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Trade-offs across densities and mixture proportions in lodgepole pine-hybrid spruce plantations

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ABSTRACT

Monocultures tend to yield higher total stand volumes and are simple to manage. Yet, mixed species stands may result in similar stand volumes while providing benefits such as mitigating damage from insects and disease. To understand the effects of stand density and species mixture and their interactions on stand yield, tree size and morphology, and damage in monocultures and mixtures, we analyzed a 25-year-old experiment in interior British Columbia, Canada. The lodgepole pine (Pl)-interior hybrid spruce (Sx) experiment included three densities—1000, 1500, and 2000 stems per hectare (SPH)—and five species mixtures—1:0, 3:1, 1:1, 1:3, and 0:1 Pl:Sx. Results 25 years after stand establishment showed that stand volume was significantly larger with an increasing proportion of Pl across all stand densities. Pl had 10% larger diameters in the 1000 SPH than in the 2000 SPH and when mixed with Sx (1:1). Pl had larger crowns in mixtures regardless of density. Mixture proportion did not affect gall rust incidence or stem form in Pl, but reduced attack in Sx by spruce weevil. Our findings suggest that mixing Pl-Sx and high planting density decrease weevil attacks in Sx, which reduce loss in timber quality. Yet, Pl quality may decrease when mixed with Sx, due to larger Pl crowns. These results may be used to improve the implementation of management strategies that decrease trade-offs between yields, desired market tree sizes, and timber loss from pest and pathogens, while making the stands more resilient to further climate change impact.

1. Introduction

The choice of monocultures versus mixtures is complex from a silvicultural point of view. Single-species plantations may be simpler to plant and manage, and the crop can be harvested more economically (Coates and Lilles, 2014). Yet, planting a mixture of species with complementary growth characteristics can reduce the effect of competition with one species having a positive effect on the other species in the stand (Forrester and Bauhus, 2016; Paquette and Messier, 2011). Temperate and boreal forest ecosystems of western Canada provide more than 60% of Canada's harvest volume (NRCan, 2020) with lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm) and interior hybrid spruce (*Picea glauca* × *engelmannii* (Moench) Voss), being the two most important native commercial conifer species in British Columbia, widely used in reforestation. The two species have very different growth characteristics: Pl (lodgepole pine) is a shade-intolerant, fast growing and deep rooted species, while Sx (interior spruce) is more shade tolerant, shallower rooted, and is an initially slower growing species that retains its growth rate longer (Eis et al., 1982). Consequently, culmination age was found to be 30–40 years longer for Sx than for Pl in interior British Columbia (BC), Canada. Interest in this mixture has increased following the unprecedented outbreaks of mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) throughout the BC interior in the late 1990s, where catastrophic losses occurred in Pl-dominated stands (Woods et al., 2010). Stands consisting of Pl, the primary host of MPB, often have a component of Sx as advance regeneration, which is a major source of canopy replacement (Coates et al. 2006). Therefore, stands are undergoing substantial conversion following MPB attacks in interior BC, towards more complex mixed forests with shade-tolerant conifers such as subalpine fir and Sx (Astrup et al., 2008; Axelson et al., 2009).

A more complex canopy structure (i.e., canopy packing and crown plasticity) could promote higher productivity in mixtures, in terms of

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stand yield, compared to monocultures (Williams et al., 2017), but evidence shows that this effect varies with tree species, site fertility, and stage of stand development (Barbeito et al., 2017; Forrester, 2014; Toïgo et al., 2015). In a comparison of 1:1 mixtures of Pl and black spruce in western Canada, stands over 50-years-old attained the same yield as Pl monocultures, but in younger stands, mixtures often had lower volumes (Chen et al., 2003). In a 34-year-old Pl-ponderosa pine mixture in central Oregon, Garber and Maguire (2004) found no difference in stand volume between Pl mixtures vs. monocultures. Pl-black spruce mixtures in western Canada had higher tree-size diversity than their respective single-species stands (Varga et al., 2005).

An often overlooked mixture attribute with important consequences for the final yield and value of products is stand density. Density determines the intensity of competition among individuals and the outcome of species interactions (Garber and Maguire, 2004). Density is a key factor in understanding inter-species mortality and growth rates when grown together (de Montigny and Nigh, 2007), and thus experiments that control mixed-species densities as well as composition are valuable (Vanclay, 2006). Effects of stand density on individual performance and stand production in monospecific populations are well characterized (Weiner and Freckleton, 2010). Few experiments have controlled for density in determining the effect of tree species mixture on growth. Generally density and initial tree size have been found to be more important to explain productivity than tree species mixture (Collet et al., 2014; Erickson et al., 2009). In a 12-year-old western hemlock-Douglas-fir experiment in the Pacific Northwest, Amoroso and Turnblom (2006) found that mixtures exhibited less volume per ha at low densities. However, the species mixtures promoted higher yield at high planting densities where competition among trees was more important. de Montigny and Nigh (2007) found that Douglas-fir was significantly larger than western red cedar in a 14-year-old Douglas-fir-western red cedar plantation in BC, but did not find any effect of density on yield or tree size. In both examples of young mixed plantations, trees were not old or big enough to detect density effects. However, it is reasonable to assume that these mixed plantations, containing one initially slower-growing species, may have higher yields than monocultures before the rotation age is reached (Coates and Lilles, 2014).

Trees of the same species may have equivalent volumes, despite having large differences in stem form described by slenderness (the ratio of height to DBH). This difference can have a large impact for stem quality as it is closely related to branch and crown structure and branch increment (Kroon et al., 2019). Both density and mixing can affect stem growth allocation and therefore slenderness (Barbeito et al., 2014; Saarinen et al., 2020). Wood properties such as wood density and fiber length are also expected to be positively correlated with increased competition at higher stand density (Karlsson et al., 2013) and negatively by mixture when competition is reduced (Rais et al., 2020).

