

EFFECT OF TREE SPECIES DIVERSITY ON SPECIES GROWTH
RATE IN THE SASKATCHEWAN BOREAL FOREST

By

Nathan Drummond-Stoyles
0885506

FACULTY OF NATURAL RESOURCES MANAGEMENT
LAKEHEAD UNIVERSITY
THUNDER BAY, ONTARIO

April 2023

EFFECT OF TREE SPECIES DIVERSITY ON SPECIES GROWTH RATE IN THE
SASKATCHEWAN BOREAL FOREST

by

Nathan Drummond-Stoyles
0885506

An Undergraduate Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of
Honours Bachelor of Science in Forestry

Faculty of Natural Resources Management
Lakehead University

April 2023

Eric Searle
Major Advisor

Doug Reid
Second Reader

LIBRARY RIGHTS STATEMENT

In presenting this thesis in partial fulfillment of the requirements for the HBScF degree at Lakehead University in Thunder Bay, I agree that the University will make it freely available for inspection.

This thesis is made available by my authority solely for the purpose of private study and may not be copied or reproduced in whole or in part (except as permitted by the Copyright Laws) without my written authority.

Date: April 27th 2023

A CAUTION TO THE READER

This HBScF thesis has been through a semi-formal process of review and comment by at least two faculty members. It is made available for loan by the Faculty of Natural Resources Management for the purpose of advancing the practice of professional and scientific forestry.

The reader should be aware that opinions and conclusions expressed in this document are those of the student and do not necessarily reflect the opinions of the thesis supervisor, the faculty or of Lakehead University.

ABSTRACT

Drummond-Stoyles, N. 2023. Effect of tree species diversity on species growth rate in the boreal forest. 32 pp.

Keywords: boreal forest, species diversity, diversity-productivity relationship

Diverse ecosystems are crucial to combating climate change. This study aims to examine the impacts of tree species diversity on growth rate of seven boreal tree species. Data from permanent sample plots located in the boreal plains ecozone of Saskatchewan will be used. Species in these plots include white spruce (*Picea glauca*), black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*) and jack pine (*Pinus banksiana*). Jack pine was the only species to have growth rates respond positively to species diversity, with black spruce and balsam fir being negatively impacted by diversity. Trembling aspen, white birch, balsam poplar and white spruce showed no significant growth response to diversity. These findings highlight the importance of considering species specific growth responses to diversity when managing boreal forest stands.

CONTENTS

LIBRARY RIGHTS STATEMENT	3
A CAUTION TO THE READER.....	4
ABSTRACT	5
ACKNOWLEDGEMENTS	10
INTRODUCTION.....	11
Objectives.....	12
Hypothesis.....	12
LITERATURE REVIEW.....	12
Resource Partitioning	12
Facilitation.....	13
Dilution.....	14
Biotic FeedBacks.....	15
Species Combinations	16
METHODS AND MATERIALS.....	18
Study Area.....	18
Data analysis.....	19
RESULTS	20

DISCUSSION 24

CONCLUSION..... 27

LITERATURE CITED 28

APPENDIX..... 32

TABLES

Table 1. Density-corrected growth response to diversity, species and other predictor variables, showing results from a Type 3 ANOVA using Satterthwaite approximation of degrees of freedom.	21
Table 2. Linear mixed model output showing coefficients of estimation, confidence intervals and significant ($p < 0.05$) effects shown in bold. Intercept represents balsam fir, as the reference level for the species variable.	32

FIGURES

Figure 1. Map showing location of plots included in the study within Saskatchewan, Canada.	19
Figure 2. State factors compared to observed average density-corrected species growth rate: stand age (a), drainage class (b), MAP (c), and MAT (d).	22
Figure 3. Relationship between growth rate and diversity by species, with model prediction shown by species. State factors are held at their mean.	23
Figure 4. Observed density-corrected mean annual increment by species.	24

ACKNOWLEDGEMENTS

I would like to thank Dr. Eric Searle for all his help and guidance in completing this thesis, as well as Dr. Doug Reid for acting as the second reader. I would also like to thank Phil Loseth from the Saskatchewan Ministry of Environment for helping with data acquisition.

INTRODUCTION

Countless benefits of biodiversity have been found across many different ecosystems and vegetation types, including ecosystem services and decreased vulnerability to stress such as extreme weather and biotic disturbances (Hooper et al. 2005; Pimentel et al. 1997; Paquette and Messier 2011; Messier et al. 2022).

Regardless of growing evidence that biodiversity can increase ecosystem productivity, monocultures are still heavily relied upon, with 45% of forests planted worldwide being monocultures (FAO 2020). This is in part due to economic profit or timber yield often being the overarching objective when managing these forests, thus managers typically want to maximize growth rates and promote complementary species combinations. Even-aged monocultures of commercially preferred species are often favoured due to easier and cheaper planting, management and harvesting (Feng et al. 2022). However, species with similar growth rates can be combined to create even aged, mixed stands with similar harvest patterns (Messier et al. 2022). Conversely, species with varying growth rates or shade tolerances can be combined to reduce competition, promoting complementarity and potentially growth rate too (Taylor et al. 2020).

Despite tree species diversity generally having a positive effect on growth, negligible and negative effects have also been found depending on several factors such as species involved and successional stage (Taylor et al. 2020; Vilà et al. 2003). The mechanisms behind this relationship and their importance are still not fully understood (Jesch et al. 2017; Trogisch et al. 2021; Brooker et al. 2008).

The literature review will outline the four main interactions between neighboring trees – niche partitioning, dilution, biotic feedbacks and facilitation, as well as the specific interactions that could be at play with some of the species combinations in this dataset.

