Forest Ecology and Management 354 (2015) 119–129

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

The influence of boreal tree species mixtures on ecosystem carbon storage and fluxes

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ARTICLE INFO

Article history:
Received 18 March 2015
Received in revised form 11 June 2015
Accepted 22 June 2015
Available online 7 July 2015

Keywords:
Boreal forest
Mixedwood management
Tree species
Trembling aspen
Carbon pools
Mixture-productivity relationships

ABSTRACT

Plant species mixtures are often seen as being able to achieve higher productivity and carbon (C) sequestration than their single-species counterparts, but it is unclear whether this is true in natural forests. Here, we investigated whether naturally-regenerated mixtures of common North American boreal tree species were more productive and stored more C than single-species stands. We also examined how closely the different C pools and fluxes were interrelated and whether these relationships varied with species composition. Single- and mixed-species stands of trembling aspen, black spruce and jack pine on mesic sites were selected in two regions of the Canadian boreal forest to assess aboveground and belowground productivity and C storage. Although previous studies conducted in these stands found synergistic effects of tree species mixtures on specific C pools and fluxes, such as higher organic layer C stocks and higher fine root productivity in some mixtures, no effects were detected on combined C pools or fluxes at the ecosystem level in the current study. Aspen abundance was linked with higher aboveground tree productivity, higher aboveground living biomass and higher soil heterotrophic respiration, indicating that aspen acts as a key driver of ecosystem C storage and fluxes in these natural forest ecosystems, more so than species richness. However, our results do not rule out the possibility of increased productivity and C storage in mixed stands under environmental conditions or stand developmental stages that are different from the ones studied here. Furthermore, when the entire forest ecosystem is considered (not only tree parts), synergistic effects of tree species mixtures may be more difficult to observe because the beneficial effect of species mixing on one specific C pool may be counterbalanced by a negative effect on another pool.

1. Introduction

Species mixtures are common in natural forests, and it has been hypothesized that mixed-species stands could be more productive than single-species stands because resources are used more completely by the companion species (Hooper et al., 2005; Kelty, 2006). Complementarity can come from niche partitioning and/or facilitation among species with different functional traits, thereby decreasing competition in diverse communities (Tilman, 1999; Brooker et al., 2008). Most studies investigating species mixture-productivity relationships using trees were conducted in plantations. Empirical evidence of wood volume production gain in naturally-regenerated mixedwoods is sparse and controversial. For example, aspen–conifer mixtures were reported as more productive than single-species stands in studies by MacPherson et al. (2001) and Légaré et al. (2004), but less productive in the Edgar and Burk (2001) study. Using large datasets of forest inventory plots in natural systems, Paquette and Messier (2011) and, more recently, Vilà et al. (2013) showed that mixed-species stands had higher tree productivity and higher wood volume, respectively, than single-species stands, though neither of these studies controlled for the potentially better edaphic conditions on which mixed stands are often established. A global meta-analysis of tree species diversity effects on aboveground productivity indicates an average 24% productivity gain in mixed-species stands compared with monocultures, and the positive diversity effects are dependent on the number of species in the mixtures, species evenness, life-history trait variation, and the stage of stand development (Zhang et al., 2012).

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http://dx.doi.org/10.1016/j.foreco.2015.06.029

Most studies assessing tree mixture-productivity relationships have focused on merchantable wood biomass or stemwood C, probably due to its economic importance. However, C is stored in a variety of pools beyond stem wood, including tree roots, understory vegetation, coarse woody debris and soil. Fine roots as well as understory plants may each represent over one third of the total ecosystem production in some forests (Jackson et al., 1997; Bisbee et al., 2001; Connell et al., 2003). Soil is also a C pool of major importance given that more C is stored in the soil than in plant biomass (Lal, 2005), though only the upper soil profile is usually affected by current vegetation (Laganière et al., 2013; Vesterdal et al., 2013). To our knowledge, there are no reported studies that have examined tree species mixture effect on C storage and sequestration at the entire ecosystem level (i.e. not only aboveground tree parts) in natural systems.

In this synthesis study, we used empirical data from single-and mixed-species stands of two regions of the Canadian boreal biome, some of which have already been published (Cavard et al., 2010; Brassard et al., 2011b; Cavard et al., 2011a; Cavard et al., 2011b; Laganière et al., 2012; Brassard et al., 2013; Laganière et al., 2013), to investigate the links between ecosystem C pools (organic layer, mineral soil, dead and live coarse, medium and fine roots, aboveground live tree parts, snags and understory vegetation) and fluxes (aboveground tree productivity, fine root productivity, understory productivity and soil heterotrophic respiration) and tree species mixture effects. Specifically, we wished to address the following questions: (1) Do mixed-species stands have greater ecosystem C storage and sequestration than single-species stands? (2) How are the sizes of the different C pools related to tree species composition? (3) Is higher ecosystem C storage associated with higher ecosystem production and/or slower decomposition?