Even if the productivity is comparable or lower in monocultures, mixing tree species increases the resistance to insect and disease attack by specialist insect herbivores or fungal pathogens (Klapwijk and Björkman, 2018; van Halder et al., 2019). In BC, mixtures could disperse the damage by interspersing species and increase the resilience to biotic and abiotic disturbances commonly occurring in the province. Although intermingling with other species would not necessarily decrease the susceptibility of a stand to MPB-infestation (Amman and Baker, 1972), the severity of an attack would be much lower in a mixture than in a Pl monoculture, simply because there is a smaller proportion of host species available (Bauhus et al., 2017). In addition to MPB, western gall rust (*Cronartium harknessii* (J.P. Moore) E. Meinecke) is among the most damaging pests to Pl in BC. Gall rust can result in growth losses, poor tree form, and reduced wood quality at rotation (Gross, 1983). Spruce leader weevil (*Pissodes strobi* Peck) is a widely distributed pest of Sx in northwestern North America (Alfaro et al., 1996). Destruction of the terminal leader results in the formation of stem defects, which reduce tree growth or even render trees unmerchantable for lumber production (Alfaro et al., 1994).

Many studies have focused on yield differences between mixtures and monocultures (Paquette and Messier, 2011; Pretzsch et al., 2015). Yet, the effects of density and mixture on yield as well as tree size and morphology, which drive the quality of many timber products, remain poorly understood. Similarly, better understanding the potential of mixtures to increase the resistance to biotic attack frequency remains a major research challenge for designing specific mixtures that economically match or outperform monocultures. This study elucidates potential trade-offs between volume, tree size, and damage in a Pl-Sx mixture that has commonly been planted in interior BC, Canada. We analyzed data 24 years after planting from a long-term experimental plantation with three planting densities and five species mixture proportions to address the following questions: (1) What are the stand density and species mixture effects on stand volume and on tree size and morphology? (2) What are the stand density and species mixture effects on the frequency of trees damaged by pest or disease? and (3) What is the severity of the damage, defined as the impact on stand volume reduction and stem form defects? Our results will help support future silvicultural decisions, such as whether to plant intimate mixtures of Pl-Sx or plant the two species separately creating mini-monocultures adjacent to each other. The latter are represented by the monocultures of Pl and of Sx in our study.

2. Methods

2.1. Study site and experimental design

The study was conducted northwest of Vernon, British Columbia, Canada (50° 20′ 30″N, 119° 38′ 00″W). The experiment (EP964.22) is at an elevation of 1560 m and is located on a gentle slope (10%), with an east-northeast aspect (Lloyd et al., 1990). The soil is classified as a Brunisol, is loamy in texture, well-drained, and has a rooting depth of 30 cm. The soil moisture regime is mesic to submesic and the soil nutrient regime is medium (Pojar et al., 1987). Site index (i.e., the average height that free growing, undamaged top height (m) trees of a given species can achieve in 50 years growth above breast height) is 16.4 for Pl and 16.9 for Sx (Mah et al., 2003). The Engelmann spruce (*Picea engelmannii* Perry) - subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) biogeoclimatic zone covers 14% of British Columbia's land (Eastham and Jull, 1999). This area is dominated by these two species, which prior to the study, occupied the site until 1991–1992, when it was clearcut (Johnstone, 1999). Lodgepole pine (Pl) is a common seral species found mainly after wildfires. In 1994, the trial was planted with Pl and Sx container seedlings (PSB, 3 cm wide by 13 cm deep) (Johnstone, 1999, 2004).

The experiment consists of a completely randomized design with two fixed effects: stand density and species mixture (Fig. 1). We examined the effects on growth and development of Pl and Sx when grown at three stand density levels (1000, 1500 and 2000 stems per hectare [SPH]) and five species mixture levels (1:0-Pl monoculture, 3:1, 1:1, 1:3, 0:1-Sx monoculture), resulting in 15 treatment combinations. Each of these 15 treatment combinations was replicated twice resulting in 30 square experimental units, which are referred to as plots. In the single species plots, 144 trees were planted in a 12 × 12 arrangement with regular spacing between trees to achieve the target planting density. Intertree distance and plot size for the single species plots were: SPH 1000: 3.16 m, 1505 m^2; SPH 1500: 2.58 m, 1050 m^2; SPH 2000: 2.24 m, 818 m^2. The mixed species plots were planted in a 15 × 15 arrangement for a total of 225 trees. The intertree distance was the same as above; the plot size was: SPH 1000: 2323 m^2; SPH 1500: 1608 m^2; SPH 2000: 1253 m^2 (see Fig. A.1 for mixture layouts).

Within each plot the outer two trees within each row are buffer trees, and there are 64 (8x8) and 121 (11x11) sample trees in monocultures and mixtures, respectively. During the first five years after planting, seedlings that died were replaced with seedlings of the same age and seedlot from an on-site reserve plantation (Johnstone, 2004). During this period, about nine percent of the plantation was replaced, with much of this early mortality being due to frost injury (Johnstone, 2004).

Fig. 1. Images of the lodgepole pine (Pl)-hybrid spruce (Sx) plantation. (A) 1:3 mixture at 1000 stems per hectare (SPH). (B) Pl monoculture at 2000 SPH. In the picture: G. O'Neill, BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development.

Competing brush and ingress was removed until 2000.

2.2. Data

The trial was re-measured every five years (1998, 2003, 2008, 2013 and 2018) after initial planting. At each measurement, species was recorded for all trees along with tree status (live versus dead), diameter at breast height (dbh, cm, with steel tape to the nearest mm), and height (ht, m, with Vertex hypsometer once trees exceeded telescoping height pole size) (Table 1). In 2018, additional measurements were recorded for each live tree: crown radii from bole to maximum crown extent in the four cardinal directions (m), measured by two people holding opposite ends of a measuring tape, and height to live crown (m), defined as the length of the stem from ground level to the lowest live branch that forms part of the uninterrupted live crown. A detailed damage survey was also conducted in 2018, in which symptoms of all disease, insect, animal and abiotic damage were recorded for all trees. Buffer trees and dead trees were removed from the dataset. We focused on the analysis of the last measurement (i.e., 2018), because (1) we expected the differences to be larger than at a younger age (see Fig. 2), and (2) additional damage and tree information was available for the 2018 measurement.

