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Positive species mixture effects on fine root turnover and mortality in natural boreal forests

Zilong Ma, Han Y.H. Chen*

Faculty of Natural Resources Management, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada

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ABSTRACT

The positive species mixture effects on both above- and below-ground productivity have been well documented in diverse ecosystem types. However, whether the results obtained on productivity can be generalized to other ecosystem processes remains unclear. We investigated the effects of tree species mixtures on fine root biomass turnover and biomass loss from mortality by sampling 18 stands dominated by *Populus tremuloides* and *Pinus banksiana*, respectively, and their relatively even mixtures in post-fire boreal forests of two stand ages (8 and 34 years following stand-replacing fire). Fine root biomass turnover and mortality were higher in mixtures than expected from those of single species-dominated stands in both stand ages, with a higher magnitude of mixture effects in the 34-year-old than in the 8-year-old stands. Mixture effects on turnover and mortality did not differ with soil depth in 8-year-old stands, but turnover increased while mortality decreased from the forest floor to the mineral layers in 34-year-old stands. Both turnover and mortality significantly increased with tree species evenness in 34-year-old stands, but not in 8-year-old stands. Root turnover and biomass loss from mortality were positively associated with annual fine root production across all stand types and ages. Our results provide the first evidence for positive mixture effects on fine root biomass turnover and biomass loss from mortality in natural forests. Moreover, our results suggest that the positive mixture effects resulted from increased competition induced by the increase of fine root biomass production in tree species mixtures.

1. Introduction

In recent decades, the biodiversity and ecosystem functioning relationship (BEF) has been a major ecological research focus to help understand the impact of global species extinction crisis on ecosystem functioning (Cardinale et al., 2012). Species mixtures positively affect both above- and belowground productivity in diverse ecosystem types (Zhang et al., 2012; Liang et al., 2016; Ma and Chen, 2016; Duffy et al., 2017; Williams et al., 2017). However, whether the positive mixture effects on productivity can be generalized to other ecosystem processes remains unclear, especially for belowground processes in long-lived natural forests. In terrestrial ecosystems, fine roots (≤ 2 mm) with high biomass turnover and mortality rates are a major contributor to nutrient cycling and carbon accumulation, translocating carbon and nutrients from roots to the long-lasting soil organic pool (Richter et al., 1999; Tefs and Gleixner, 2012; Jackson et al., 2017). Fine root turnover rate ($year^{-1}$) is the inverse of fine root lifespan, and it is calculated by dividing annual fine root production by the average fine root biomass over a year (Aber et al., 1985; Yuan and Chen, 2010). Fine root biomass mortality at the stand level refers to annual biomass loss from fine root senescence ($Mg\ ha^{-1}\ year^{-1}$) (Yuan and Chen, 2013; Feng et al., 2018).

In the boreal forest, approximately 50–70% of soil carbon results from the mortality of roots and root-associated microorganisms (Clemmensen et al., 2013). Unlike leaves, the timing and rate of root growth and root death are difficult to study, especially at the stand level. This is because sampling plant roots to represent the overall root pool of the stand is destructive, laborious and technically challenging (Hendricks et al., 2006; Brassard et al., 2009). Particularly, although fine root mortality and turnover differ with species traits and root sizes (Chen and Brassard, 2013; McCormack et al., 2015, 2017), detailed maps of fine root distributions are currently almost impossible to construct at the stand level (Brassard et al., 2011). The limited appreciation of the effects of species mixture on fine root turnover and mortality at the stand level is a major omission in our understanding of how species mixture affects ecosystem functions and hinders efforts to model terrestrial biogeochemistry (Ostle et al., 2009).

Species mixture may increase fine root turnover and biomass loss from mortality. A few existing studies, conducted in temperate forests at the stand level, however, have reported contrasting results. Fine root biomass turnover rate was found to increase with tree species richness

* Corresponding author.
E-mail addresses: zma2@lakeheadu.ca (Z. Ma), hchen1@lakeheadu.ca (H.Y.H. Chen).

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in an 80- to160-year-old natural temperate forest (Jacob et al., 2014) as well as in a 5- to 6-year-old temperate plantation (Lei et al., 2012). In contrast, a study conducted in an 8- to 14-year-old temperate plantation did not observe higher biomass turnover rate in mixtures than monocultures (Domisch et al., 2015). Because (*i*) above- and belowground biomass and production are higher in species mixtures (Zhang et al., 2012; Liang et al., 2016) and (*ii*) high fine root production and biomass lead to great resource scarcity, and reduce root lifespans and increase turnover rates (McCormack et al., 2012, 2014; Chen and Brassard, 2013; McCormack and Guo, 2014), our first hypothesis was that fine root biomass turnover and mortality would be higher in species mixtures than expected from monocultures. Since positive mixture effects on productivity tend to increase with stand development (Zhang et al., 2012; Ma and Chen, 2017), we also expect that positive mixture effects on turnover and mortality would increase with stand development. Because species mixture increases species evenness (Kirwan et al., 2007; Hillebrand et al., 2008; Brassard et al., 2013), we expect that fine root turnover and mortality would increase with species evenness.