Objectives

The goal of this study is to examine the impact of species diversity on seven boreal tree species growth in Saskatchewan, while controlling for climate and site conditions. Growth data from permanent sample plots were used to test this.

Hypothesis

Growth rates of at least one species is expected to increase with species diversity. The null hypothesis is that there will be no significant relationship between species diversity and species growth rate.

LITERATURE REVIEW

RESOURCE PARTITIONING

Tree species that have evolved to coexist in mixtures typically exhibit niche partitioning: they occupy different niches spatially and temporally to reduce competition and increase overall resource use (Trogisch et al. 2021). Spatially, this can involve aboveground (mainly light) or belowground (nutrients and water) resources. This could apply to mixtures of aspen and white spruce, or jack pine and black spruce (Man and Lieffers 1999; Cowie 2009).

In closed canopy forests, neighboring tree species often have complementary crown profiles, allowing them to form denser, more productive canopy (Trogisch et al. 2021; Jucker et al. 2015). One example of this is vertical stratification, where neighboring species have contrasting vertical crown profiles, maximizing use of available light and growing space (Jucker et al. 2015). This is

common in stands with mixtures of shade tolerant and intolerant species, such as white spruce and trembling aspen, where the shade tolerant spruce have physiological adaptations that allow them to grow in the low light conditions under the canopy of faster growing species like aspen (Man and Lieffers 1999; Chen and Popadiouk 2002).

Another explanation for mixed forests having denser canopies is the high variation in intraspecific crown structure, known as crown plasticity, where trees have been shown to modify their crown size and shape in response to differing levels of competition (Jucker et al. 2015). In some cases, species have been shown to increase the size of their crowns when growing in mixtures (Jucker et al. 2015).

There is less agreement on if belowground niche partitioning contributes to the aboveground diversity-productivity relationship (Trogisch et al. 2021; Jesch et al. 2018). Some evidence for belowground resource partitioning has been found in boreal forests, even if it doesn't always correlate to aboveground overyielding in the same stands (Brassard et al. 2013). For example, Brassard et al. (2011) found fine root productivity to be higher in mixtures of trembling aspen, spruce and balsam and fir compared to aspen monocultures. Additionally, coexisting boreal species often have contrasting rooting habits, for example occupying different soil horizons, thus spatially partitioning their uptake of belowground resources (Strong and La Roi 1983). Mixtures have also been shown to have increased soil volume filling through space and time by fine roots (Brassard et al. 2013).

FACILITATION

Facilitation is the process where one species can reduce stresses on neighboring trees of different species, for example by altering wind speed, humidity, and radiation (Trogisch et al. 2021; Richter et al. 2022; Wright et al. 2017). Facilitation must involve an environmental factor

that limits one species' growth and can be altered by another species (Trogisch et al. 2021). These facilitative effects are expected to be increasingly important with increasing levels of stress, based on the stress gradient hypothesis (He and Bertness 2014). For example, shade tolerant, late successional species often don't perform well under full sun exposure, but this can be mitigated when they commonly grow below a canopy of early successional pioneer species (Man and Lieffers 1999). This canopy shelter reduces solar radiation and high temperatures reaching understory species such as white spruce that are often sensitive to extreme conditions (Man and Lieffers 1999).

Water stresses are expected to become more important as climate change progresses (Allen et al. 2010). Facilitative interactions between neighboring species in mixtures can mitigate the impacts of water stress (Trogisch et al. 2021). For example, hydraulic lift is a process where deeper rooting species are sometimes capable of redistributing soil water upwards to drier, shallower soil horizons, increasing water availability and growth of neighbouring shallow rooting species (Dawson 1993).

In conifer dominated stands managed mainly for timber production, a common factor limiting tree growth is soil nitrogen availability, with one solution being mixed stands of conifers and hardwoods due to hardwood foliage/litter often having a higher nitrogen concentration (Kelty 1992). In the context of this study, this could apply to mixtures of jack pine and white birch, aspen or poplar.

DILUTION

Herbivory and pathogens are common natural disturbance agents in the boreal forest, playing important roles in the structure and dynamics of these ecosystems (Jactel et al. 2017). Species diversity is known to play a significant role in regulating damage from these pests, through the

dilution effect, where diverse stands provide less food or resources for specialized herbivores or species-specific pathogens (van der Putten et al. 2001; Jactel and Brockerhoff 2007; Castagneyrol et al. 2014).

An example is the lodgepole pine dwarf mistletoe (*Arceuthobium americanum*), a native parasitic plant capable of causing severe swelling, deformation and brooming in various species of pine across western North America (Brandt et al. 1998; Callan 2001). Since jack pine is the only pine species found in the area surveyed, dwarf mistletoe damage would be expected to decrease with increasing species diversity as the relative abundance of jack pine would be lower. However, the strength of this dilution effect depends on the degree of specialization of the herbivores, with oligophagous and polyphagous herbivores being less effected by the relative abundance of a given host species compared to monophagous herbivores (Castagneyrol et al. 2014).

The degree of phylogenetic relatedness between neighboring trees is also important for mitigating herbivory, with more phylogenetic distance between neighbors often correlating with lower herbivore damage (Castagneyrol et al. 2014; Ness et al. 2011). For example, mixtures of conifers and hardwoods may be more important than mixtures of either conifers or hardwoods alone (Castagneyrol et al. 2014). Disease pressure is also influenced by how closely related neighboring trees are, with pathogen spillover to neighboring hosts theoretically decreasing when neighbors are more distantly related (Parker et al. 2015).

BIOTIC FEEDBACKS

Biotic feedback effects are complex interactions involving three trophic levels or food sources. This could involve a primary producer (tree), primary consumer (insect herbivores) and secondary consumers (herbivore predators) (Trogisch et al. 2021; van der Putten et al. 2001).