2.3. Characterizing stand volume

Individual tree volumes (m^3) were calculated using the taper function defined by Kozak (1988) and used to calculate stand volume (Vol; m^3 ha^{-1}) by species for each treatment in 2018. Relative yield totals (RYT) (Harper, 2010) were defined as the sum of the ratio between yield (i.e., stand volume per ha) for species A in mixture vs. monoculture plus the ratio between yield for species B in mixture vs. monoculture in 2018. In a 1:1 mixture, if there is no effect of one species on the other, relative yield is 0.5 per species for a RYT of 1. An RYT $>$ 1 indicates a potential productivity gain for the mixture (Harper, 2010).

Table 1
Mean values for Pl and Sx by density and mixture in 2018. Yield metrics: volume (stand volume, m^3 ha^{-1}); size and morphology metrics: dbh (diameter at breast height, cm), ht (height, m), CPA (crown projection area, m^2), CR (crown ratio), and damage metrics: Rust (Western gall rust in stem, %), Weevil (spruce leader weevil, %).

Density	Mixture Pl:Sx	Volume (m^3 ha^{-1})		dbh (cm)		ht (m)		CPA (m^2)		CR		Rust (%)	Weevil (%)
		Pl	Sx	Pl	Sx	Pl	Sx	Pl	Sx	Pl	Sx	Pl	Sx
1000 SPH	1:0	63.32		14.3		9.14		9.78		0.85		7.1	
	3:1	39.60	3.24	13.89	7.30	8.48	5.62	8.77	3.09	0.89	0.91	3.6	5.1
	1:1	24.67	4.84	13.96	6.68	8.45	5.15	10.47	2.72	0.91	0.90	3	7.5
	1:3	17.34	6.63	14.48	6.97	8.05	5.04	11.56	2.95	0.93	0.92	5.7	2.8
	0:1		11.67		7.83		5.23		2.80		0.93		16.7
1500 SPH	1:0	70.69		12.82		8.79		7.24		0.82	0.91	4.3	
	3:1	52.91	5.59	13.06	7.29	8.47	6.01	6.94	2.70	0.84	0.91	5.4	7
	1:1	37.70	6.74	13.41	6.47	8.33	5.23	9.07	2.68	0.88	0.90	3.4	6.4
	1:3	29.56	12.76	15.38	7.20	8.78	5.56	12.13	2.74	0.91	0.93	4.5	4
	0:1		12.14		6.87		4.71		2.69				11.7
2000 SPH	1:0	71.49		11.19		8.23		4.42		0.79		4.8	
	3:1	64.75	5.24	12.42	6.11	8.82	5.44	6.45	2.04	0.79	0.86	5.5	3
	1:1	49.63	10.73	13.42	6.87	8.82	5.85	6.60	2.52	0.84	0.90	4.7	1.9
	1:3	33.66	17.03	14.32	7.29	8.82	5.80	7.73	2.45	0.89	0.90	3.1	11.6
	0:1		17.61		6.58		4.76		2.55		0.89		6.8

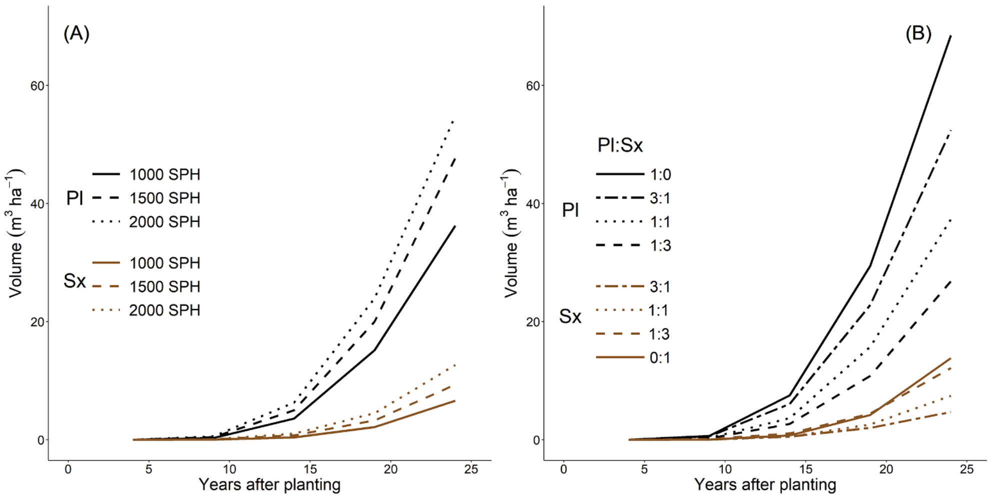

Fig. 2. Volume (m^3ha^{-1}) for Pl (black) and Sx (grey) by (A) density: 1000 SPH, 1500 SPH, and 2000 SPH averaged across all mixtures; and (B) mixture proportion: 1:0 Pl monoculture, 3:1, 1:1, 1:3 and 0:1 Sx monoculture averaged across all densities.

