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Differences in fine root productivity between mixed- and single-species stands

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Summary

1. The diversity–productivity debate has so far been focused above-ground, despite that below-ground production can account for approximately half of total annual net primary production, mostly from fine roots.

2. Here, we investigate the fine root productivity of mature, fire-origin stands of *Populus tremuloides* – *Picea* spp. – *Abies balsamea* (mixed-species stands) and relatively pure *P. tremuloides* (single-species stands) in two regions of North American boreal forest to better understand the link between plant diversity and below-ground productivity in forest ecosystems. We hypothesized that: (i) mixed-species stands have higher fine root productivity compared with single-species stands and (ii) this difference may be the result of greater soil space filling by the fine roots due to the contrasting rooting traits of the component species in the mixed-species stands.

3. We found that fine root productivity, measured by annual production and total biomass, was higher in mixed- than single-species stands. We also found that mixed-species stands had lower and higher horizontal and vertical fine root biomass heterogeneity, respectively, indicating that soil space is more fully occupied by fine roots in the mixed- than single-species stands.

4. In all, our study supports that below-ground niche differentiation may be a key driver of higher fine root productivity in mixed stands of species with contrasting rooting traits than single-species stands by facilitating greater soil space filling of fine roots and soil resource exploitation.

Key-words: boreal forest, over-yielding, plant competition, resource use, spatial rooting heterogeneity, species complementarity

Introduction

Ever since Darwin & Wallace (1858) first proposed that higher crop species diversity may be linked to higher crop yields, the question of whether or not plant diversity is related to net primary productivity has remained highly contested amongst the scientific community. During the past two decades, various experimental and observational studies have reported that polycultures can have higher above-ground biomass production than the average above-ground biomass production of monocultures under similar site conditions, i.e. over-yielding. Two hypotheses have been proposed to explain the observed positive diversity effect on productivity. The species complementarity hypothesis predicts that a mixture of two or more species of plants can achieve higher productivity than monocultures of the same component species via either facilitation, i.e. the presence of one species benefits the other by improving growing conditions, or niche differentiation, i.e. coexisting species occupy different ecological niches that results in more complete resource use (Tilman *et al.* 1997; Loreau & Hector 2001; Spehn *et al.* 2005; Marquard *et al.* 2009). Critics of the species complementarity hypothesis, however, argue that a selection effect, i.e. that a more diverse plant community has a higher probability of containing the most productive species, could alternatively explain the observed higher productivity of polycultures than monocultures in some studies (Špaèková & Lepš 2001; Cardinale *et al.* 2006;

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Schmid *et al.* 2008). A recent meta-analysis by Cardinale *et al.* (2007) has shown that species mixtures are more productive than the average of all monocultures in 79% of 44 diversity–productivity experiments, but achieve higher biomass in only 12% of these experiments, indicating that positive diversity–productivity relationships are likely attributable to both selection and species complementarity effects.

The majority of diversity–productivity studies to date have occurred in grasslands on above-ground components, where parameters can be more easily controlled and measured (e.g. Tilman, Wedin & Knops 1996; Hector *et al.* 1999, 2002; Loreau & Hector 2001; Flombaum & Sala 2008; Marquard *et al.* 2009). By contrast, diversity–productivity relationships have been less studied in forests, as the complex structure of this ecosystem type, and the relatively long life span of trees, make direct manipulation difficult. Especially lacking are studies that examine this relationship below-ground, despite that below-ground production can account for approximately half of total annual net primary production in forest ecosystems (Gower, Vogt & Grier 1992; Helmisaari *et al.* 2002).

The objective of this study was to examine fine root (≤2 mm in diameter) productivity and rooting patterns in single-species stands of *Populus tremuloides* Michx. and mixed stands of *P. tremuloides*, *Picea mariana* (Mill.) BSP, *Picea glauca* (Moench) Voss, and *Abies balsamea* L. Fine roots are primarily responsible for nutrient and water acquisition from the soil, and their production can account for well over three quarters of annual below-ground production in forest ecosystems (Jackson, Mooney & Schulze 1997; Brassard, Chen & Bergeron 2009). We attempted to test: (i) whether *P. tremuloides* – *Picea* spp. – *A. balsamea* mixtures have higher fine root productivity, measured by annual fine root production and total fine root biomass (live roots), than pure *P. tremuloides* stands (over-yielding hypothesis) and (ii) the niche differentiation hypothesis, i.e. that the difference in productivity between stand types may be the result of greater soil space filling by the fine roots due to the contrasting rooting traits of the component species in the mixed stands. To avoid a potential selection effect, this study was designed to compare the fine root productivity of the most productive single-species stand type in the North American boreal forest, pure *P. tremuloides* stands, with mixed stands of *P. tremuloides*, *P. mariana*, *P. glauca* and *A. balsamea*. To test the second hypothesis, we use a heterogeneity index to characterize stand-level horizontal and vertical fine root biomass distributions as an indicator of how fully below-ground growing space is being utilized within a stand. To our knowledge, this study is the first to investigate the link between fine root spatial biomass heterogeneity and below-ground productivity.