The enemies hypothesis states that species diverse forests should provide habitat to more diverse populations of insect herbivores, leading to increased predation and diversity of predator species (Muiruri et al. 2016; Moreira et al. 2015). This can be explained by mixtures having more niches and more diverse habitats and resources for predator species (Moreira et al. 2015). For example, Muiruri and coworkers (2016) studied avian predation of artificial larvae in various forest types and found increased predation when the artificial larvae were placed on a tree with a higher diversity of neighbors. Erskine (1977) found that pure jack pine stands in Saskatchewan provided limited habitat for birds, who can be important herbivore predators. Tree diversity has also been shown to increase the stability of these interactions involving multiple trophic levels (Fornoff et al. 2019).

SPECIES COMBINATIONS

One common species combination in the data set is white spruce and trembling aspen. These species are expected to exhibit overyielding in combination compared single species stands of either species for a number of reasons, mainly niche partitioning and facilitative interactions (Man and Lieffers 1999). Aspen and white spruce have contrasting crown profiles, physically separating their crowns in the canopy (Man and Lieffers 1999). Additionally, the two species have different phenological strategies for leaf development, allowing understory white spruce to extend their growing season in the spring and fall when aspen is without its leaves (Constabel and Lieffers 1996). aspen and white spruce mixtures can avoid competition for belowground resources through differences in rooting habits, although it is unclear if this correlates to aboveground overyielding. Strong and La Roi (1983) used destructive sampling techniques to show aspen fine roots reached as low as 100 cm belowground, whereas fine roots of white spruce were typically limited to 50 cm. An example of facilitative interactions between aspen and white

spruce is improved rates of litter decomposition and subsequent nutrient cycling (Man and Lieffers 1999). coniferous boreal forests often exhibit slow litter decomposition and nutrient cycling, potentially due to factors such as lower soil temperature or conifer needle litter inhibiting microbial decomposition (Prescott et al. 1989; Van Cleve et al. 1981). Combining a deciduous species such as aspen can improve growth rates due to creating nutrient rich leaf litter (Man and Lieffers 1999). Additionally, overstory aspen can protect the more sensitive white spruce from harsh environmental conditions. For example, mixed aspen and white spruce stands have been shown to decrease the vulnerability of white spruce to blowdown (Man and Lieffers 1999).

Another common species combination in the dataset is jack pine and black spruce. These species could perform well together due to physical separation and morphological and physiological differences (Cowie 2009). Jack pine are capable of rooting in deeper soil horizons to avoid competition with the shallower rooting black spruce, the latter mainly being restricted to the organic soil layer and the upper 10 cm of the mineral layer (Cowie 2009). Physiological differences include black spruce being more shade tolerant, in part due to a lower photosynthetic capacity (Kröner 2005). This correlates with spruce being the slower growing of the two species, leading to a stratified canopy (Cowie 2009). Jack pine has a lower leaf area index and more open crown structure, allowing sufficient light levels to reach spruce growing below a pine canopy (Cowie 2009).

METHODS AND MATERIALS

STUDY AREA

This study used publicly available data from permanent sample plots (PSPs) located in Saskatchewan, Canada (from -107.19° to -104.22° N and 53.63° to 54.80° E) (Figure 1). These plots were established and measured by the Saskatchewan Ministry of Environment, Weyerhaeuser Canada and MacMillan Bloedel starting in 1949, with mature, fully stocked stands being subjectively targeted for plot location/establishment (Ministry of Environment 2022). Plots were predominantly 20 m x 30m (0.06 ha) or 20 m x 40m (0.08 ha), and on average 3 measurements per plot were used. Measurement intervals ranged from 1 to 19 years. All trees with a diameter than 9.0 cm had species identity, diameter at breast height (DBH) and tree number recorded greater electronically in the field. Tree number was marked on each tree using tree marking paint to keep track of trees between measurement years. For this study, 30 plots that were within the boreal plains ecozone and had drainage class data were randomly selected, from a total of 2,048 plots in the province.



Figure 1. Map showing location of plots included in the study within Saskatchewan, Canada.

DATA ANALYSIS

Drainage class, stand age, mean annual temperature (MAT) and mean annual precipitation (MAP) were considered state factors in the model. Species diversity was calculated using Shannon's diversity index (H) as follows, where p is species proportion by basal area and i is each species.

$$H = - \sum_{i=1}^i p_i \ln p_i$$

Shannon's diversity index is widely used to represent species diversity. It was chosen here because it accounts for both richness and evenness, although it can be sensitive to sample size. Growth rate was expressed as mean annual increment (MAI) in square centimetres per stem, per

year. Climate data (MAT and MAP) was obtained using plot coordinates, for a 30-year reference period from 1970-2000 (Fick and Hijmans 2017). The ministry provided drainage class data for each plot, which was determined based on several factors, including topographic features, humus, mineral soil and water table depths, pore patterns and permeability (Searle and Chen 2017). Drainage was classified as very rapid, rapid, well, moderately well, imperfect, poor, or very poor. All stands were assumed to originate from stand replacing wildfire, with stand age determined by ring count after coring the largest stem in each plot. Microsoft Excel and the programming language 'R' were used for calculations and to perform a linear regression between species growth rate and species diversity (R Core Team 2022).

RESULTS

Shannon's index varied across all plots from 0 to 1.02, with species richness ranging from 1 to 5. Stand age varied from 27 to 145 years, with a mean age of 74 years. Mean annual temperature ranged from -1.1 to 0.5 °C. Mean annual precipitation ranged from 431 to 505 mm. The drainage classes encountered ranged from poor to rapid.

