An Evaluation of the Main Factors Affecting Yield Differences between Single- and Mixed-species Stands

Discussion Paper

Erica B. ***Lilles****, Bulkley Valley Research Centre; K. David* ***Coates****, B.C. Ministry of Forests, Lands and Natural Resource Operations.*

Abstract

In British Columbia, many of our second-growth stands have regenerated as mixed-species stands and yet our understanding of how to manage these stands to achieve multiple goals is limited. There is considerable interest and need to identify management strategies that will optimize timber production and carbon storage while maintaining biodiversity in the province's managed forests. Careful use of mixed-species management may contribute to meeting these goals. This discussion paper reviews the published literature that compares yield in single-and mixed-species stands. The review shows that drawing any definitive conclusions on whether mixed-species stands had a higher yield than single-species stands is not possible because of the confounding influence of four key factors: 1) species composition; 2) site type; 3) density and pattern; and 4) assessment age. To plan mixed-species plantations with native species that may out-yield monocultures and have other potential benefits, silviculturists will need to extrapolate from past research and pay close attention to these factors.

KEYWORDS: competition; diversity; facilitation; monoculture; productivity

Introduction

Forest management must maintain productive and fully functional forest ecosystems. To this end, silviculturists need to evaluate the short- and long-term viability of specific practices using a framework that promotes adaptability and self organization, while minimizing the risk of undesirable future outcomes (Messier et al. 2013). In British Columbia, we have extensive experience with yield prediction of single-species plantations and the further potential benefits of genetic improvement, vegetation management, spacing, and fertilization (Di Lucca 1999). Our understanding of how mixed-species stands perform is still poor, even though many of our second-growth stands are planted to more than one species or have regenerated as mixtures of two or more species because of natural ingress after planting (B.C. Ministry of Forests 2008).

It is imperative that we better understand the relationship between tree species diversity and forest productivity. It is probably fair to say that management of mixed stands in British Columbia is currently *ad hoc* with little specific guidance for meeting timber or other objectives. Given threats associated with global change, including a changing climate, there is considerable interest and need to identify management strategies that will optimize forest yield and carbon storage, reduce risk, and maintain biodiversity in the province's managed forests (Campbell et al. 2009).

Lilles, E.B. & K.D. Coates. 2013. An evaluation of the main factors affecting yield differences between single- and mixed-species stands. Journal of Ecosystems and Management 14(2):1–14.
Published by FORREX Forum for Research and Extension in Natural Resources.
http://jem.forrex.org/index.php/jem/article/viewFile/552/497

JEM
Vol 14, No 2
JOURNAL OF Ecosystems & Management

Silviculturists have long compared the advantages and disadvantages of single-species versus mixed-species stands (e.g., Kelty 1992) and have more recently examined specific mixture combinations (e.g., Chen et al. 2003; Pretzsch et al. 2010). Interestingly, the main issues regarding single- versus mixed-species management have not changed much over the years. The conclusions drawn by Toumey and Korstian in 1937 (quoted in Nichols et al. 2006) are still quite informative:

> Although, silviculturally considered, pure crops are usually undesirable, there are often economic advantages which overbalance silvicultural disadvantages. The most important of these advantages are:
>
> - Management is much simplified
> - The crop can be harvested more economically
> - Artificial restocking is simpler
>
> The formation of pure stands, however, is sometimes indicative of insufficient silvicultural knowledge on the part of the forester. … In France, where silviculture is understood and practiced, mixed-stands form about three-fourths of the forest … are likely to be of superior economic value as well. The more important advantages that may result from mixed crops are:
>
> - Where a mixture is suitably arranged the site is most completely utilized.
> - A mixture of shallow-rooted species with deep-rooted species forms a stand that suffers less from wind and more fully utilizes the soil.
> - Fungi and insects are less harmful in mixed stands.
> - Mixed crops are more successful on poor sites than are most pure stands.
> - When early thinnings of a species in pure stands are of little economic value, more valuable thinnings may be realized by mixing with it a species which brings better prices in small sizes.
> - Serious mistakes made in the selection of species for artificial regeneration are more easily corrected in mixed stands than in pure crops.
> - mixed stand is more easily transformed or modified to meet present or probable future demands of the market or to overcome a serious fungus or insect pest than is a pure stand. (pp. 278–280)

Our scientific understanding of forest dynamics and the processes controlling forest productivity has increased considerably since Toumey and Korstian's 1937 publication. We now understand that forests are heterogeneous, highly dynamic, and contain many biotic and abiotic elements that interact across different levels of organization with various feedback loops and that all these factors in turn can affect productivity (Messier et al. 2013). Yet, the emphasis on one or two dominant commercial species in plantation management has remained quite constant over time in British Columbia.