This study was conducted in two regions, a drier and warmer central region and a cooler and wetter eastern region of the North American boreal forest. The studied stand types are mostly common on mesic sites in both regions. *Populus tremuloides* is a shade-intolerant broadleaf species that roots deeper than the more shade-tolerant conifers *P. mariana*, *P. glauca*, and *A. balsamea*, while having a higher rate of above- and below-ground growth (Burns & Honkala 1990). All four of these tree species can establish immediately after stand-replacing crown fire, but *P. glauca* and *A. balsamea* can also recruit later in stand development by seeding in from neighbouring stands (Galipeau, Kneeshaw & Bergeron 1997; Bergeron 2000; Ilisson & Chen 2009).

Materials and methods

STUDY AREA

One study region was located west of Lake Nipigon in the Upper English River (B.11) Forest Region (Rowe 1972), approximately 150 km north of Thunder Bay, Ontario, Canada (49°23′N–49°37′N, 89°31′W–89°45′W). The average annual precipitation for Thunder Bay (1971–2000), the location of the closest weather station, is 712 mm, and the average annual temperature is 2·5 °C (Environment Canada 2010). The second was located east of Lac Turgeon approximately 100 km northeast of La Sarre, Quebec, Canada (49°08′N–49°12′N, 89°46′W–89°54′W) in the Northern Clay (B.4) Forest Region. The closest weather station is located in La Sarre, where the average annual precipitation and temperature is 823 mm and 0·6 °C respectively. Short summers and moderately dry cool climate is common to both study regions, and topographic features were shaped by the retreat of the Laurentide Ice Sheet approximately 10 millennia ago. Stand-replacing crown fire is the most common natural stand initiating disturbance in both regions (Johnson 1992).

SAMPLING

We selected, using forest resource inventory maps and random stratified sampling, six mature fire-origin stands in each study region (time since fire: Ontario sites = 85 and Quebec sites = 92 years) that belonged to one of two discrete stand types: (i) stands containing mixtures of *P. tremuloides*, *Picea* spp., and *A. balsamea* (hereafter referred to as 'mixed-species stands') and (ii) relatively pure stands of *P. tremuloides* (hereafter referred to as 'single-species stands'). Similar to other studies that investigate the species mixture effect in naturally established mature stands (e.g. Wang *et al.* 2002; Brassard *et al.* 2008; Cavard *et al.* 2010), and in following the definitions for single- and mixed-species stands in the forest resource inventory, criteria for stand selection was that mixed-species stands would contain > 20% stand basal area of *Picea* spp. and *A. balsamea*, while single-species stands would have < 20%. The average percent basal area of *Picea* spp. and *A. balsamea* in the mixed-species stands was 33%, ranging from 24% to 48%, whereas that in the single-species stands was 3% and ranged from 0% to 9% (Table 1).

Common understory plant species in the Quebec stands were *Rubus pubescens* Raf., *Diervilla lonicera* Mill., *Viburnum edule* (Michx.) Raf., *Gaultheria hispidula* (L.) Muhl. ex Bigelow, *Alnus* spp., *Cornus canadensis* L., *Viola* spp., *Linnea borealis* L., *Maianthemum canadense* Desf. and *Mitella nuda* L. In the Ontario stands, common understory plants included *Acer spicatum* Lam., *R. pubescens*, *Alnus* spp., *Corylus cornuta* Marsh., *D. lonicera*, *C. canadensis*, *Clintonia borealis* (Aiton) Raf., *M. canadense*, *Coptis trifolia* (L.) Salisb., *Viola* spp. and *Aster macrophyllus* L.