The impact of species diversity on growth rate of seven species was assessed using a linear mixed model. There was a statistically significant interaction between species and diversity ($F = 6.05$), indicating that the effect of diversity on growth rate varied depending on the species, and this interaction explained more variation in growth than any other term in the model. Age ($F = 1.10$), MAP ($F = 2.59$) and MAT ($F = 1.19$) had significant effects on growth rate. There was no significant effect for drainage class (Table 1).

Table 2. Density-corrected growth response to diversity, species and other predictor variables, showing results from a Type 3 ANOVA using Satterthwaite approximation of degrees of freedom.

Predictor	Sum Sq	Mean Sq	F value
Species	26.70	4.45	1.74
H	3.19	3.19	1.25
Age	2.80	2.80	1.10
MAP	6.61	6.61	2.59
MAT	3.30	3.03	1.19
Drainage Class	5.15	1.28	0.50
SPECIES:H	92.65	15.44	6.05

The fixed and random effects combined accounted for 83.0% of the variation in growth (conditional R^2), with the fixed effects (species, diversity, MAT, MAP and stand age) accounting for 43.6% of the variation in growth (marginal R^2 , Table 2). Of the variation explained by the fixed effects, the interaction between species and diversity accounted for 66% of this variation (Table 1).

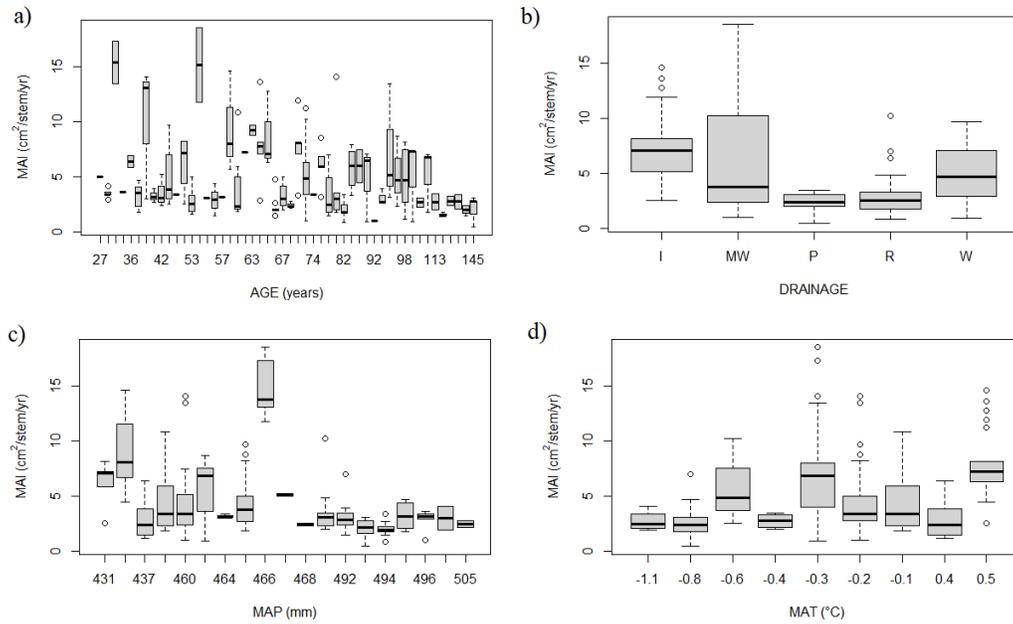


Figure 2. State factors compared to observed average density corrected growth rate: stand age (a), drainage class (b), mean annual precipitation (c), and mean annual temperature (d). Bold line indicates median, boxes show upper and lower 25th percentile, and whiskers show upper and lower 5th percentile.

While controlling for climatic conditions (temperature and precipitation), stand age, and drainage class, the effect of species diversity on growth rate varied from negative, to neutral, to positive, depending on the species. There was a significant, positive relationship between diversity and jack pine growth ($p < 0.05$). Growth rates of black spruce and balsam fir showed a significant negative relationship with diversity ($p < 0.05$) (Figure 2). Growth of balsam poplar, white birch, white spruce, and trembling aspen were not significantly affected by diversity. Balsam fir responded the strongest to diversity, with its growth rate decreasing by $8.27 \text{ cm}^2 \text{ stem}^{-1} \text{ year}^{-1}$ for every unit increase in Shannon's diversity index. Conversely, jack pine growth increased by $4.82 \text{ cm}^2 \text{ stem}^{-1} \text{ year}^{-1}$ for every unit increase in Shannon's index.