Although other reviews have summarized information on mixtures versus monocultures in the last 10 years (Forrester et al. 2006; Kelty 2006; Nichols et al. 2006; Piotto 2008; Pretzsch 2009; Griess & Knoke 2011; Zhang et al. 2012), we felt that a review specific to native tree species could highlight the opportunities and challenges pertinent to mixed-species management in our province. During our literature search, we realized how few yield comparisons of mixed- and single-species stands have been made for provincial species, so we broadened our search criteria to include other boreal and temperate tree species with the same genus as native species (see Appendix 1).

We found even fewer studies had specifically examined biodiversity or risk of damage differences between mixed- and single-species stands, so we focused this paper on differences in yield, defined as the total productivity of the stand (measured by volume, basal area, stem mass, net primary productivity, or growth rate) regardless of end economic value (see sidebar, "Future stand value"). While reviewing the literature, it became apparent that four key factors confounded comparisons of yield between mixtures and monocultures: 1) species composition; 2) site type; 3) density and pattern; and 4) assessment age. Instead of drawing any definitive conclusions about whether mixed- or single-species stands performed better in terms of yield, we sought to bring attention to these factors and how they affect interactions among species. This information can help silviculturists in British Columbia make educated decisions about which species combinations and stocking arrangements are suitable for mixed plantations on specific sites (e.g., Table 1).

Table 1: A guide to logical mixtures of British Columbia tree species with potential benefits over monocultures

Species combination	Site type	Potential benefits
Mixtures with potential yield gain		
Red alder with Douglas-fir	Poor sites or dry ecosystems	• Revenue at different times • Increased stand biodiversity • Improved Douglas-fir bole characteristics • Decreased risk of damage or catastrophic loss
Trembling aspen or paper birch with lodgepole pine	Poor sites or dry ecosystems	• Revenue at different times • Increased stand biodiversity • Decreased risk of damage or catastrophic loss
Mixtures with other benefits and no yield loss		
Douglas-fir with western hemlock	Unknown	• Increased stand biodiversity • Improved Douglas fir bole characteristics • Decreased risk of damage or catastrophic loss
Ponderosa pine with grand fir	Unknown	• Increased stand biodiversity • Decreased risk of damage or catastrophic loss
Interior spruce, lodgepole pine, and subalpine fir	Medium or rich sites	• Increased stand biodiversity • Decreased risk of damage or catastrophic loss
Trembling aspen or paper birch with interior spruce or white spruce	Medium or rich sites	• Revenue at different times • Increased stand biodiversity • Decreased risk of damage or catastrophic loss

Review of current research

Toumey and Korstian (1937) mention several reasons why mixtures can outperform monocultures in terms of yield, including decreased windthrow, decreased pests and disease, increased use of the site resources (both below- and above-ground), and different timing of harvest among species. A recent global review supports their assertion about the positive effect of mixtures on resistance to windthrow and pests (Griess & Knoke 2011). In British Columbia's interior Douglas-fir forests, Simard et al. (2013) recognized many other positive benefits of species interactions for healthy forest functioning.

The assertion about mixtures more fully utilizing site resources is supported for species that spatially stratify their roots and/or leaves and have higher yields in mixture (Kelty 1992; Pretzsch 2009). In general, it is well known that negative interactions among trees of different species are often less than those among trees of the same species, and this has been clearly documented for the interior cedar-hemlock and sub-boreal spruce forests of northwest British Columbia (Coates et al. 2009; Coates et al. 2013). This is because "neighbours that are similar in their resource needs or physiological ecology have greater overlap of their 'niche space' and less opportunity for resource partitioning, leading to more intense competition" (Boyden et al. 2008).

Species composition

Whether or not mixtures have higher yields than monocultures (suggesting that they are more fully utilizing site resources) depends on species composition. Overall, the studies in this review indicated that mixing species with very similar characteristics is less likely to produce higher yields than monocultures. Two species combinations that had lower yields for mixtures than monocultures involved conifers that were both shade-intolerant (e.g., lodgepole pine with western larch; see Table 2 for all scientific names) or both very shade-tolerant (e.g., western redcedar with western hemlock). Strong negative effects of competition between these two sets of similar species decreased the growth of at least one species in a pair when they were grown together (Klinka et al. 2001a, 2001b; Chen et al. 2003). Other combinations of two conifers with similar shade tolerance (Douglas-fir with western white pine [both intermediate in shade tolerance] and Ponderosa pine with lodgepole pine [both shade-intolerant]) had no change in performance between mixtures and monocultures (Garber & Maguire 2004; Erickson et al. 2009). For those species combinations, competition within each species was similar to competition between species.

Future stand value

The end economic value of a forest stand in British Columbia is liable to change during the 50–100 years that the stand takes to reach its rotation age. Fifty years from now, carbon credits may be more valuable than wood products. Many other issues that affect how forests are valued could change in the future. These issues include the type and number of mills demanding certain species and specific wood quality attributes, the economic evaluation of non-timber values, export markets, and national and provincial policies on value-added forestry.