2.4. Characterizing size and morphology

Tree size and morphology metrics were calculated for each tree and averaged for every treatment and species to identify differences between mixtures and monocultures (Table 1). To characterize size, in addition to dbh and ht, we calculated quadratic mean diameter (QMD, cm) and height-to-diameter ratio (slenderness, m:cm). The quadratic mean radius obtained from the four crown radii was used to calculate the crown projection area (CPA, m^2) based on the formula of the area of a circle. Crown ratio (CR) was defined as the ratio of crown length to total tree height. Slenderness describes the relationship between ht and dbh, with a higher slenderness indicating a greater ht over dbh. CPA was calculated using the four crown radii, and CR was calculated as the ratio of crown length to tree height.

$$Y_{ij} = \mu + stand\ \ density_i + species\ \ mixture_j + (stand\ \ density \times species\ \ mixture)_{ij} + \varepsilon_{ij}$$

2.5. Evaluating damaging agents

We tested for differences among treatments in the percent of Pl trees affected by western gall rust (hereafter rust) and the percent of Sx trees affected by spruce leader weevil (hereafter weevil), the two most prevalent types of detected biotic damage affecting the plantation (measured by % of affected trees) (Fig. A.2). Rust and weevil incidence were calculated as the number of live trees with rust or weevil status, respectively, divided by the total number of live trees. Only trees with galls occurring on the main stem were considered as diseased (i.e., can lead to growth loss and early mortality), while trees with galls on branches were considered as healthy (i.e., little damage for the host tree and rarely lethal, but represent the major source of spores for further infection) (Sattler et al., 2019). In Pl trees, in addition to assessing rust incidence, we tested for differences among treatments in major stem form defects (crooks and forks) likely caused by *Pissodes terminalis* (Maclauchlan and Borden, 1996). In Sx trees, in addition to trees currently affected by weevil, we analyzed how treatments affected weevil attacks prior to 2018 that created leader damage. We further tested for differences among treatments in weevil-induced severity of stem defects (Maclauchlan and Borden, 1996). Stem defects were aggregated in two categories of severity: major defects composed of staghead trees (three or more lateral branches of equal dominance due to a single attack or consecutive attacks on the same tree), forks (two laterals assume dominance), and major crooks (a lateral assuming dominance is offset from the main stem by at least half the stem diameter); and minor defects attributed to minor crooks (little stem curvature at the point of attack).

2.6. Statistical analysis

We fit linear models for each dependent variable (volume, size, morphology) (Table 1) for each species separately. The following model was used:

where: Y_{ij} is volume, the size variable (QMD) or morphology variable (HD ratio, CPA, or CR) for Pl or for Sx at the i^{th} level of density and j^{th} level of mixture (Table 1), μ is the overall mean, stand density and species mixture (as categorical variables) are fixed effects, and ε_{ijk} is the random error term. The models were fit using the lm function contained in the R statistical programming environment (R Development Core Team, 2020). If statistically significant differences were detected for a variable, then Tukey (HSD) tests were conducted to detect which treatments differed ($p < 0.05$). Standardized residuals were visually checked for all models to assess model assumptions of equal variance and normality. To meet model assumptions, volume was log-transformed.

The proportion of trees with rust and weevil per plot were treated as binomial variables with a logit link. Generalized linear models (GLMs; McCullagh and Nelder, 1989) were used to test for differences over mixture proportions and planting densities using the R package MASS (Venables and Ripley, 2002). In addition, we used GLMs to test whether weevil attack severity (with distinction between major and minor defects) was affected by mixture and density.

3. Results

3.1. Stand volume

Overall, differences between treatments increased over time (Fig. 2). 24 years after planting, in 2018, differences between treatments in dbh, ht, and crown morphology were evident, particularly for Pl (Table 1).

Volume was higher in Pl than in Sx across all densities and mixture combinations (Table 1, Fig. 2A). We did not find any interactions in volume between density and mixture 24 years after planting ($p = 0.47$ for Pl; $p = 0.54$ for Sx). Highest planting densities resulted in highest volumes for Pl (Fig. 2A; Table 1) with significant differences between the 2000 and 1000 SPH ($p = 0.005$) and between the 1500 and 1000 SPH ($p = 0.031$). Multiple comparisons indicated that Pl volume was higher in the monoculture (1:0) than in the 1:1 ($p = 0.005$) and 1:3 ($p = 0.0006$) mixtures, higher in the 3:1 mixture than in the 1:3 mixture ($p < 0.0001$; Fig. 2B), and higher in the 3:1 than the 1:1 ($p = 0.006$), while volume in the 1:1 and 1:3 mixtures ($p = 0.72$) were not significantly different.

For Sx, highest densities also resulted in highest volumes (Table 1; Fig. 2A) with significant differences between the 2000 and 1000 SPH ($p = 0.0004$) and between the 1500 and 1000 SPH ($p = 0.047$; Fig. 2A). Volume of Sx in the Sx monoculture (0:1) was higher than in the 1:1 ($p = 0.016$) and 3:1 ($p = 0.001$) mixtures. Sx volume was also significantly higher in the 1:3 (1 pine to 3 spruce) mixture than in the 3:1 mixture (3 pine to 1 spruce) ($p = 0.003$).

A higher complementary yield effect was found at higher densities with RYT values exceeding one for the 1500 SPH (1.4 for the 1:3, 1.1 for the 1:1, and 1.2 for the 3:1 mixture) and for the 2000 SPH (1.4 for the 1:3, 1.3 for the 1:1, and 1.2 for the 3:1 mixture). For the 1000 SPH, RYT values were below one for the three mixtures (0.8 for the 1:3 and 1:1, and 0.9 for the 3:1 mixture).

3.2. Size and morphology

Higher QMDs indicated more Pl in larger diameter classes as Sx proportion increased (Table 1; Fig. 3). At 2000 SPH, QMD at 1:0 Pl was significantly lower than Pl QMD at 1:1 ($p = 0.009$) and 1:3 ($p = 0.002$). At 1500 SPH, 1:0 Pl was only significantly lower than at 1:3 ($p = 0.004$) and this difference disappeared at 1000 SPH ($p > 0.05$). QMD was slightly higher (but not significantly) for Pl monocultures at 1000 SPH (14.24 ± 0.34 cm) than for the 1:1 mixture at 2000 SPH (13.72 ± 0.47 cm), suggesting that density and mixture have a similar effect in Pl's QMD. For Sx, no differences in QMD were detected among densities ($p = 0.12$) or mixtures ($p = 0.67$).