To limit site variability, all selected stands were > 1 ha in area, fully stocked, visually homogeneous in structure and composition, and were located on relatively flat, upland, mid-slope positions. Following

Table 1. Characteristics (mean and range) of the twelve study stands sampled in northwestern Ontario and northwestern Quebec, Canada. Each stand type was replicated three times in each region

Study region	Ontario		Quebec	
Stand type	Mixed-species	Single-species	Mixed-species	Single-species
Stand volume (m^3 ha^{-1})*	341·5 (262·8–404·1)	378·6 (222·7–478·9)	413·4 (269·4–501·4)	505·8 (364·6–636·9)
Stand density (trees ha^{-1})	1600 (1350–1850)	734 (675–775)	1350 (1100–1500)	825 (650–1000)
Shrub, herb and moss biomass (kg ha^{-1})†	2413 (1260–4709)	25 749 (3176–43 316)	1716 (1251–2125)	21 860 (14 002–37 460)
Abies balsamea basal area (m^2 ha^{-1})	2·63 (0·71–4·31)	0	0·02 (0–0·06)	0·04 (0–0·12)
Picea glauca basal area (m^2 ha^{-1})	1·86 (0–5·59)	0	0	0
Picea mariana basal area (m^2 ha^{-1})	7·61 (1·80–10·95)	0	14·79 (10·25–17·13)	2·74 (1·04–6·11)
Pinus banksiana basal area (m^2 ha^{-1})	1·59 (0·28–3·24)	1·09 (0·35–1·87)	2·16 (0–3·33)	0·86 (0–2·58)
Populus tremuloides basal area (m^2 ha^{-1})	25·60 (18·39–31·51)	32·50 (20·17–38·75)	25·31 (14·76–33·59)	37·34 (27·57–42·41)

*Stand volume was determined using individual tree volumes that were summed to the plot level and scaled up to per ha. Individual tree volumes were estimated using the diameter at breast-height and height measurements and species-specific volume equations developed for tree species of central and eastern Canada (Honer, Ker & Alemdag 1983).

†Shrub, herb, and moss biomass was determined by harvesting all above-ground components of each type in three randomly located 1 m^2 quadrates. All samples were brought back to the laboratory, oven-dried for 48 h at 65 °C, and weighed. Sample weights were pooled by plot and scaled up to per ha.

the procedure described in Taylor *et al.* (2000), a soil pit was dug in each sampled stand to ensure site condition was mesic in Ontario and subhydric in Quebec, the typical site type for boreal mixedwoods in the respective regions. All sampled sites in Quebec belonged to the Luvisolic soil order, while those in Ontario were Brunisolic (Cavard *et al.* 2010).

At each site, a 400 m^2 circular plot was established to represent the stand, where no trees had survived from the last fire. The diameter at breast-height (DBH), taken 1·3 m above the root collar, height, and species of all live trees DBH ≥2 cm were measured and recorded. Stand basal area by species was summed to the plot level and used for assigning stand type classification.

Within each plot, seven soil cores (6·75 cm diameter) were randomly extracted from the forest floor surface to a mineral soil depth of 30 cm using a power auger in mid July and late October of 2007, which are generally regarded in northern forests as the timings of maximum and minimum fine root biomass respectively (Steele *et al.* 1997; Wang, Bond-Lamberty & Gower 2003). To facilitate extraction by layers, and to minimize compaction during coring, we extracted the forest floor layer (FF) and two mineral soil sections: MS1 (0–15 cm) and MS2 (15–30 cm) subsequently after removing the upper layer.

Soil core sections were transported in an ice-filled cooler from the field to the laboratory and stored in a freezer for approximately 1–2 months at −20 °C until processing. Thawed samples were soaked in water to separate roots from soil and gently washed over a 0·5 mm sieve. Coarse roots (> 2 mm in diameter) and coarse fragments were removed. Remaining root fragments were rinsed with water and sorted according to vitality class, i.e. live versus dead. Roots were considered 'live' if they were pale-coloured on the exterior, elastic and flexible, and free of decay with a whitish cortex, while roots were classified as 'dead' if they were brown or black in colour, rigid and inflexible, in various stages of decay, and had a dark coloured cortex (Persson 1983; Bennett, Andrew & Prescott 2002).

Live fine roots were further divided into the following species-based classes: (i) *P. tremuloides*, (ii) *Picea* spp. and *A. balsamea*, (iii) non-tree (shrubs and herbs) and (iv) *P. banksiana* using a combination of morphological characteristics. These included: (i) colour (*P. tremuloides* and non-tree roots were more white or yellow in colour, while conifer roots were more red or brown in colour), (ii) size (*Picea* spp. and *A. balsamea* and non-tree roots were generally finer-structured than those of *P. tremuloides* and *P. banksiana*), (iii) branching angle (approximately 90° for conifer roots and 45° for *P. tremuloides* and non-tree roots), (iv) branching pattern (sections of *Picea* spp. and *A. balsamea* and non-tree roots were more branched than those of *P. tremuloides* and *P. banksiana*) and (v) presence or absence of root hairs (non-tree roots contained small hairs that were not present on tree roots). These criteria were developed previous to root sorting using samples of known origin from our study sites. The fine roots were then oven-dried to a constant mass at 65 °C and weighed.