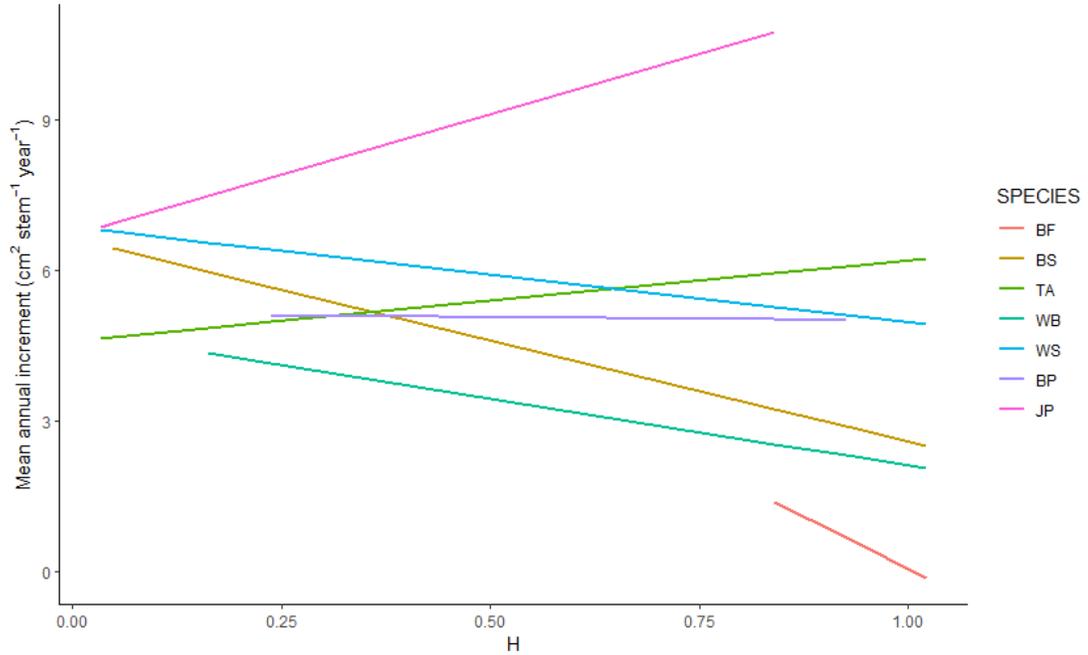


Figure 3. Relationship between growth rate and diversity by species., with model prediction for the observed range of Shannon's diversity index by species. BF = balsam fir, BP = balsam poplar, BS = black spruce, JP = jack pine, TA = trembling aspen, WB = white birch, WS = white spruce.

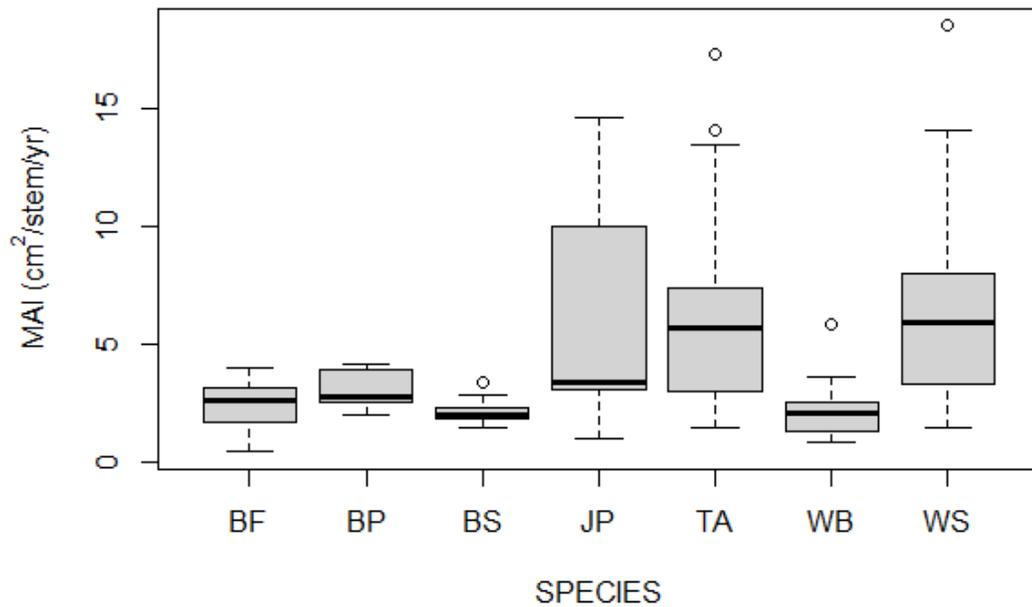


Figure 4. Observed mean annual increment by species. Median growth rate shown by bold line, box showing upper and lower 25th percentile, whiskers showing upper and lower 5th percentile.

DISCUSSION

Shade intolerant species, like jack pine and trembling aspen, generally benefited from diversity compared to more conservative, shade tolerants, which is supported by other studies (Fichtner et al. 2017).

Taylor et al. (2020) found differing results for balsam fir, finding a positive diversity effect in older stands, though at certain stand ages, only small balsam fir stems showed any growth response to diversity. This was potentially due to complementarity effects when paired with aspen or birch, such as increased understory light availability, or facilitative litter effects of these hardwood species (Taylor et al. 2020). In the dataset used for this study, balsam fir was only observed in stands with a high diversity index.

The negative diversity effect on fir found here could be explained by beneficial complementarity effects when only paired with one other species, for example birch or aspen, whereas the most diverse fir stands are more likely to contain functionally or phylogenetically similar species such as spruce. The mean stand age was 74 years, meaning the more diverse stands containing balsam fir might have a closed canopy of faster growing shade intolerants, that are potentially outcompeting the understory fir (Chen and Popadiouk 2002). Other studies have found fir did not benefit from diversity before the canopy transition stage, indicating that the negative diversity effect this study found might shift to positive as the stands age (Taylor et al. 2020).

Longpré et al. (1994) found also found a positive effect of diversity on jack pine growth, showing that jack pine diameter but not height growth increased when combined with white birch. They attributed this to lower levels of competition among pine stems in mixtures, though only with white birch as a companion species over aspen. This could be due to aspen and pine having similar vertical growth patterns and thus increased competition for light in in the canopy, whereas birch was found to grow slower vertically, indicating the possibility for vertical stratification and lower competition for light to explain pine overyielding in mixtures (Longpré et al. 1994). Taylor et al. (2020) found a positive diversity effect on jack pine growth, but not for larger stems, potentially due to hardwood companion species such as aspen or birch facilitating better soil resource availability.