Table 2: Common and scientific names of tree species included in this review

Common name	Scientific name	Common name	Scientific name
Grand fir	*Abies grandis* (Dougl. ex D. Don) Lindl.	Lodgepole pine	*Pinus contorta* Dougl. ex Loud.
Subalpine fir	*Abies lasiocarpa* (Hook.) Nutt.	White pine	*Pinus monticola* Dougl. ex D. Don
Red maple	*Acer rubrum* L.		
Green alder	*Alnus crispa* (Ait.) Pursh	Ponderosa pine	*Pinus ponderosa* Dougl. ex Laws
Red alder	*Alnus rubra* Bong.		
Caucasian alder	*Alnus subcordata* C.A.Mey	Scots pine	*Pinus sylvestris* L.
Paper birch	*Betula papyrifera* Marsh	Eastern cottonwood	*Populus deltoides* Marsh.
Silver birch	*Betula pendula* Roth	Trembling aspen	*Populus tremuloides* Michx.
Downy birch	*Betula pubescens* Ehrh.	Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco
European beech	*Fagus sylvatica* L.		
Western larch	*Larix occidentalis* Nutt.	Red oak	*Quercus rubra* L.
Norway spruce	*Picea abies* (L.) Karst.	Western redcedar	*Thuja plicata* Donn ex D. Don
Interior spruce	*Picea glauca* × *engelmannii* (Moench) Voss	Eastern hemlock	*Tsuga canadensis* (L.) Carr.
Black spruce	*Picea mariana* (Mill.) BSP	Western hemlock	*Tsuga heterophylla* (Raf.) Sarg.
Sitka spruce	*Picea sitchensis* (Bong.) Carr.		
Jack pine	*Pinus banksiana* Lamb.		

Several species combinations did not have a greater yield in mixture than in monoculture because the more productive species was diluted by the less productive species, even though neither species' growth rate was negatively affected by the other. These combinations were lodgepole pine and black spruce (Chen et al. 2003), Douglas-fir and red alder on rich sites (Binkley 1983), Sitka spruce and red alder (Wipfli et al. 2003), Scots pine and Norway spruce (Lindén & Agestam 2002), and eastern cottonwood and Caucasian alder (Sayyad et al. 2006). For many of these combinations, no yield loss was evident in mixtures compared to monocultures, and other benefits may have occurred, such as improved tree form (Wierman & Oliver 1979), decreased risk of damage (Griess & Knoke 2011), and increased biodiversity (Deal 1997; Wipfli et al. 2003; Varga et al. 2005).

Species combinations that did exhibit higher yield in mixtures than monocultures often included a nitrogen-fixing species. This was the case for jack pine and green alder (Vogel & Gower 1998) and for Douglas-fir and red alder on poor sites (Binkley 1983). Other mixtures that outperformed monocultures in yield consisted of pairs of conifers with different shade tolerances (Ponderosa pine and grand fir plantations; Garber & Maguire 2004), or consisted of broadleaved and conifer species grown together (Norway spruce with European beech [Pretzsch et al. 2010] or silver and downy birch [Johansson 2003]; black spruce with trembling aspen [Légaré et al. 2004]; hardwood stands, primarily red oak and red maple, with an Eastern hemlock understorey [Kelty 1989]; see sidebar, "Why broadleaves and conifers make sense").

Why broadleaves and conifers make sense

Two main hypotheses explain why mixed plantations of broadleaved and conifer species are more likely to outperform conifer monocultures on sites of low soil fertility. Most broadleaved trees have higher water requirements than conifers, so their leaf area index and ability to compete for light are reduced on poor sites. Positive effects of litter from broadleaved trees on soil fertility are more important on poor sites than on sites that already have medium or rich soil fertility. Other facilitative interactions between broadleaves and conifers are also possible. For example, in Douglas-fir and paper birch mixed stands, Douglas-fir benefits from mycorrhizal transfer of carbon from paper birch and reduction of root disease (Simard et al. 2005; Simard & Vyse 2006).

Site types

In the 1930s, Toumey and Korstian (1937) also recognized the importance of soil productivity on the outcomes of competition. Since then, extensive research has shown how competition changes along soil resource gradients, but the competition–soil fertility relationship remains poorly understood (Maestre et al. 2009). For this review, we sought to find studies that examined the effect of soil resources on the performance of mixtures versus monocultures, but we found that most studies looked at plantations growing on sites of medium fertility only. The two studies that did compare mixtures and monocultures across different sites found that mixtures performed better in terms of yield compared to monocultures as soil resources decreased for European beech and Norway spruce (Pretzsch et al. 2010) and for Douglas-fir and red alder (Binkley 2003).

In British Columbia, some research on competition between conifers and broadleaved deciduous species has also found reduced negative effects of broadleaf species on planted lodgepole pine on lower fertility sites (Simard et al. 2005). Trembling aspen also has lower competitive effects on lodgepole pine in drier and colder biogeoclimatic units (Newsome et al. 2012). Unfortunately, the yield of trembling aspen and other species such as paper birch is usually not considered in competition studies because these species are not currently of broad commercial value in British Columbia.