We also installed 10 ingrowth cores (6·75 cm diameter, 30 cm length) at each site to give a second estimate of annual fine root production (Steele *et al.* 1997; Hendricks *et al.* 2006). A power auger was again used to drill holes at each site. A plastic mesh core was then inserted into each hole, filled with root-free soil (medium-textured sand), covered with leaf litter, and marked by a steel rod. All ingrowth cores were installed in October 2007 and removed after one calendar year. Roots were separated from the soil, dried, and weighed as described above, with the exception that roots were not separated by soil layer or species class. No roots > 2 mm in diameter were present in any of the ingrowth cores.

DATA ANALYSIS

Total fine root biomass and necromass (dead roots) (kg ha^{-1}) was calculated for each sampling period (July and October) at each site by summing the dry weight of live and dead fine roots, respectively, in each soil core and scaling up to per ha. Annual fine root production (kg ha^{-1} year^{-1}) based on the minimum–maximum method was then calculated as the difference between total July and October fine root biomass. Annual fine root production based on the ingrowth core method was calculated at each site by summing the dry weight of live and dead roots in each ingrowth core and scaling up to per ha.

Horizontal fine root biomass heterogeneity was calculated as the standard deviation of the fine root biomass values of all soil layers combined among the seven soil cores at each site for both sampling periods. Vertical fine root biomass heterogeneity was calculated for both sampling periods as the standard deviation of the fine root biomass values among the three soil layers averaged from all soil cores. A higher standard deviation value would imply that fine root biomass is less evenly distributed, i.e. more heterogeneous, among the soil cores or soil layers, respectively. As detailed maps of fine root distributions are currently almost impossible to construct at the stand level, using among soil core fine root biomass heterogeneity to approximate how variable fine roots are distributed horizontally within a stand provides a practical tool for assessing fine rooting patterns in the horizontal dimension.

To determine if annual fine root production, total July and October fine root biomass and necromass, July and October horizontal and vertical fine root biomass heterogeneity, and the biomass of fine roots in July and October by species – soil layer class differed with stand type and study region, we used the following general linear model (eqn. 1):

$$Y_{ijk} = \mu + T_i + R_j + T \times R_{ij} + \varepsilon_{(ij)k} \quad eqn1$$

where Y_{ijk} is annual production, biomass or necromass, or biomass heterogeneity, μ is the overall mean, T_i is stand type ($i = 1, 2$), R_j is study region ($j = 1, 2$), $T \times R_{ij}$ is the stand type – study region interaction, and $\varepsilon_{(ij)k}$ is the random error. Simple linear regression analysis was then used to determine if total July and October fine root biomass were related to July and October horizontal or vertical fine root biomass heterogeneity, respectively. Normality and homogeneous variances were confirmed following Kutner *et al.* (2005). Statistical significance was based on $\alpha = 0{\cdot}05$, and all analyses were performed using SPSS® version 16.0 (SPSS Inc., Chicago, IL, USA).

Results

Both the minimum–maximum and ingrowth core methods indicated that annual fine root production was significantly higher in mixed- than single-species stands in both study regions (Table 2, Fig. 1). Total July and October fine root biomass were significantly and marginally significantly ($\alpha = 0{\cdot}10$) higher in mixed- than single-species stands, respectively, in both study regions. Total July fine root necromass, however, did not differ with stand type or study region, whereas total October fine root necromass was significantly higher in mixed- than single-species stands in both study regions (Table 2, Fig. 2).

Table 2. Effects (*P*-values) of stand type (*T*) and study region (*R*) on annual fine root production, the total biomass and necromass of fine roots in July and October, and horizontal and vertical fine root biomass heterogeneity in July and October. Bold indicates significant or marginally significant effects

		Source*		
Characteristic	R^2	*T*	*R*	*T* × *R*
Annual fine root production				
Minimum–maximum method	0·597	**0·011**	0·582	0·401
Ingrowth core method	0·604	**0·008**	0·749	0·988
Total fine root biomass				
July	0·510	**0·022**	0·920	0·630
October	0·427	**0·071**	0·657	0·272
Total fine root necromass				
July	0·124	0·467	0·842	0·495
October	0·419	**0·046**	0·975	0·654
Horizontal fine root biomass heterogeneity				
July	0·554	**0·038**	**0·089**	0·981
October	0·462	0·541	**0·057**	0·250
Vertical fine root biomass heterogeneity				
July	0·446	**0·061**	0·261	0·623
October	0·609	**0·016**	0·667	0·117

*Source is explained in eqn 1.

