
- Schmid, I. (2002). The influence of soil type and interspecific competition on the fine root system of Norway spruce and European beech. *Basic and Applied Ecology*, 3, 339-346.
- Senici, D., Chen, H.Y.H., Bergeron, Y. & Cyr, D. (2010). Spatiotemporal Variations of Fire Frequency in Central Boreal Forest. *Ecosystems*, 13, 1227-1238.
- Smart, D.R., Schwass, E., Lakso, A. & Morano, L. (2006). Grapevine rooting patterns: a comprehensive analysis and a review. *American Journal of Enology and Viticulture*, 57, 89-104.
- Steele, S.J., Gower, S.T., Vogel, J.G. & Norman, J.M. (1997). Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. *Tree physiology*, 17, 577-587.
- Steinaker, D.F. & Wilson, S.D. (2008). Phenology of fine roots and leaves in forest and grassland. *Journal of Ecology*, 96, 1222-1229.
- Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294, 843-845.
- Valverde-Barrantes, O.J., Smemo, K.A., Feinstein, L.M., Kershner, M.W. & Blackwood, C.B. (2015). Aggregated and complementary: symmetric proliferation, overyielding, and mass effects explain fine-root biomass in soil patches in a diverse temperate deciduous forest landscape. *New Phytol*, 205, 731-742.

- Wardle, D.A., Zackrisson, O., Hörnberg, G. & Gallet, C. (1997). The influence of island area on ecosystem properties. *Science*, 277, 1296-1299.
- Xiang, W., Fan, G., Lei, P., Zeng, Y., Tong, J., Fang, X. *et al.* (2015). Fine root interactions in subtropical mixed forests in China depend on tree species composition. *Plant and Soil*, 395, 335-349.
- Yuan, Z.Y. & Chen, H.Y.H. (2010). 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, 204-221.
- Yuan, Z.Y., Chen, H.Y.H. & Ostle, N. (2012). Fine root dynamics with stand development in the boreal forest. *Functional Ecology*, 26, 991-998.
- Zeng, G., Birchfield, S.T. & Wells, C.E. (2008). Automatic discrimination of fine roots in minirhizotron images. *New Phytol*, 177, 549-557.
- Zhang, Y., Chen, H.Y.H. & Reich, P.B. (2012). Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *J Ecol*, 100, 742-749.