Poor sites do not always have higher yields with mixtures, however. Other provincial research (lacking total yield data but still pertinent here) found that the effect of soil re-

sources on competitive interactions among trembling aspen, lodgepole pine, interior spruce, and subalpine fir depended on species, neighourhood composition, and type of competition (Coates et al. 2013), suggesting that site type and species composition should be considered together (see sidebar, "The quandary of the alternate species"). For lodgepole pine, the negative effects of below-ground competition from neighbouring conifers on growth rates were worse on low-fertility sites. Interior spruce also experienced increased negative effects of competition on low-fertility sites with lodgepole pine neighbours but not with interior spruce or subalpine fir neighbours. For subalpine fir, the type of competition controlled whether soil fertility decreased or increased the negative effects of competition on growth (Coates et al. 2013).

The quandary of the alternate species

In most instances, a secondary non-target tree species will decrease the yield of the primary tree as the density of the non-target species increases. For example, trembling aspen is considered a non-commercial species in many studies of young lodgepole pine stands; in the Sub-Boreal Spruce zone, it decreases production of the desirable species except at low densities of less than 1000 stems per hectare (O'Neill 2006; Newsome et al. 2012). Likewise, if red alder is not considered part of the stand volume, it decreases yield in Douglas-fir and red alder mixtures on rich sites and has no effect on poor sites; however, if it is considered part of the stand volume, it has no effect on yield on rich sites and increases yield on poor sites (Binkley et al. 2003).

Assessment age

Toumey and Korstian (1937) recognized that species with different growth rates can be harvested at different times, leading to economic flexibility for stand management. Different growth rates between species in a mixture also affect the age at which a mixture might have higher yields than a monoculture. Assessment age plays a key role in spruce and pine mixtures, which have different size–growth curves. For example, lodgepole pine grows very fast initially but slows down in the larger size classes, whereas interior spruce grows slowly at first but maintains higher growth rates later and maintains them for longer than lodgepole pine (Coates et al. 2009; Lilles & Astrup 2012). In comparisons of 50:50 mixtures of lodgepole pine and black spruce, stands over 50-years-old at breast height attained the same yield as lodgepole pine monocultures, but in younger stands mixtures often have lower volumes (Chen et al. 2003). Lindén and Agestam (2002) showed that Scots pine and Norway spruce mixtures also had differences in volume increment over time that could lead to differences in yield performance with stand age (see sidebar, "The problem with total yield").

Douglas-fir with western hemlock is another species combination for which age of assessment is a critical factor in comparing mixed- and single-species stands. In young plantations (12-years-old) of these two species, stands with the slower-growing western hemlock were less productive or as productive (depending on stand density, see below) as monocultures of the faster-growing Douglas-fir (Amaroso & Turnblom 2006). In 35–80-year-old natural stands, mixtures of Douglas-fir and western hemlock outperformed stands of pure Douglas-fir (Wierman & Oliver 1979). It is reasonable to assume that other species combinations of young mixed plantations, containing one initially slower-growing species, may have higher yields than monocultures before the rotation age is reached, even if early assessments do not show higher yields compared to a monoculture of the initially faster-growing species.

Species density and pattern

Although total stocking density is another mixture attribute with important consequences for yield comparisons, it has received relatively little attention in the literature. In the one

study we found that directly addressed this question, Amaroso & Turnblom (2006) compared yield in 12-year-old Douglas-fir and western hemlock mixed and monoculture plantations of different densities. They found that mixtures underperformed monocultures at lower densities because western hemlock diluted the more productive Douglas-fir. At high planting density (1729 trees per hectare), competition among trees was a more important factor, western hemlock had a lower negative effect, and the mixed stands could equal the yield of the pure Douglas-fir plantation.

Recent neighbourhood studies of growth dynamics in mixed forests have provided insight into how specific spatial patterns of species combinations could optimize yield in mixed forests (Canham et al. 2006; Coates et al. 2009; Baribault & Kobe 2011). For example, it is clear that species-specific competitive interactions vary widely among species in the interior cedar-hemlock and sub-boreal spruce forests of northern British Columbia and that certain species combinations will have lower competitive interactions than others (Coates et al. 2009, 2013). Opportunities to use data from neighbourhood studies in growth simulators such as SORTIE-ND will provide a means to test the yield implications of different species and spatial arrangements that would otherwise require costly long-term empirical experiments. Simulation models may offer some of the best information we have on long-term yields of mixed stands until more mixed plantation studies reach rotation age.

The problem with total yield

Although total yield is an attractive way to compare productivity in single- or mixed-species stands, it has its drawbacks, especially for operational forestry decisions, where considerations of merchantable or economically recoverable yield may be more important. Two species planted in mixture may very well make better use of the site resources and produce a higher level of total biomass, but if one species reaches merchantability before the other, harvesting that yield may be difficult and expensive (partial cut, single tree selection) or need to be delayed until the lower strata has reached maturity, resulting in a net loss of value. In current clearcutting operations, it is not uncommon for "potentially merchantable" volume to be cut down and left on site because it is not up to the required size when the other species is harvested. Resolving these issues will be important for British Columbia silviculturists when considering mixed-species management.