The biomass of *P. tremuloides* fine roots did not differ between stand types and study regions for all three soil layers in both sampling periods (Table 3, Fig. 2). The biomass of *Picea* spp. and *A. balsamea* fine roots was significantly higher in mixed- than single-species stands in all three soil layers for both sampling periods. July and October *Picea* spp. and *A. balsamea* fine root biomass were marginally higher in the Ontario than Quebec region in the FF and MS1 layer, respectively, but did not differ between study regions in the MS2 layer for either sampling period (Table 3, Fig. 2). By contrast, non-tree fine root biomass was significantly or marginally higher in single- than mixed-species stands in the FF and MS1 layers, but did not differ between stand types in the MS2 layer, for either sampling period. Non-tree fine root biomass in the FF layer was marginally higher in the Quebec than Ontario region in July, but did not differ between study regions in the other two soil layers in July, or any of the soil layers in October (Table 3, Fig. 2). The fine root biomass of all species combined was higher in mixed- than single-species stands in the FF layer, while both stand types had similar total fine root biomass in the MS1 and MS2 layers, in both sampling periods. Stands in the Ontario region, however, contained higher total fine root biomass in the MS2 layer, but similar biomass in the other two soil layers, compared with those in the Quebec region, in both sampling periods (Table 3, Fig. 2).

July horizontal fine root biomass heterogeneity was significantly higher in single- than mixed-species stands, and marginally higher in stands of the Ontario than Quebec regions (Table 2, Fig. 3). October horizontal fine root biomass heterogeneity, however, did not differ between stand types, but showed a similar regional trend. By contrast, July and October vertical fine root biomass heterogeneity were marginally and significantly higher in mixed- than single-species stands, respectively, but did not differ between study regions (Table 2, Fig. 3). Total July fine root biomass increased with decreasing horizontal fine root biomass heterogeneity and increasing vertical fine root biomass heterogeneity. Total October fine root biomass, however, was not significantly affected by horizontal fine root biomass heterogeneity, but did increase with increasing vertical fine root biomass heterogeneity (Fig. 4).

Discussion

Our data supported our first hypothesis that fine root productivity, measured by annual fine root production and total fine root biomass, is higher in mixed- than single-species stands. Although this study is the first, to our knowledge, to examine fine root production in different stand types of similar age

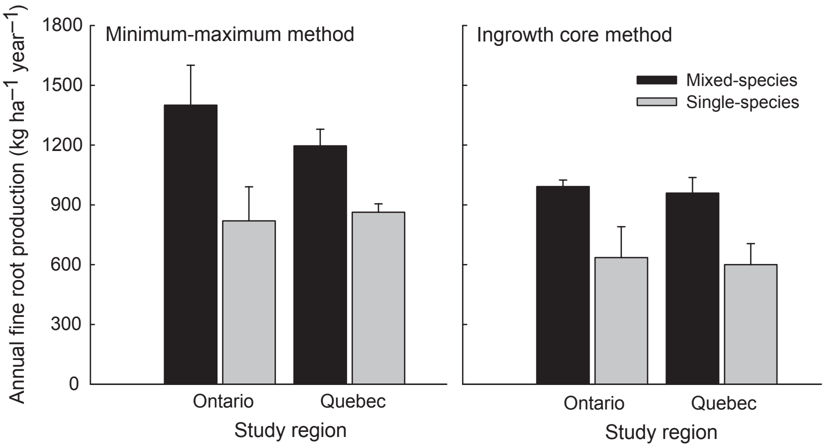

Fig. 1. Annual fine root production by stand type (mixed-species and single-species), study region (Ontario and Quebec), and method of sampling (minimum–maximum method and ingrowth core method). Error bars represent 1 SEM.