Pl trees in 1:0 Pl monocultures had higher slenderness at 2000 SPH than at 1500 SPH ($p = 0.03$) and 1000 SPH ($p = 0.0002$). Across all densities, for a given diameter, Pl in monocultures (1:0) were overall more slender than pines in stands with increasing Sx proportion (Fig. 4A), indicating reduced competition in mixtures. However, the difference among mixture levels depended on density (interaction, $p = 0.048$). Slenderness for 1:0 Pl was greater at all densities than slenderness for the 1:3 mixtures ($p < 0.001$). At 1500 SPH and 2000 SPH, Pl also had significantly higher slenderness between the 3:1 and the 1:3 mixtures ($p < 0.01$). At 2000 SPH, Pl had significantly higher slenderness between 1:0 Pl and 1:1 ($p = 0.004$) and between 3:1 and 1:1 mixtures ($p = 0.03$). Slenderness for Sx trees in 0:1 Sx monocultures were not significantly different among densities ($p > 0.5$). For Sx trees, mixture effect on slenderness also depended on density ($p = 0.025$) with no significant mixture effect at 1000 SPH. At 1500 SPH and 2000 SPH, for a given diameter, Sx trees in 1:1 and 1:3 mixtures had higher slenderness than the 0:1 Sx monoculture ($p < 0.05$; Fig. 4B). In the 2000 SPH density, slenderness was also significantly higher in the 1:3 than in the 1:1 mixtures ($p = 0.03$).

CPA of Pl was affected by density, with significantly smaller crown projection for 2000 SPH than for 1500 SPH ($p = 0.0009$) and 1000 SPH ($p < 0.0001$; Fig. 5A). CPA of Pl in the 1:3 mixture was significantly larger than of the 3:1 mixture ($p = 0.001$) and the Pl monoculture (1:0) ($p = 0.0007$). CPA of Sx was not affected by mixture, but was significantly smaller for 2000 SPH than for 1000 SPH ($p = 0.039$; Fig. 5B). No interactions between density and mixture were observed for CPA in Pl ($p = 0.22$) and Sx ($p = 0.87$).

CR of Pl was significantly lower at 2000 SPH than at 1000 SPH for the 1:1 and 1:3 mixtures (Fig. 6A). At 2000 SPH, the 1:1 and 1:3 mixtures had a larger CR for Pl than in the 3:1 mixture and the 1:0 Pl monoculture ($p < 0.0001$; Fig. 6A). CR of Sx was significantly lower at 2000 SPH than at 1000 SPH ($p = 0.04$), but was not affected by mixture ($p = 0.22$; Fig. 6B).

3.3. Damaging agents

Thirteen percent of all Pl trees across all densities and mixtures had rust infections, and an average of 6 percent had stem galls (Table 1). On

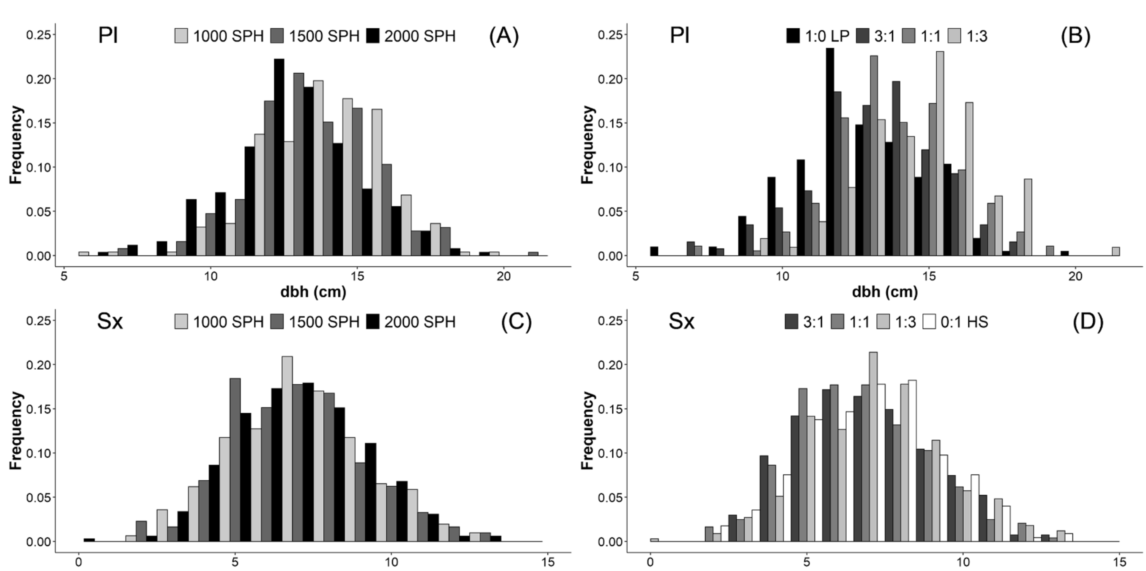

Fig. 3. Pl diameter at breast height (dbh) distribution by (A) density: 1000 SPH, 1500 SPH, and 2000 SPH; and (B) mixture proportion: 1:0 Pl monoculture, 3:1, 1:1 and 1:3; and Sx dbh distribution by (C) density (as in Pl); and (D) mixture: 3:1, 1:1, 1:3 and 0:1 Sx monoculture.