Conclusion

Many instances are evident in which trees in mixtures grow faster in height and diameter than trees in monocultures (Piotto 2008). By inference, mixtures can produce higher yields than monocultures, and potentially higher end value, if all species are considered economically valuable. Here in British Columbia, we found it difficult to estimate the yield impacts of mixed plantations compared to monocultures (or vice versa) because often the results of mixed plantation research were confounded by four factors that varied among studies: 1) species composition; 2) site type; 3) stand age; and 4) density and pattern. It is necessary to carefully consider these factors to achieve equal or greater productivity in a mixed tree plantation compared to a monoculture plantation.

First, it is clear that strong differences in characteristics, or traits, between or among species in a mixture can promote positive interactions and decrease negative interactions and hence more fully utilize soil and light resources in a stand. Species characteristics will also determine the effects of site type, density and pattern, and age of assessment on stand productivity.

Second, species-specific responses to site type will affect growth rate comparisons and the degree of positive versus negative interactions among trees. For example, mixed plantations of broadleaved and conifer species are more likely to out-produce monocultures on sites with low soil fertility than on sites with medium or rich soil fertility.

Unfortunately, specific information about native tree species mixtures is especially lacking across different site types.

A third factor to consider is the age of assessment. Different growth patterns over time among species will affect the age at which a mixture out-produces a monoculture. Frequently, stands must be over 20–25 years old before positive effects of mixed-species on growth rates become evident.

The final factor is the effect of density and pattern on yield. Decreased competitive effects between or among species in a mixed stand may not be apparent if tree density is low and there is slight overall competition. Furthermore, a slower-growing species in a mixture can have very low yield if high densities of a faster-growing species overtop it during early stand development. We also believe that mixture spatial distribution is important, but this attribute has been poorly studied

Silviculturists exploring the option of establishing plantations of mixed species have a long history of practical and scientific knowledge to guide them. Prescriptions for specific combinations of species, site, rotation age, and stocking that will produce higher yields than monocultures are lacking for most species in British Columbia. Consequently, silviculturists will need to extrapolate from available research to make educated decisions for their particular cases (e.g., Table 1). As more mixed plantations are established and reach rotation age, more yield data will be available to support these kinds of silvicultural decisions.

Acknowledgements

We are thankful for the assistance of three anonymous reviewers. The B.C. Ministry of Forests, Lands and Natural Resource Operations provided funding for this review.

References

Amaroso, M.M., & E.C. Turnblom. 2006. Comparing productivity of pure and mixed Douglas-fir and western hemlock plantation in the Pacific Northwest. Canadian Journal of Forest Research 36(6):1484–1496.

B.C. Ministry of Forests and Range. 2008. Tree species composition and diversity in British Columbia. Forest Practices Branch, Victoria, BC. FREP Report No. 14. http://www.for.gov.bc.ca/ftp/hfp/external/!publish/frep/reports/FREP_Report_14.pdf (Accessed October 2013).

Baribault, T.W., & R.K. Kobe. 2011. Neighbourhood interactions strengthen with increased soil resources in a northern hardwood forest. Journal of Ecology 99(6):1358–1372.

Binkley, D. 1983. Ecosystem production in Douglas-fir plantations: interaction of red alder and site fertility. Forest Ecology and Management 5(3):215–227.

_____. 2003. Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. Canadian Journal of Forest Research 33(11):2274–2279.

Boyden, S., D. Binkley, & J.L. Stape. 2008. Competition among *Eucalyptus* trees depends on genetic variation and resource supply. Ecology 89(10):2821–2859.

Campbell, E.M., S. Saunders, K.D. Coates, D.V. Meidinger, A.J. MacKinnon, G.A. O'Neill, D.J. MacKillop, S.C. DeLong, & D.G. Morgan. 2009. Ecological resilience and complexity: a theoretical framework for understanding and managing British Columbia's forest ecosystems in a changing climate. B.C. Ministry of Forests and Range, Forest Science Program, Victoria, B.C. Technical Report No. 055. http://www.for.gov.bc.ca/hfd/pubs/Docs/Tr/Tr055.htm (Accessed October 2013).

Canham, C.D., M.J. Papiak, M. Uriarte, W.H. McWilliams, J.C. Jenkins, & M.J. Twery. 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecological Applications 16(2):540–554.

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.

Coates, K.D., C.D. Canham, & P.T. LePage. 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. Journal of Ecology 97(1):118–130.

Coates, K.D., E.B. Lilles, & R. Astrup. 2013. Competitive interactions across a soil fertility gradient in a multispecies forest. Journal of Ecology 101(3):806–818.