2. Material and methods

2.1. Study area

The study was conducted in two regions of the North American boreal forest, in Canada. One study region was located in northwestern Ontario (named "ON" hereafter), approximately 150 km north of Thunder Bay (49°23′N to 49°37′N, 89°31′W to 89°45′W). The climate is boreal with mean annual precipitation (MAP) of 712 mm and a mean annual temperature (MAT) of 2.5 °C (Environment Canada, 2014). Four stands dominated by jack pine, *Pinus banksiana* Lamb. (abbreviated as "JP"), five stands dominated by trembling aspen, *Populus tremuloides* Michx. (abbreviated as "TA"), and thirteen mixed-species stands of jack pine, aspen and/or black spruce, *Picea mariana* (Mill.) BSP (abbreviated as "BS"), (see Table 1) were selected for sampling in a 250 km^2 area with a maximum distance of 30 km between stands (total: 22 stands). The understory vegetation in the jack pine stands consisted mainly of the herbs *Cornus canadensis* L., *Maianthemum canadensis* Desf. and *Linnea borealis* L. and feathermosses, whereas the understory in the trembling aspen stands was dominated by the shrubs *Acer spicatum* Lamb., *Rubus pubescens* Raf. and *Ribes glandulosum* Grauer ex Weber and the herbs *M. canadensis*, *Mitella nuda* L. and *Aster macrophyllus* (L.) Cass. The understory in the mixedwood stands contained plant species found in both the jack pine and aspen stands (Bartels and Chen, 2013). Soils were well-drained silty loam to sandy loam, classified as Brunisols that originated from glacial till deposits (Soil Classification Working Group, 1998). The topography was relatively flat, and all stands originated from the same 1923 wildfire (Senici et al., 2010).

The second region was located in western Quebec (named "QC" hereafter), approximately 50 km northeast of La Sarre (49°08′N to 49°11′N, 78°46′W to 78°53′W). The climate is boreal with MAP of 890 mm and MAT of 0.7 °C (Environment Canada, 2014). Six stands dominated by black spruce, eight stands dominated by trembling aspen, and seven mixed stands comprising a relatively uniform component of both tree species were selected for sampling in a 100 km^2 area with a maximum distance of 10 km between stands (total: 21 stands). The understory vegetation in the black spruce stands consisted mainly of the herbs *C. canadensis*, *Rhododendron groenlandicum* (Oeder) Kron and Judd and *Vaccinium* spp. and big red stem moss (*Pleurozium schreberi* (Bird.) Mitt.). In the aspen stands, by contrast, the understory was dominated by the shrubs *R. pubescens*, *Diervilla lonicera* Mill. and *Viburnum edule* (Michx.) Raf. and the herbs *C. canadensis*, *Viola* spp., *L. borealis* and *M. canadensis*, while the mixedwood stands had an understory of plant species that were found in both the black spruce and aspen stands. Soils were moderately-drained silty clay, classified as Luvisols that originated from glaciolacustrine deposits (Soil Classification Working Group, 1998). The topography was flat, and all stands originated from the same 1916 wildfire (Bergeron et al., 2004).

2.2. Sampling design

Similar to other studies that investigated tree species mixture effects in naturally established mature stands (e.g. Wang et al., 2002; Brassard et al., 2008), the criteria for stand selection were that mixed-species stands should have relatively equal proportions of component tree species by stand basal area, while for single-species stands, the basal area of a single tree species would be >80% of total stand basal area (Table 1).

Table 1
Overstory characteristics and mean annual soil temperature (at 5 cm depth) of the study plots (mean ± 1 SE). Other species consist of balsam fir, white spruce and paper birch in the Ontario region and jack pine and balsam fir in the Quebec region.

Stand type	Number of stands	Total basal area (m^2 ha^{-1})		Total density (stems ha^{-1})		Species composition by basal area (%)								Soil temperature (°C)	
						BS		TA		JP		Other species			
Ontario															
JP	4	49.4	(3.6)	2445	(128)	7.5	(2.0)	0.0	(0.0)	83.2	(1.9)	9.3	(1.6)	4.8	(0.2)
TA	5	43.3	(3.8)	780	(43)	0.0	(0.0)	95.2	(1.2)	0.7	(0.7)	4.1	(0.9)	5.5	(0.1)
JP + BS	3	47.6	(1.2)	2450	(240)	29.2	(3.9)	3.6	(2.3)	64.1	(4.9)	3.0	(1.5)	4.5	(0.1)
TA + BS	4	53.9	(3.3)	2045	(205)	20.6	(3.7)	68.8	(4.3)	3.5	(1.9)	7.0	(1.9)	4.8	(0.1)
JP + TA	4	44.6	(2.0)	1300	(168)	6.7	(1.4)	30.7	(7.0)	48.2	(6.4)	14.4	(6.1)	5.4	(0.1)
JP + TA + BS	2	44.3	(1.9)	2463	(238)	26.0	(4.8)	27.1	(3.6)	44.0	(10.9)	2.9	(2.5)	4.4	(0.1)
Quebec															
BS	6	43.4	(2.3)	3115	(380)	89.4	(4.2)	1.8	(0.7)			8.8	(4.0)	4.7	(0.1)
TA	8	57.7	(3.6)	1065	(105)	8.9	(1.8)	88.5	(2.6)			2.6	(2.3)	4.9	(0.1)
BS + TA	7	52.2	(2.7)	1578	(128)	33.8	(3.6)	59.5	(3.5)			6.7	(1.6)	5.2	(0.1)

Note: BS, black spruce; JP, jack pine; TA, trembling aspen. Numbers in parentheses are ±1 SE. Modified from Cavard et al. (2011).