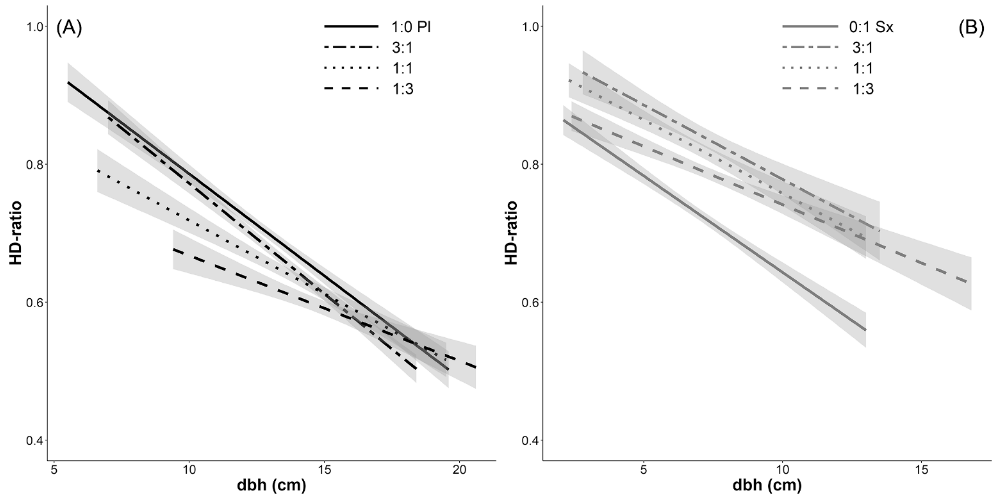

Fig. 4. Slenderness averaged across all densities for Pl (A) and Sx (B) by mixture proportion across all densities: 1:0 Pl monoculture, 3:1, 1:1, 1:3 and 0:1 Sx monoculture. The grey shaded areas indicate 95% confidence intervals.

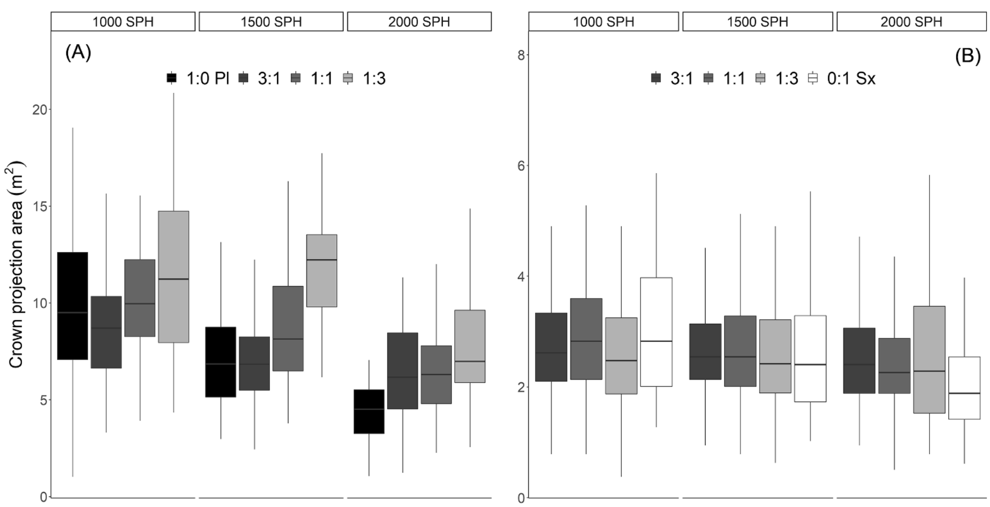

Fig. 5. Crown projection area of Pl (A) and Sx (B) by density and mixture.

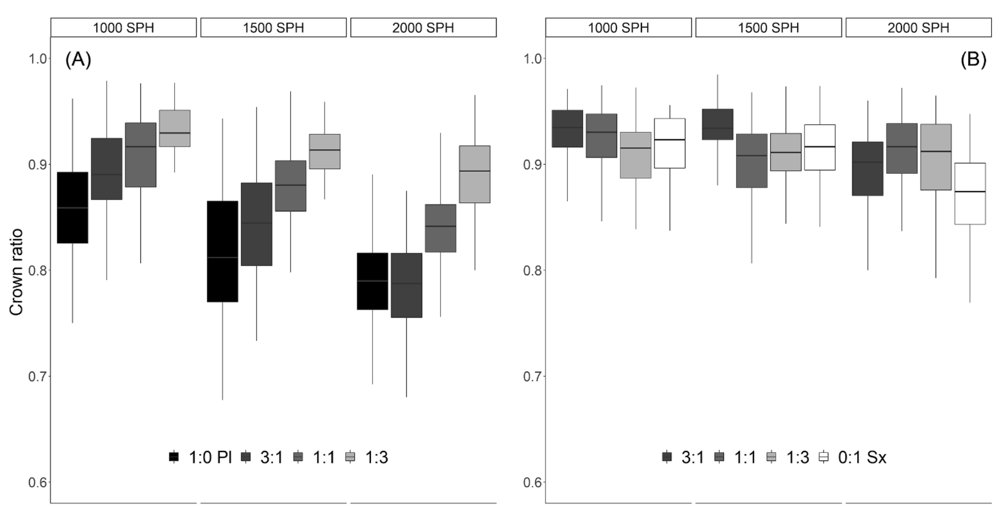

Fig. 6. Crown ratio of Pl (A) and Sx (B) by density and mixture.