Deal, R.L. 1997. Understory plant diversity in riparian alder-conifer stands after logging in south-east Alaska. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oreg. Research Note PNW-RN-523. http://www.fs.fed.us/pnw/pubs/pnw_rn523.pdf (Accessed October 2013).

Di Lucca, C.M. 1999. TASS/SYLVER/TIPSY: systems for predicting the impact of silvicultural practices on yield, lumber value, economic return and other benefits. In: Stand Density Management Conference: Using the Planning Tools. C.R. Bamsey (editor). Alberta Environmental Protection, Conference Proceedings, pp. 7–16.

Erickson, H.E., C.A. Harrington, & D.D. Marshall. 2009. Tree growth at stand and individual scales in two dual-species mixture experiments in southern Washington State, USA. Canadian Journal of Forest Research 39(6):1119–1132.

Forrester, D.I., J. Bauhus, A.L. Cowie, & J.K. Vanclay. 2006. Mixed-species plantations of *Eucalyptus* with nitrogen-fixing trees: a review. Forest Ecology and Management 233(2–3):211–230.

Garber, S.M., & D.A. Maguire. 2004. Stand productivity and development in two mixed-species spacing trials in the central Oregon cascades. Forest Science 50(1):92–105.

Griess, V.C., & T. Knoke. 2011. Growth performance, windthrow, and insects: meta-analyses of parameters influencing performance of mixed-species stands in boreal and northern temperate biomes. Canadian Journal of Forest Research 41(6):1141–1159.

Johansson, T. 2003. Mixed stands in Nordic countries: a challenge for the future. Biomass & Bioenergy 24(4–5):365–372.

Kelty, M.J. 1989. Productivity of New England hemlock/hardwood stands as affected by species composition and canopy structure. Forest Ecology and Management 28(3–4):237–257.

_____. 1992. Comparative productivity of monocultures and mixed-species stands. In: The Ecology and Silviculture of Mixed-Species Forests. M.J. Kelty, B.C. Larson, & C.D Oliver (editors). Kluwer Academic Publishers, Dordrecht, Boston, Mass., pp. 125–141.

_____. 2006. The role of species mixtures in plantation forestry. Forest Ecology and Management 233(2–3):195–204.

Klinka, K., D.B. Collins, & C. Chourmouzis. 2001a. Investigation into the productivity of single- and mixed-species, second growth stands of western hemlock and western redcedar. University of British Columbia, Forest Sciences Department, Vancouver, BC. Scientia Silvica Extension Series No. 36. https://circle.ubc.ca/bitstream/handle/2429/698/SSES036.PDF?sequence=1 (Accessed October 2013).

Klinka, K., P. Varga, L.E.M. de Montigny, & C. Chourmouzis. 2001b. The structure of single- and mixed-species, second-growth stands of western hemlock and western redcedar. University of British Columbia, Forest Sciences Department, Vancouver, BC. Scientia Silvica Extension Series No. 35. https://circle.ubc.ca/bitstream/handle/2429/708/SSES035.PDF?sequence=1 (Accessed October 2013).

Légaré, S., D. Paré, & Y. Bergeron. 2004. The responses of black spruce growth to an increased proportion of aspen in mixed stands. Canadian Journal of Forest Research 34:405–416.

Lilles, E.B., & R. Astrup. 2012. Multiple resource limitation and ontogeny combined: a growth rate comparison of three co-occurring conifers. Canadian Journal of Forest Research 42(1):99–110.

Lindén, M., & E. Agestam. 2002. Increment and yield in mixed and monoculture stands of *Pinus sylvestris* and *Picea abies* based on an experiment in southern Sweden. Scandinavian Journal of Forest Research 18(2):155–162.

Maestre, F.T., R.M. Callaway, F. Valladares, & C.J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. Journal of Ecology 97(2):199–205.

Messier, C., K.J. Puettmann, & K.D. Coates (editors). 2013. Managing forests as complex adaptive systems: building resilience to the challenge of global change. Routledge, New York, N.Y.

Newsome, T.A., J.L. Heineman, & A.F.L. Nemec. 2012. Identifying and characterizing important trembling aspen competitors with juvenile lodgepole pine in three south-central British Columbia ecosystems. International Journal of Forestry Research Volume 2012, Article ID 573640. http://dx.doi.org/10.1155/2012/573640 (Accessed October 2013).

Nichols, J.D., M. Bristow, & J.K. Vanclay. 2006. Mixed species plantations: prospects and challenges. Forest Ecology and Management 233(2–3):383–390.

O'Neill, M. 2006. Review of lodgepole pine growth and yield within mixed-wood canopies. University of Victoria, Department of Biology, Victoria, BC. Work Term Report. http://www.for.gov.bc.ca/hfd/library/FIA/2007/FSP_Y072051c.pdf (Accessed October 2013).

Piotto, D. 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. Forest Ecology and Management 255(3–4):781–786.