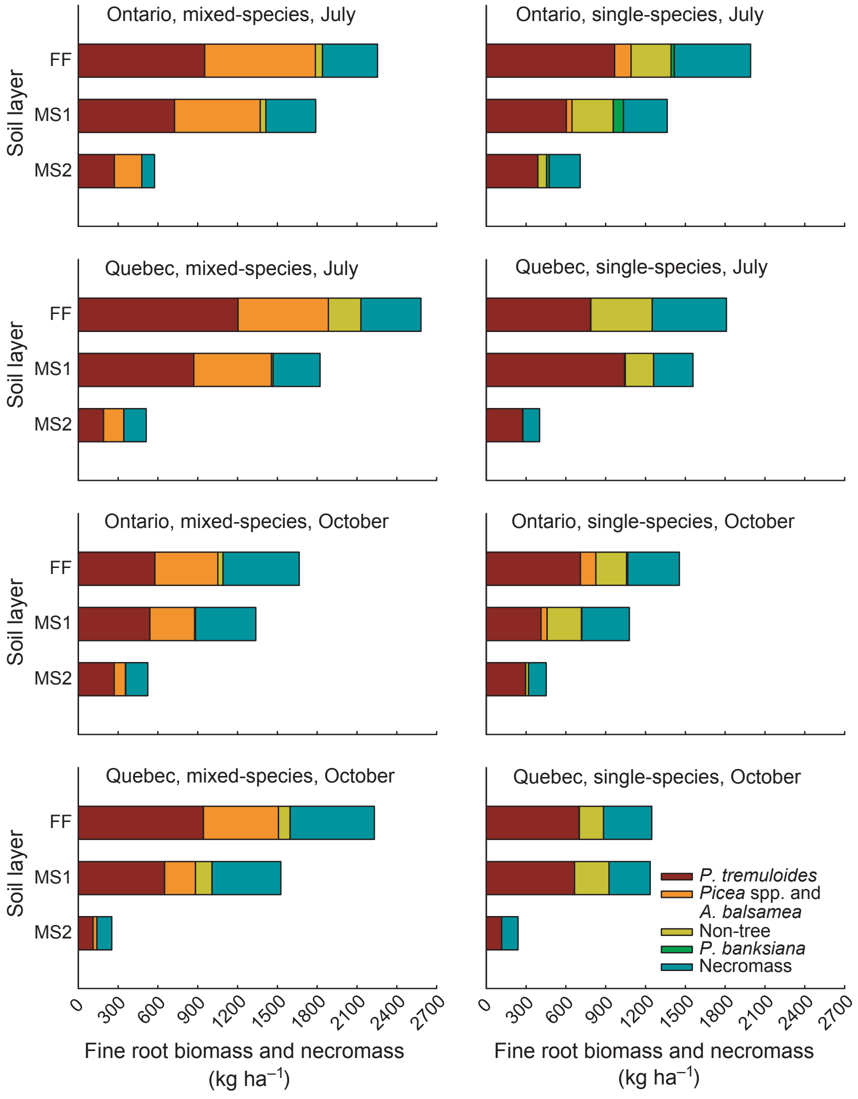

Fig. 2. The biomass (*Populus tremuloides*, *Picea* spp. and *Abies balsamea*, non-tree, and *Pinus banksiana*) and necromass of fine roots by soil layer (FF, MS1 and MS2), stand type (mixed-species and single-species), study region (Ontario and Quebec), and sampling period (July and October).

and site conditions, fine root biomass has been compared between mixed- and single-species stands in a limited number of other studies. For example, Fredericksen & Zedaker (1995) found that *Pinus taeda* L. – *Robinia pseudoacacia* L. mixtures contained higher fine root biomass than relatively pure *P. taeda* stands. Similarly, Wang *et al.* (2002) reported that root biomass in *Tsuga heterophylla* (Raf.) Sarg. – *Thuja plicata* Donn ex D. Don mixtures was almost double that compared with single-species stands of *T. heterophylla* and *T. plicata*. By contrast, Leuschner *et al.* (2001) did not find a

Table 3. Effects (*P*-values) of stand type (*T*) and study region (*R*) on the biomass of fine roots in July and October by species – soil layer class. Bold indicates significant or marginally significant effects

	July				October			
		Source*				Source*		
Species – soil layer class	R^2	T	R	$T \times R$	R^2	T	R	$T \times R$
Populus tremuloides								
FF layer	0·317	0·229	0·827	0·198	0·384	0·650	0·172	0·152
MS1 layer	0·447	0·650	0·153	0·286	0·281	0·639	0·151	0·559
MS2 layer	0·326	0·201	0·208	0·823	0·399	0·837	0·171	0·492
Picea spp. and *Abies balsamea*								
FF layer	0·925	**< 0·001**	**0·090**	0·819	0·844	**< 0·001**	0·881	0·188
MS1 layer	0·901	**< 0·001**	0·503	0·870	0·856	**< 0·001**	**0·095**	0·466
MS2 layer	0·940	**< 0·001**	0·133	0·133	0·591	**0·023**	0·210	0·280
Non-tree								
FF layer	0·597	**0·026**	**0·072**	0·867	0·676	**0·005**	0·984	0·216
MS1 layer	0·568	**0·015**	0·426	0·662	0·402	**0·066**	0·531	0·538
MS2 layer	0·437	0·177	0·208	0·183	0·529	0·138	0·106	0·148
All species†								
FF layer	0·491	**0·031**	0·812	0·388	0·559	**0·057**	0·361	0·103
MS1 layer	0·328	0·123	0·432	0·626	0·182	0·455	0·326	0·805
MS2 layer	0·330	0·691	**0·093**	0·724	0·527	0·669	**0·018**	0·920

*Source is explained in eqn 1.