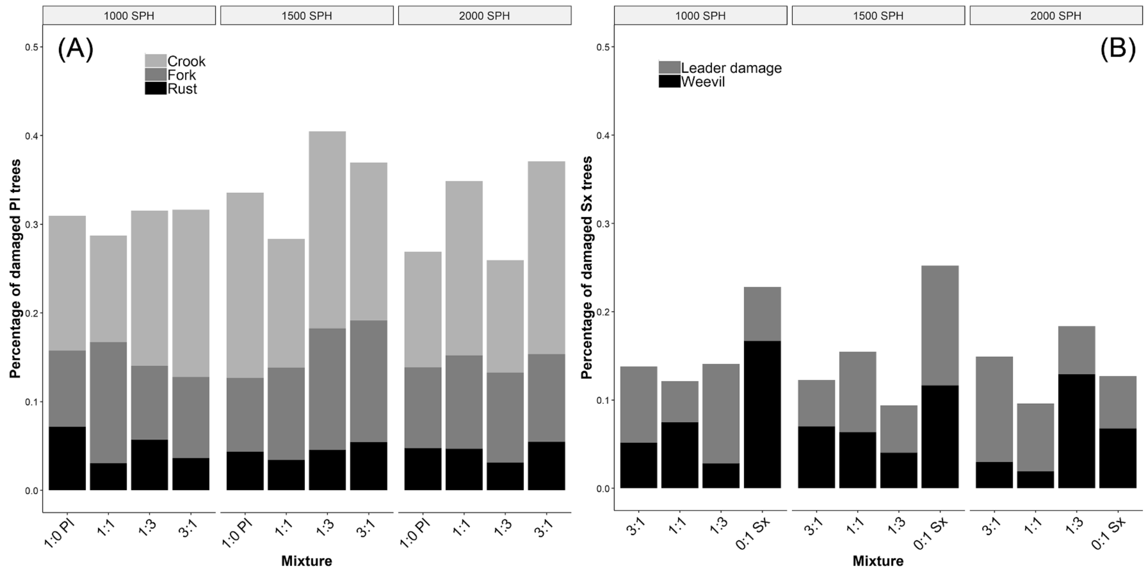

Fig. 7. Proportion of Pl (A) and Sx (B) trees with common damage types by density and mixture. For Pl trees, proportions affected by stem gall rust, crooks, and forks (A) are distinguished. For Sx trees, proportions of trees attacked by weevil in 2018 and with leader damage (i.e., weevil attack prior to 2018) (B) are distinguished.

average, crooks and forks occurred on 20 and 11 percent of Pl, respectively. No differences in stem rust incidence or crooks or forks presence were noticed with dbh ($p = 0.322$) and over the three planting densities ($p = 0.887$) or over the four mixture proportions ($p = 0.382$) (Fig. 7A). Weevil incidence was 8 percent for all Sx trees across all densities and treatments (Table 1). Sx trees with larger dbh were significantly more frequently attacked by weevil ($p < 0.001$). They also presented higher leader damage (i.e., more attacks prior to 2018) ($p = 0.002$). The proportion of Sx trees with weevil was significantly lower at 2000 SPH than at 1000 SPH ($p = 0.017$). Weevil incidence was also significantly lower for the three mixture combinations than in the Sx monoculture at 1000 SPH and at 1500 SPH, and lower for the 3:1 and the 1:1 combinations than for the Sx monoculture at 2000 SPH ($p < 0.05$; Fig. 7B).

When the leader damage from previous attacks was accounted for, weevil attack was still significantly lower in all mixtures ($p < 0.02$) than in the 0:1 Sx monoculture at 1000 and 1500 SPH (Fig. 7B). Weevil attack was also lower at 2000 SPH than at 1000 SPH ($p = 0.029$; Fig. 7B). The percentage of Sx trees with major defects showed no significant pattern with the different densities ($p > 0.4$) or mixture proportions ($p > 0.36$) (Fig. A.3). For a given diameter, Sx trees affected by weevil were shorter (Fig. A.4).

4. Discussion

In this study of mixed Pl and Sx, 24 years after planting, the outcome of planting at a given mixing proportion depended on the initial stand density. The highest total volume was found in Pl monocultures as expected. Mixtures decreased volume production, but differences were small, suggesting that Pl-Sx plantations could be a viable alternative from a production perspective. Mixture effects in Pl-Sx plantations were generally larger at higher densities and less relevant in open stands, which had not yet reached crown closure. Reduced competition with Sx, particularly at the 2000 SPH density, resulted in larger Pl trees with larger crowns than in monocultures, which is likely linked to lower wood quality. The mixture was favourable for Sx, overtopped by Pl, which was significantly less frequently attacked by weevil even when it was mixed with only 25% of Pl in the 1500 and 2000 SPH with larger average dbh and ht (Table 1).

4.1. Overyielding is stronger at higher densities

Our findings partially support previous studies that found a larger effect of the mixture at higher densities in stratified conifer mixtures (Amoroso and Turnblom, 2006; Forrester et al., 2013; Garber and Maguire, 2004) and in spruce-fir-beech stands in a simulation study (Brunner and Forrester, 2020). No differences between densities and mixture levels had been observed at age 10 (Johnstone, 2004). A total relative yield value greater than 1, such as found for the closest densities (1500 SPH and 2000 SPH) in this study, indicates that the two species are using resources differently or are avoiding competition (Harper, 2010). Our results agree with Garber and Maguire (2004), who found a marginally significant greater complementarity yield effect for *Pinus ponderosa* – *Abies grandis* mixtures at a 1.8 m spacing (~3100 SPH) than at spacings of 3.7 and 5.5 m (~730 SPH and ~330 SPH). One mechanism explaining the overyielding found in the studied mixed stands at 1500 SPH and 2000 SPH is crown complementarity (Barbeito et al., 2017; Williams et al., 2017). Similar studies (Amoroso and Turnblom, 2006; Debell et al., 1997; Garber and Maguire, 2004) have found relative yield totals greater than 1 for a variety of species mixtures, concluding that the yield sacrifice of the mixture relative to the most productive species in the pure stands is partly mitigated by overyielding. Mason and Connolly (2014) found evidence of overyielding in 1:1 mixtures of Scots pine with Norway spruce and with Sitka spruce at over 4500 SPH, where basal area growth was about 40 percent greater in the mixtures than that predicted from the pure plots of the same species. Several other studies have shown that species with different characteristics can utilize site resources differently and more efficiently than if they were to compete for the same resources, resulting in higher productivity than in single species stands (Assmann, 1970). Chen et al. (2003) found that mixed stands with one shade intolerant species, such as Pl, and one shade tolerant species, such as Sx, tended to be more productive than single species stands in direct contrast to mixtures of only shade-tolerant species and mixtures of only shade-intolerant species where productivity was equal to or lower than in the monocultures.