Mixture effects on turnover rate may also change with soil depth. When stimulated by more resource competition such as higher production and biomass in species mixtures, plants can adjust their rooting depths and grow more fine roots to soil layers with more resources or with less root competition (Brassard et al., 2013; Mueller et al., 2013; Ma and Chen, 2017). These rooting strategies may change with stand development. Low root biomass in young stands may underutilize soil space and other resources (water and nutrients) with little resource competition and interspecific root interaction in mixtures (de Kroon et al., 2012; Yuan and Chen, 2012), which may result in minimal alteration of fine root distribution (Ma and Chen, 2017). Increasing root biomass and production with stand development (Yuan and Chen, 2012), as well as increasing tree sizes, requires roots to grow deeper, especially in mixtures in which fine root production is higher than the average of those in monocultures (Ma and Chen, 2017). Our second hypothesis was that positive mixture effects on turnover would be stronger in deep soil layers, especially in older stands. Since fine root biomass loss from mortality is closely related to turnover rates (Persson, 1980; Hendrick and Pregitzer, 1993; Gill et al., 2002; Iversen et al., 2008), we also expect that mixture effects on mortality would also be stronger in deep soil layers.

The three previous studies have attributed high biomass turnover rates to high competition intensity in species mixtures (Lei et al., 2012; Jacob et al., 2014; Domisch et al., 2015). This attribution is plausible since more fine roots per unit soil volume or nutrient in species mixtures would indicate less available soil volume and nutrients per individual roots (Leuschner et al., 2001; Beyer et al., 2013). The reduced soil resource availability decreases fine root longevity because their maintenance costs exceed the benefits of resource acquisition (Chen and Brassard, 2013; McCormack and Guo, 2014). Fine root turnover increases with fine root production under resource enrichment such as elevated CO_2 (Norby et al., 2004). Yet, it remains unclear whether fine root biomass turnover and biomass loss from mortality are positively associated with fine root biomass and production across natural forest stands with varying species composition from monocultures to mixtures. Our third hypothesis was that fine root biomass turnover rate and biomass loss from mortality would be positively associated with fine root biomass and annual fine root production.

As the most common natural disturbance in boreal forests, wildfire has resulted in a diversity of forest mosaic ranging in composition from pure deciduous and mixed deciduous-coniferous to pure coniferous stands. Here, we examined the mixture effects on fine root turnover and mortality in 8-, and 34-year-old single-species-dominated and mixed stands of natural boreal forest. We specifically tested whether (*i*) species mixtures would have higher fine root turnover and mortality than expected from those of single species-dominated stands, the species mixture effects on turnover and mortality would increase with stand development, and fine root turnover and mortality would increase with tree species evenness; (*ii*) positive mixture effects on turnover and mortality would be stronger in deep soil layers, especially in older stands; (*iii*) fine root turnover and mortality rates would be positively associated with both fine root biomass and production because increased resource competition associated with high biomass and production reduces fine root longevity (Beyer et al., 2013; Chen and Brassard, 2013; McCormack and Guo, 2014).

2. Material and methods

2.1. Study area and experimental design

Our study area was located approximately 150 km north of Thunder Bay, Ontario, between 49°27′ N to 49°38′ N, and 89°29′ W to 89°54′ W. The mean annual temperature and annual precipitation between 1981 and 2010 was 1.9 °C and 824 mm, respectively, at the closest climatic station of Cameron Falls (Environment Canada, 2016). The topographical features were shaped by the retreat of the Laurentide Ice Sheet approximately ten millennia ago. Soils are relatively deep glacial tills of the Brunisolic order on the upland sites (Soil Classification Working Group, 1998). Wildfire is the primary stand-replacing natural disturbance in our study area, with an average fire return of approximately 100 years over the last century (Senici et al., 2010). Full details of the experimental design were described in Ma and Chen (2017). Here, a brief description is given.

We sampled two post-fire stand age classes (i.e., 8 and 34 years since fire) and three overstory types (single-species stands dominated by *Populus tremuloides* Michx. (*Populus*) and dominated by *Pinus banksiana* Lamb. (*Pinus*) to mixtures (*Populus* + *Pinus*)) at mesic sites in the study area. We replicated each of the stand age classes and overstory types three times. Stand ages were derived from fire records and verified by sampling dominant trees (Senici et al., 2010). Similar to other studies in natural forests and in following the definitions of single- and mixed species stand in the forest resource inventory (MacPherson et al., 2001; Brassard et al., 2011), we defined single- and mixed-species stands as stands which contained a ≥80% stand basal area of a single species and stands in which none of the component species had a ≥80% stand basal area, respectively. Understorey vegetation accounts for the majority of species diversity and has strong affiliations with overstorey composition (Bartels and Chen, 2013). We used ecological classification approach to ensure that all sample stands were similar based on topography and soil texture (Taylor et al., 2000). We allocated all sites on mid-slope positions of well-drained glacial moraines with > 50 cm in thickness. The soil moisture regime class was confirmed by a soil profile examination, dug to the parent material, within each selected stand. The similarity of the sites was further validated through a comparison of the physical and chemical properties of soils; that is, the concentrations of total nitrogen and total carbon, cation exchange capacity, and soil texture composition of the mineral soil at a depth of 30–55 cm, following the method described by Laganiere et al. (2012). Stands were allocated several kilometers apart from each other to minimize neighborhood and unknown environmental influence that might be spatially correlated.

2.2. Data collection

A circular plot (400 m^2 in the 34-year-old stands, and 50 m^2 in the 8-year-old stands due to high stem densities) (Hart and Chen, 2008) was randomly established to represent each sample stand. All live trees with diameter at breast height (DBH) over 2 cm were measured and recorded. The characteristics of our study stands were described in detail (Table S1). Species richness was the number of tree species in the plot. We calculated Shannon's index (Shannon and Weaver, 1949) using the species proportions based on their relative stand basal area (Table S1). Species evenness was calculated using *J′* index (Pielou, 1969) as the ratio of Shannon's index to the natural logarithm of species richness.