Morris et al. (2014) found similar results for black spruce, with single species plantations outperforming natural, mixed conifer stands, accrediting this to relatively high levels of competition with hardwoods, due to the natural stands reaching crown closure sooner than plantations.

The neutral diversity effect on aspen growth found in this study potentially indicates the proportion of aspen compared to companion species was well balanced, to avoid one species outcompeting another. This neutral effect on aspen is contrasted by other studies that have shown a negative effect of diversity on growth of aspen (Taylor et al. 2020; MacPherson et al. 2001). Taylor et al. (2020) attributed their negative diversity effect to increased competition for light in mixtures, and conifer litter impacting soil chemical properties.

Muiruri et al. (2015) showed similar results for diversity effects on birch, finding no effect of tree diversity on overall birch diameter growth, though they also found that moose browsing intensity altered the effect of diversity on tree growth. They found the growth rate of birch in more species rich stands less affected by moose herbivory compared to browsed birch in monocultures.

Several factors limited the comprehensiveness of this analysis, for example, the relationship between species diversity and growth rate might not be best represented by a linear model, which was used here. Another limitation was not including neighbor identity or species composition in the statistical analysis. Neighbor characteristics such as crown structure and resource acquisition strategies (shade tolerance, responses to competition) could impact growth rates of the focal tree (Trogisch et al. 2021). Natural stands such as the plots used here typically have random or clumped spatial species arrangement patterns, whereas diversity effects, specifically competitive reduction, rely on diversity at the neighborhood scale (MacPherson et al. 2001). This is especially important in a management planning context, where specific knowledge of ideal species compositions and companion species would be required for maximizing diversity effects for focal/commercial species. The proportion of companion species could also be an important factor, for example tolerant species like spruce can get outcompeted by faster growing

aspen if the proportion of aspen is too high (Man and Lieffers 1999). Within the overall stand level results presented here, there could be variation in diversity effects at the stem level, as mentioned above. In this study, growth rates were calculated only using diameter growth, meaning vertical growth was ignored. Specifically, shade tolerant species are known to prioritize vertical over diameter growth depending on competition levels and resource (space and light) availability (Man and Lieffers 1999; Morris et al. 2014). Additionally, the absence of an effect of drainage class on growth indicates that more plots should have been used to provide a wider range of variation in drainage classes.

CONCLUSION

This analysis of natural stands shows boreal forest tree species exhibit varying growth responses to stand level species diversity, potentially due to differing competitive abilities or shade tolerances. Species with positive or neutral diversity effects could be planted in commercial plantations as mixtures to maintain or improve growth rate compared to their respective monoculture, while promoting resilience and shifting towards multiple-use forestry (Messier et al. 2022). These results suggest mixtures of jack pine with trembling aspen or white birch, or mixtures of white spruce and aspen should optimize beneficial diversity effects on growth. More research could provide a better understanding of optimal species combinations with respect to the changing climate, today and in the future.

LITERATURE CITED

- Allen, C.D., A.K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D.D. Breshears, E.H. Hogg, et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259(4): 660-684.
- Brandt, J.P., R.D. Brett, K.R. Knowles, A. Sproule. 1998. Distribution of severe dwarf mistletoe damage in west-central Canada. Natural Resources Canada. Canadian Forest Service
- Brassard, B.W., H.Y.H. Chen, X. Cavard, J. Laganier, P.B. Reich. 2013. Tree species diversity increases fine root productivity through increased soil volume filling. *Journal of Ecology* 101(1): 210-219.
- Brooker, R.W., F.T. Maestre, R.M Callaway, C.L. Lortie, L.A. Cavieres, G. Kunstler, P. Liancourt, K. Tielborger, J.M.J. Travis, et al. 2008. Facilitation in plant communities: the past, present, and future. *Journal of Ecology* 96(1): 18-34.
- Callan, B. 2001. Introduction to forest diseases. Natural Resources Canada. 16pp.
- Castagneyrol, B., H. Jactel, C. Vacher, E.G. Brockerhoff, and J. Koricheva. 2014. Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. *Journal of Applied Ecology* 51:134-141.
- Cavard, X., Y. Bergeron H.Y.H. Chen, Paré, D., Laganier and Brassard, B. 2011. Competition and facilitation between tree species change with stand development. *Oikos*, 120: 11(1673-1695).
- Chen, H. Y., & Popadiouk, R. V. 2002. Dynamics of North American boreal mixedwoods. *Environmental Reviews* 10(3): 137–166.
- Chen, H.Y.H., K. Klinka, A.H. Mathey, X. Wang, P. Varga, C. Chourmouzis. 2003. Are mixed-species stands more productive than single-species stands: an empirical test of three forest types in British Columbia and Alberta. *Canadian Journal of Forest Research* 33(7): 1227-1237.
- Constabel, A.J. and V.J. Lieffers. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. *Canadian Journal of Forest Research* 26(6): 1008-1014.
- Cowie, T.L. 2009. Assessing above- and belowground competitive effects in pure and mixed stands of jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*). MScF Thesis, Lakehead University. 118 pp.
- Dawson, T.E. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia* 95: 565-574.
- Erskin, A.J. 1977. Birds in boreal Canada: Communities, densities and adaptations. Canadian Wildlife Service Report Series 41. ISBN-0-660-01185-9
- Feng, Y., Schmid, B., Loreau, M., Forrester, D. I., Fei, S., Zhu, J., Tang, Z., Zhu, J., Hong, P., Ji, C., Shi, Y., Su, H., Xiong, X., Xiao, J., Wang, S., and Fang, J. 2022. Multispecies forest