Pretzsch, H. 2009. Forest dynamics, growth and yield: from measurement to model. Springer-Verlag, Berlin, Germany.

Pretzsch, H., J. Block, J. Dieler, P.H. Dong, U. Kohnle, J. Nagel, H. Spellmann, & A. Zingg. 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Annals of Forest Science 67(7):712–723.

Sayyad, E., S.M. Hosseini, J. Mokhtari, R. Mahdavi, S.G. Jalali, M. Akbarinia, & M. Tabari. 2006. Comparison of growth, nutrition and soil properties of pure and mixed stands of *Populus deltoides* and *Alnus subcordata*. Silva Fennica 40(1):27–35.

Simard, S.W., S.M. Hagerman, D.L. Sachs, J.L. Heineman, & W.J. Mather. 2005. Conifer growth, *Armillaria ostoyae* root disease, and plant diversity responses to broadleaf competition reduction in mixed forests of southern interior British Columbia. Canadian Journal of Forest Research 35(4):843–859.

Simard S., K. Martin, A. Vyse, & B. Larson. 2013. Meta-networks of fungi, fauna and flora as agents of complex adaptive systems. In: Managing Forests as Complex Adaptive Systems: Building Resilience to the Challenge of Global Change. C. Messier, K.J. Puettmann, & K.D. Coates (editors). Routledge, New York, N.Y. pp. 133–164.

Simard, S.W., & A. Vyse. 2006. Trade-offs between competition and facilitation: a case study of vegetation management in the interior cedar-hemlock forests of southern British Columbia. Canadian Journal of Forest Research 36(10):2486–2496.

Toumey, J.W., & C.F. Korstian. 1937. Foundations of silviculture upon an ecological basis. John Wiley and Sons, New York, N.Y.

Varga, P., H.Y.H. Chen, & K. Klinka. 2005. Tree-size diversity between single- and mixed-species stands in three forest types in western Canada. Canadian Journal of Forest Research 35(3):593–601.

Vogel, J.G., & S.T. Gower. 1998. Carbon and nitrogen dynamics of boreal jack pine stands with and without a green alder understory. Ecosystems 1(4):386–400.

Wierman, C.A., & C.D. Oliver. 1979. Crown stratification by species in even-aged mixed stands of Douglas-fir–western hemlock. Canadian Journal of Forest Research 9(1):1–9.

Wipfli, M.S., R.L. Deal, P.E. Hennon, A.C. Johnson, R.T. Edwards, T.L. De Santo, T. Gomi, E.H. Orlikowska, M.D. Bryant, M.E. Schultz, C. LeSage, R. Kimbirauskus, & D.V. D'Amore. 2003. Compatible management of red alder-conifer ecosystems in southeastern Alaska. In: Compatible forest management. R.A. Monserud, R.W. Haynes, & A.C. Johnson (editors). Kluwer Academic Publishers, the Netherlands, pp. 55–81. http://www.fs.fed.us/pnw/pubs/journals/pnw_2003_wipfli001.pdf (Accessed October 2013).

Zhang, Y., H.Y.H. Chen, & P.B. Reich. 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. Journal of Ecology 100(3):742–749.

Author information

Erica B. Lilles – Soil and Vegetation Scientist, Bulkley Valley Research Centre, 3883 3rd Avenue, PO Box 4274, Smithers, BC V0J 2N0. Email: erica.lilles@bvcentre.ca

K. David Coates – Research Silviculturist, B.C. Ministry of Forests, Lands and Natural Resource Operations, Bag 6000, Smithers, BC V0J 2N0. Email: dave.coates@gov.bc.ca

ARTICLE RECEIVED: October 23, 2012 • ARTICLE ACCEPTED: August 4, 2013

Test Your Knowledge

How well can you recall the main messages in the preceding article? Test your knowledge by answering the following questions.

An evaluation of the main factors affecting yield differences between single- and mixed-species stands

1) In general, which is more severe: competition within a species or competition between species?

   a. Between species

   b. Within a species

   c. Does not matter

2) What is the concept of dilution?

   a. The overall stocking level is too low and no yield benefit of mixtures is observed

   b. A productive species always dilutes a less productive species

   c. The less productive species reduces overall yield even though neither species negatively affects the other

3) Mixed plantations of broadleaved and conifer species are more likely to have higher yield than single-species plantations on:

   a. Poor sites

   b. Average sites

   c. Rich sites

ANSWERS: 1 = b; 2 = c; 3 = a

Appendix 1: Yield comparisons between mixtures and monocultures from studies in this review with total yield data. British Columbia species codes are western hemlock (Hw), western redcedar (Cw), lodgepole pine (Pl), western larch (Lw), and black spruce (Sb).