†Includes *P. tremuloides*, *Picea* spp. and *A. balsamea*, non-tree, and *Pinus banksiana* fine root biomass.

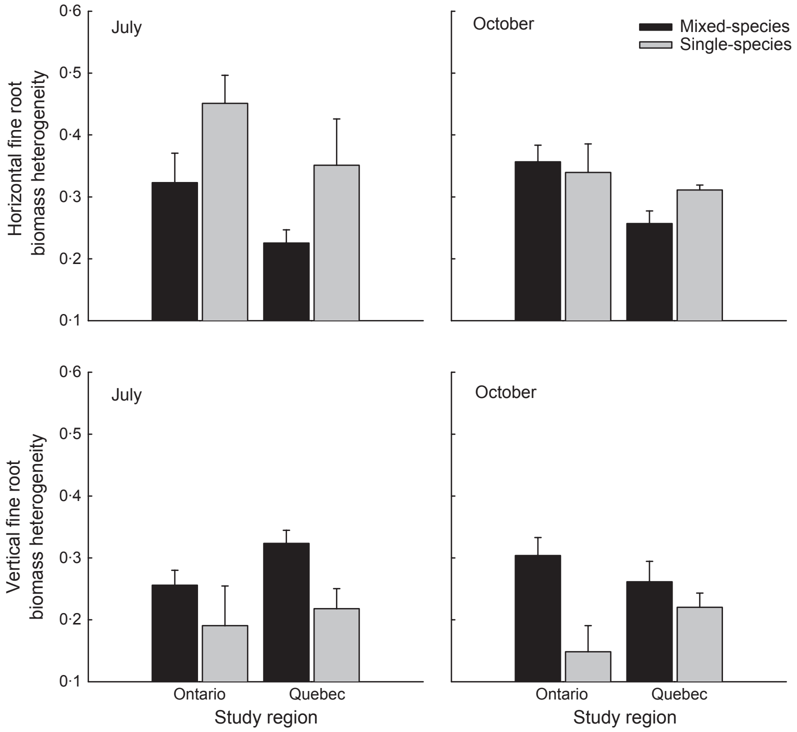

Fig. 3. Horizontal and vertical fine root biomass heterogeneity (standard deviation of the seven soil cores within a stand and that of the three soil layers, respectively) by stand type (mixed-species and single-species), study region (Ontario and Quebec), and sampling period (July and October). Error bars represent 1 SEM.

difference in fine root biomass between single- and mixed-species stands of *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. Likewise, Meinen, Hertel & Leuschner (2009) did not find a species diversity effect on fine root biomass between single- and mixed-species broadleaf stands. It would appear, therefore, that whether mixed-species stands can yield higher fine root productivity than single-species stands may depend on the presence of contrasting rooting traits among component species in mixture affecting the number of individuals that can occupy a stand and the magnitude to which the soil

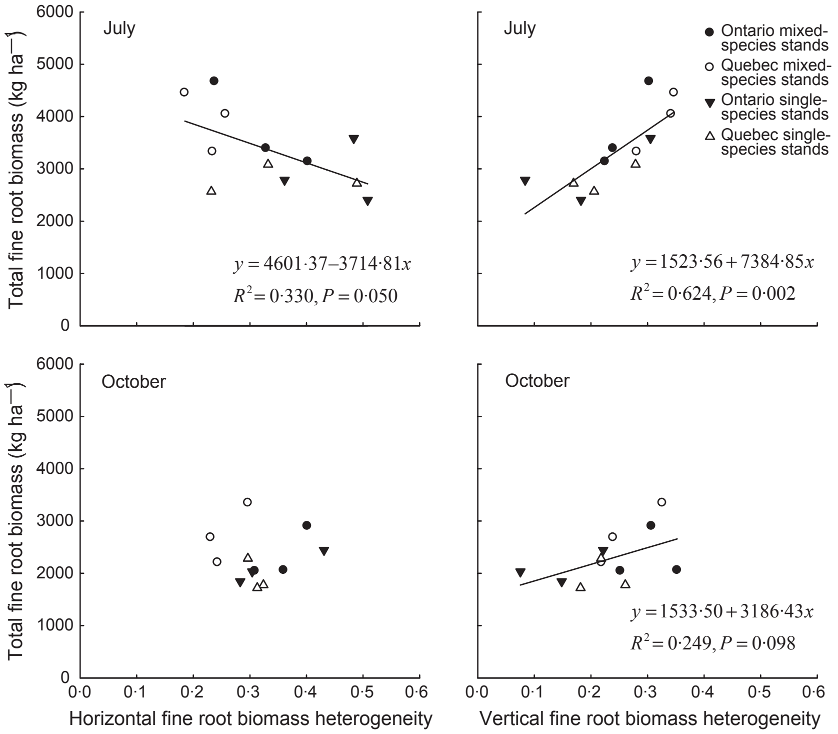

Fig. 4. Relationship between total fine root biomass and horizontal and vertical fine root biomass heterogeneity (standard deviation of the seven soil cores within a stand and that of the three soil layers, respectively) in July and October, respectively.

space and resources of a stand can be filled and used by the fine roots respectively (Köstler, Brueckner & Bibelriether 1968; Brassard, Chen & Bergeron 2009).