- plantations outyield monocultures across a broad range of conditions. *Science* 376(6595): 865–868. <https://doi.org/10.1126/science.abm6363>
- Fichtner, A., Härdtle, W., Li, Y., Bruelheide, H., Kunz, M., & von Oheimb, G. 2017. From competition to facilitation: How tree species respond to neighbourhood diversity. *Ecology Letters* 20(7): 892–900.
- Fick, S.E. and R.J. Hijmans. 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37(12): 4302–4315.
- Food and Agriculture Organization of the United Nations (FAO). 2020. Global Forest Resources Assessment 2020: Main report. <https://doi.org/10.4060/ca9825en>
- Fornoff, F., A.-M. Klein, N. Blüthgen and M. Staab. 2019. Tree diversity increases robustness of multitrophic interactions. *Proceedings of the Royal Society B: Biological Sciences* <https://doi.org/10.1098/rspb.2018.2399>
- He, Q. and M.D. Bertness. 2014. Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology* 95(6): 1437–1443.
- Hildebrand, M., M.D. Perles-Garcia, M. Kunz, W. Hardtle, G. von Oheimb, A. Fichtner. 2021. Tree-tree interactions and crown complementarity: The role of functional diversity and branch traits for canopy packing. *Basic and Applied Ecology* 50: 217–227.
- Hooper, D.U., F.S. Chapin, J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D.M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A.J. Symstad, J. Vandermeer and D.A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75(1): 3–35.
- Jactel, H. and E.G. Brockerhoff. 2007. Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10(9): 835–848.
- Jactel, H., J. Bauhus, J. Boberg, D. Bonal, B. Castagneyrol, B. Gardiner, J. Ramon Gonzalez-Olabarria, J. Koricheva, N. Meruisse, and E.G. Brockerhoff. 2017. Tree diversity drives forest stand resistance to natural disturbances. *Curr. Forestry Rep.* <https://doi.org/10.1007/s40725-017-0064-1>.
- Jesch, A., K.E. Berry, J.M. Ravenek, D. Bachmann, T. Strecker, A. Weigelt, N. Buchmann, H. de Kroon, A. Gessler, L. Mommer, C. Roshcer and M. Scherer-Lorenzen. 2017. Below-ground resource partitioning alone cannot explain the biodiversity–ecosystem function relationship: A field test using multiple tracers. *Journal of Ecology* 106(5): 2002–2018.
- Kelty, M.J. 1992. Comparative productivity of monocultures and mixed-species stands. 124–141 pp. *in* Kelty, M.J., Larsson, B.C. and Oliver, C.D. 1992. *The ecology and silviculture of mixed-species forests*. Kluwer Academic Publishers, Netherlands.
- Körner, C.H. 2005. An introduction to the functional diversity of temperate forest trees. Pp 13–37 *in* Scherer-Lorenzen, M., M.C. Körner and E.D. Schulze (eds). *Forest Diversity and Function: Temperate and Boreal Systems*. Springer. 400pp.
- Longpré, M.-H., Bergeron, Y., Paré, D., & Béland, M. 1994. Effect of companion species on the growth of jack pine (*Pinus banksiana*). *Can. J. For Res.* 24(9): 1846–1853.

- MacPherson, D. M., Lieffers, V. J., & Blenis, P. V. (2001). Productivity of aspen stands with and without a spruce understory in Alberta's boreal mixedwood forests. *The Forestry Chronicle*: 77(2): 351–356.
- Man, R. and V.J. Lieffers. Are mixtures of aspen and white spruce more productive than single species stands? *Forestry Chronicle* 75(3): 505-513.
- Messier, C., Bauhus, J., Sousa-Silva, R., Auge, H., Baeten, L., Barsoum, N., Bruelheide, H., Caldwell, B., Cavender-Bares, J., Dhiedt, E., Eisenhauer, N., Ganade, G., Gravel, D., Guillemot, J., Hall, J. S., Hector, A., Hérault, B., Jactel, H., Koricheva, J., Kreft, H., Mereu, S., Muys, B., Nock, C.A., Paquette, A., Parker, J.D., Perring, M.P., Ponette, Q., Potvin, C., Reich, P.B., Scherer-Lorenzen, Schnabel, F., Verheyen, K., Weih, M., Wollni, M. and Zemp, D. C. 2022. For the sake of resilience and multifunctionality, let's diversify planted forests! *Conservation Letters*, 15(1), e12829.
<https://doi.org/10.1111/conl.12829>
- Moreira, X., Abdala-Roberts, L., Rasmann, S., Castagneyrol, B., & Mooney, K. A. (2016). Plant diversity effects on insect herbivores and their natural enemies: Current thinking, recent findings, and future directions. *Current Opinion in Insect Science*: 14, 1–7.
- Morris, D. M., Reid, D. E. B., Kwiaton, M., Hunt, S. L., & Gordon, A. M. 2014. Comparing growth patterns of jack pine and black spruce in mixed natural stands and plantations. *Ecoscience*: 21(1): 1–10.
- Muiruri, E. W., Milligan, H. T., Morath, S., & Koricheva, J. 2015. Moose browsing alters tree diversity effects on birch growth and insect herbivory. *Functional Ecology* 29(5): 724–735.
- Muiruri, E. W., Rainio, K., & Koricheva, J. (2016). Do birds see the forest for the trees? Scale-dependent effects of tree diversity on avian predation of artificial larvae. *Oecologia*: 180(3): 619–630.
- Ness, J.H., E.J. Rollinson and K.D. Whitney. 2011. Phylogenetic distance can predict susceptibility to attack by natural enemies. *Oikos* 120(9): 1327-1334.
- Parker, I. M., Saunders, M., Bontrager, M., Weitz, A. P., Hendricks, R., Magarey, R., Suiter, K., & G. S. Gilbert. 2015. Phylogenetic structure and host abundance drive disease pressure in communities. *Nature*, 520(7548). <https://doi.org/10.1038/nature14372>
- Pimentel, D., C. Wilson, C. McCullum, R. Huang, P. Dwen, J. Flack, Q. Tran, T. Saltman, B. Cliff. 1997. Economic and environmental benefits of biodiversity. *BioScience* 47(11): 747-757.
- Prescott, C.E., J.P. Corbin and D. Parkinson. 1989. Input, accumulation and residence times of carbon, nitrogen, and phosphorus in four Rocky Mountain coniferous forests.
- Pretzch, H. 2005. Diversity and productivity in forests: evidence from long-term experimental plots. pp. 41-64 in Scherer-Lorenzen, M., Ch. Korner and E.D. Schulze. *Forest Diversity and Function*. Springer, Germany. 399 pp.
- Pretzch, H., G. Schütze and E. Uhl. 2013. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by interspecific facilitation. *Plant Biology* 15(3): 483-495.