4.2. Pines in mixtures with spruce grow like pines at low density

The design of the experimental plantation enabled us to confirm the hypothesis that Pl (i.e., the strongest competitor of the two species) in the mixture with Sx (i.e., the less competitive species) has a growth pattern similar to growth at low density, with larger dbh. A similar mechanism was proposed by Holmström et al. (2018) for a Norway spruce-Scots pine mixture, but only one density was available, so the hypothesis could not be tested. Crown dimensions, through their relationship with branch length, branch diameter, and consequently the size of knots, have a strong influence on stem quality (e.g., Groot and Schneider, 2011). Consequently, the larger crown sizes for Pl found in our study suggest that Pl could produce wood with inferior mechanical properties in mixtures with Sx, which can downgrade lumber value. Increased spacing was found to increase the diameter of the largest branches in 23 year-old Pl in Southern Sweden (Liziniewicz et al., 2012) and increased mean knot size on Pl boards sawn from logs in northern Sweden (Liziniewicz and Lula, 2019). Hébert et al. (2016) found similar increasing size of the largest branch diameter and knots with increasing spacing in *Pinus banksiana* plantations in Quebec. However, they found that wood properties such as wood density and the moduli of elasticity and rupture did not change significantly with spacing.

4.3. No effect of density or mixture on stem rust

Larger Pl were not more likely to be infected by stem rust than smaller trees even if they have more surface area for spore deposition (Bella, 2011). Conforming to previous findings, planting density was not a significant predictor of rust incidence in the main stem (Sattler et al., 2019). Our study did not support previous claims suggesting that mixtures had a significantly lower frequency of rust incidence on main stems relative to pure stands (Roach et al., 2015). Two mechanisms could be responsible for the lack of treatment effect. First, wide inter-tree distances between Pl trees (1000 SPH and mixtures) resulted in less transference of rust among trees (LeMay and Ahmed, 2015). Second, higher height to crown base 24 years after planting at 2000 SPH and in the Pl monocultures resulted in less opportunity for infection given fewer live lower branches (van der Kamp, 1994). The lack of treatment effect on rust incidence could also be related to the specific site characteristics, because rust incidence in southern interior BC was found to be affected by the interaction between planting density and climate (e.g., summer precipitation) or soil moisture regime (Mather et al., 2010).

4.4. Reduced weevil attack in mixtures at all densities

Larger Sx trees with vigorously growing leaders were more attacked by weevils in our study in agreement with previous results (Alfaro et al., 1994). Similarly, the largest Pl trees were preferred by *Pissodes terminalis* in south central BC (Maclauchlan and Borden, 1996). More frequent weevil damage was also reported for longer and thicker leaders of fertilized trees at three interior spruce fertilization research installations in central BC (vanAkker et al., 2004). The reduced weevil attack at the highest density agrees with previous studies that found significantly lower attack rates in Sitka spruce plantations and by *P. terminalis* in Pl at the highest densities of about 1500 SPH (Alfaro and Omule, 1990). This reduction is caused by competition reducing spruce leader size and hence attractiveness to weevil because they contain less food. We found that weevil attack decreased significantly in mixtures. This could be related to the effect of Pl overstory causing shading that decreases the leader growth (Taylor et al., 1996). Previous studies in Sitka spruce found that shading by Douglas-fir (Alfaro, 2019) or by red alder (McLean, 1989) reduced leader growth and consequently weevil incidence. Simard and Hannam (2000) found no effect of birch density on weevil attack but they suggested that these effects may have been over-ridden by the dense canopy of overtopping conifers, which may have played a similar protective role as birch. A higher proportion of Pl could also just reduce the overall food supply for the weevil resulting in low weevil populations and damage (van Halder et al., 2019). More complex mechanisms may also reduce weevil activity such as non-host volatiles reducing success of mate or host finding (Koopmans et al., 2009). Volume loss caused by weevil was still very moderate 24 years after planting as a result of height reduction (Fig. A.4), but repeated attacks and overtopping by competing Pl can lead to reduced yield in the less favourable treatments over the rotation length.

4.5. Implications for designing mixed-species plantations

Plantation forests have continued to increase globally in the last decades (Payn et al., 2015) and will undoubtedly play a critical role in BC's future wood supply. However, the lack of experimental evidence may be hampering the adoption of mixed-species plantations (Nichols et al., 2006). It is therefore important to document how mixing and density will affect yield and health of plantations. Pl plantations face extensive health problems that are expected to increase with climate change (Mather et al., 2010). Likewise, Sx plantations could also be negatively affected by climate change, which is expected to increase the severity of bark beetles in Canada (Bentz et al., 2010). The levels of stand density tested in our study correspond well to the range planted between 1995 and 2020 in interior BC across over 100,000 operational planting units that resulted from silvicultural regeneration cuts or natural disturbances that were planted to Pl and Sx (RESULTS database of silviculture activities, 2014). The median density for the openings was about 1400 SPH with the 0.5 and 95% quantiles being about 800 SPH and 1800 SPH, respectively. Unfortunately, no information is available about the mixture levels that were planted in the openings.

Long-term experiments including mixture and density combinations are rare, but are key to demonstrating that stand structures for a given pair of species are not constant across a wide range of SPH and thus for designing multi-species plantations. We provide evidence of trade-offs between achieving the highest total volume in the highest densities in monocultures and larger tree sizes and lower damage in the mixtures of the intermediate and highest densities. Hence, managers should implement combinations of SPH and mixing ratios that result in stand structures that are more resilient to climate change impacts affecting lumber value, while providing a higher delivery of ecosystem goods and services relative to pure stands (Huuskonen et al., 2021). Results of this study may change over the course of a rotation since self-thinning has only started at the highest density. Until this mixed experimental plantation and others reach rotation age, complementing empirical studies with a modelling approach on long-term yields, introducing mixed-species into growth and yield stand simulators (Calama et al., 2020), may offer the best information for managers to make decisions.

CRediT authorship contribution statement

Ignacio Barbeito: Conceptualization, Methodology, Formal analysis, Writing - original draft. **Bianca N.I. Eskelson:** Conceptualization, Data curation, Methodology, Writing - review & editing. **Grace Carsky:** Conceptualization, Data curation, Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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