Evidence to support our second hypothesis is manifested by both the heterogeneity analyses and biomass plots. The lower July horizontal fine root biomass heterogeneity in mixed-species stands would appear to indicate that greater horizontal space filling is occurring in this stand type than single-species stands. The higher July and October vertical fine root biomass heterogeneity in mixed-species stands, attributable to the significantly higher fine root biomass in the FF layer in this stand type than single-species stands, suggests that the mixed-species stands allow for greater soil space filling of fine roots in this nutrient-rich layer than the single-species stands. Furthermore, since the biomass of *P. tremuloides* fine roots did not differ between stand types in the FF layer, this among stand type difference is largely the result of the higher *Picea* spp. and *A. balsamea* fine root biomass in the FF layer of the mixed-species stands compared to the non-tree fine root biomass in the FF layer of the single-species stands. These findings support our heterogeneity analyses that a certain amount of growing space is not being utilized by fine roots in single-species stands, so that total soil space filling and soil resource exploitation by fine roots is lower in single- than mixed-species stands.

Three of the four heterogeneity indices indicated a direct link between total fine root biomass and fine root biomass heterogeneity. This result suggests that fine root biomass heterogeneity, as an indicator of the total soil space filling of fine roots within a stand, may be a key driver for the observed below-ground productivity–plant diversity relationships found in this study, supporting the existence of below-ground niche differentiation in the mixed-species stands we studied. Furthermore, above-ground functional trait differences between *P. tremuloides* and *P. mariana*, *P. glauca*, and *A. balsamea* (e.g. the more shade-tolerant *Picea* spp. and *A. balsamea*, with their narrow, conical-shaped crowns (Burns & Honkala 1990) may position themselves between the larger crowns of *P. tremuloides* despite the relatively closed canopy), in conjunction with their different rooting traits, may also be important for facilitating greater below-ground space filling and higher fine root productivity in our mixed- compared to single-species stands. However, these hypotheses must be tested in other forest and ecosystems types before any broader generalizations can be made.

Based on the results from both forest and grassland studies, it appears that contrasting and similar above- and below-ground diversity–productivity relationships can occur within the same plant communities. Although fine root productivity, for example, was found to be higher in our mixed- than single-species stands, the single-species stands were found to contain higher above-ground biomass than the mixed-species stands (Cavard *et al.* 2010). By contrast, Chen & Klinka (2003) reported that above-ground productivity did not differ between mixed- and single-species stands of *T. heterophylla* and *T. plicata*, whereas Wang *et al.* (2002) found that *T. heterophylla* and *T. plicata* mixtures contained higher root biomass than relatively pure *T. heterophylla* and *T. plicata* stands at the same sites. Furthermore, while Spehn *et al.* (2005), De Boeck *et al.* (2008) and Fornara & Tilman (2008) found that more diverse grassland communities contained greater above- and below-ground biomass than less diverse communities, Bessler *et al.* (2009) and Wacker *et al.* (2009) reported that above-ground biomass production was greater, but below-ground biomass production similar, in more than less diverse grassland communities. However, Hooper (1998) did not find a significant relationship between functional group diversity and above-ground or below-ground biomass production in a serpentine grassland. It is apparent, therefore, that certain functional trait differences between component species in mixture that promote below-ground over-yielding may not necessary do so above-ground, while the same is true regarding the expression of above- but not below-ground over-yielding. What still remains to be determined, however, is what functional trait differences are key to facilitating below-ground over-yielding, and which are important for above-ground over-yielding.

In summary, this study is one of the first to not only demonstrate a positive relationship between plant diversity and below-ground productivity in forest ecosystems that is unrelated to a selection effect, but also to present empirical evidence, through characterization of stand-level fine root biomass distributions, that below-ground niche differentiation is a key driver of higher fine root productivity in species mixtures with contrasting rooting traits in comparison to single-species stands. Given that the biodiversity effect on productivity can vary between natural and artificial systems (Flombaum & Sala 2008), future plant diversity–productivity studies should strive to study this process in natural ecosystems, despite the added challenges of separating selection from species complementarity effects that this approach presents.

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