- R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Richter, R., H. Ballasus, R.A. Engelmann, C. Zeilhofer, A. Sanaei and C. Wirth. 2022. Tree species matters for forest microclimate regulation during the drought year 2018: disentangling environmental drivers and biotic drivers. *Scientific Reports* (12): <https://doi.org/10.1038/s41598-022-22582-6>
- Saskatchewan Ministry of Environment. 2022. Natural stand permanent sample plot (PSP) field re-measurement procedures. Unpublished manuscript.
- Searle, E. B., & Chen, H. Y. H. 2017. Climate change-associated trends in biomass dynamics are consistent across soil drainage classes in western boreal forests of Canada. *Forest Ecosystems* 4(1):18.
- Strong, W.L. and G.H. La Roi. 1983. Root-system morphology of common boreal forest trees in Alberta, Canada. *Can. J. For. Res* 13(6): 1164-1173.
- Taylor, A.R., B. Gao and H.Y.H. Chen. 2020. The effect of species diversity on tree growth varies during forest succession in the boreal forest of central Canada. *Forest Ecology and Management* <https://doi.org/10.1016/j.foreco.2019.117641>
- Trogisch, S., X. Liu, G. Rutten, K. Xue, J. Bauhaus, U. Brose, W. Bu, s. Cesarz, D. Chesters, J. Connolly, X. Cui, N. Eisenhauer, L. Guo, S. Haider, W. Hardtle, M. Kunz, L. Liu, Z. Ma, S. Neumann, W. Sang, A. Schuldt, Z. Tang, N.M. van Dam, G. von Oheimb, M.Q. Wang, S. Wang, A. Weinhold, C. Wirth, T. Wubet, X. Xu, B. Yang, N. Zhang, C.D. Zhu, K. Ma, Y. Wang and H. Brulheide. 2021. The significance of tree-tree interactions for forest ecosystem functioning. *Basic and Applied Ecology* 55(2021):33-52.
- Van Cleve, K., R. Barney, and R. Schlenker. 1981. Evidence of temperature control of production and nutrient cycling in two interior Alaska black spruce ecosystems. *Can. J. For Res.* 11: 258-273.
- Van der Putten, W.H., L.E.M. Vet, J.A. Harvey and F.L. Wäckers. 2001. Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends in Ecology and Evolution* 16(10): 547-554.
- Vilà, M., Vayreda, J., Gracia, C. and J.J. Ibáñez. 2003. Does tree diversity increases wood production in pine forests? *Oecologia* 135: 299-303.
- Wright, A.J., D.A. Wardle, R. Callaway and A. Gaxiola. 2017. The overlooked role of facilitation in biodiversity experiments. *Trends in Ecology and Evolution* 32(5): 383-390.

APPENDIX

Table 3. Linear mixed model output showing coefficients of estimation, confidence intervals and significant ($p < 0.05$) effects shown in bold. Intercept represents balsam fir, as the reference level for the species variable.

<i>Predictors</i>	MAI		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	120.33	-18.30 – 258.96	0.088
SPECIES [BP]	-3.20	-8.22 – 1.83	0.211
SPECIES [BS]	-1.71	-4.95 – 1.53	0.299
SPECIES [JP]	-1.65	-5.22 – 1.93	0.364
SPECIES [TA]	-3.75	-7.22 – -0.27	0.035
SPECIES [WB]	-3.56	-7.52 – 0.40	0.078
SPECIES [WS]	-1.48	-4.81 – 1.85	0.382
H	-8.27	-13.18 – -3.37	0.001
AGE	-0.01	-0.04 – 0.01	0.296
MAP	-0.25	-0.55 – 0.06	0.109
MAT	-8.30	-23.33 – 6.73	0.277
DRAINAGE [MW]	2.00	-2.45 – 6.45	0.375
DRAINAGE [P]	0.97	-4.11 – 6.06	0.706
DRAINAGE [R]	0.23	-4.05 – 4.50	0.917
DRAINAGE [W]	1.53	-2.48 – 5.55	0.452
SPECIES [BP] × H	8.13	0.78 – 15.48	0.030
SPECIES [BS] × H	4.23	-0.61 – 9.06	0.086
SPECIES [JP] × H	13.09	7.71 – 18.47	<0.001
SPECIES [TA] × H	9.87	4.99 – 14.75	<0.001
SPECIES [WB] × H	5.61	0.04 – 11.17	0.048
SPECIES [WS] × H	6.38	1.69 – 11.07	0.008
Random Effects			
σ^2	2.55		
τ_{00} PLOT_ID	5.91		
ICC	0.70		
N PLOT_ID	30		
Observations	179		
Marginal R ² / Conditional R ²	0.436 / 0.830		