Paper	Type of mixture	Site conditions	Yield	Explanation
Amaroso & Turnblom 2006	Douglas-fir and western hemlock mixtures and monocultures	Not considered	• Stand volume was as high in mixture as monoculture once planting density was 1729 stems per hectare. • Lower densities had higher volume in the Douglas-fir monoculture.	At higher planting density, interspecific competition was less than intraspecific and canopy stratification was developing to reduce competition.
Binkley 1983	Douglas-fir stands with and without red alder	One rich site and one poor site	• Douglas-fir dbh increased 10% on the poor site with alder and decreased 13% on the rich site with alder. • If alder basal area is included, basal area was 150% higher on poor sites with alder and unchanged on rich sites with alder.	Site type has an important influence on species interactions.
Binkley 2003	70-year-old Douglas-fir and red alder monocultures and mixtures	N-rich site and N-poor site	• A 50% decrease in stem mass for monoculture on nitrogen-poor site. • A 48% decrease in stem mass for mixture on nitrogen-rich site.	Site type has an important influence on species interactions.
Chen et al. 2003	Western hemlock–western redcedar; lodgepole pine–western larch; and lodgepole pine–black spruce mixtures and monocultures	Hw–Cw: fresh and medium; Pl–Lw: moderately dry and poor; Pl–Sb: fresh and poor	• Redcedar decreased the volume of hemlock in proportion to its abundance. • Pure pine and larch stands had higher volume than mixed stands. • Pine–spruce stands had the same volume as pure pine stands.	Important species-specific effects were noted: hemlock is a productive species that was diluted by the slower-growing redcedar; pine had a negative effect on larch; and spruce had little effect on pine, but its volume did not increase stand volume at the stand age in this study.
Erickson et al. 2009	Douglas-fir mixed with white pine or western hemlock compared to monocultures of all three species after 24 years	Not considered	• Douglas-fir diameter was 33% greater and individual tree volume was 100% greater in a mixed stand with western hemlock compared with a monoculture or mixture with white pine. • Yield was the same in mixture and monoculture with white pine and western hemlock.	Species similarities are important for outcomes of mixtures. Douglas-fir had a relative yield higher than 0.5 in hemlock mixtures and hemlock relative yield was unchanged; therefore, over time or depending on stocking, the Douglas-fir–hemlock mixture would potentially over-yield.

Appendix 1: Yield comparisons between mixtures and monocultures from studies in this review with total yield data. British Columbia species codes are western hemlock (Hw), western redcedar (Cw), lodgepole pine (Pl), western larch (Lw), and black spruce (Sb) [continued]

Paper	Type of mixture	Site conditions	Yield	Explanation
Garber & Maguire 2004	34-year-old ponderosa pine and lodgepole pine mixtures, 26-year-old ponderosa pine and grand fir mixtures and monocultures	Not considered	• No difference in stand volume was noted for ponderosa and lodgepole pine mixtures vs. monocultures. • The ponderosa pine and grand fir mixture had the same volume as the ponderosa pine monoculture but more than the grand fir monoculture. • Relative yield was slightly higher than 1 for ponderosa pine and grand fir mixtures.	Density and species composition both influenced yield comparisons between mixtures and monocultures. Ponderosa pine had better canopy stratification with grand fir than with lodgepole pine because grand fir is a slower-growing, shade-tolerant species.
Johansson 2003	Norway spruce with silver and downy birch	Not considered	• A 32% increase was noted in mean annual increment (MAI) in mixed birch-spruce stands compared to pure spruce stands. • Spruce MAI was lower in mixed stands, but the birch increase made up the difference.	Stocking and timing of planting or thinning is important for successful mixed-wood management in Europe.
Kelty 1989	Hardwood stands (primarily red oak and red maple) with and without an eastern hemlock understorey	Not considered	• Hardwood-hemlock stands had 64% and 43% greater basal area than hardwood only. • Hardwood yield was similar in stands with and without hemlock, so hemlock had an additive effect. • Modelling suggested that yield was similar to a pure hemlock stand if measured by volume but greater than pure hemlock if measured by basal area.	Productivity in mixture was increased by niche separation, highlighting an additive effect of hemlock, which could survive in the understorey.
Klinka et al. 2001a, 2001b	Pure and mixed 55–63-year-old stands of western hemlock and western redcedar	Fresh, nutrient-medium	• No change was noted for redcedar. • A 12% diameter decrease was noted for hemlock in mixed stands. • 15% height decrease was noted for hemlock in mixed stands.	With no canopy stratification, positive interactions were lacking and redcedar negatively affected hemlock. Density was high in redcedar stands, whereas hemlock self-thinned.
Légaré et al. 2004	Black spruce and trembling aspen	Plots had similar abiotic conditions, but site may still have been a confounding factor.	• Stands with less than 41% aspen increased spruce dbh by 24% and height by 29%. • Greater amounts of aspen decreased spruce growth. • At the stand level, increases in volume with increasing aspen (up to 41%) were attributed to the aspen fibre.	Volume increase was attributed to competitive reduction and improved nutrient cycling through aspen litter.

Appendix 1: Yield comparisons between mixtures and monocultures from studies in this review with total yield data. British Columbia species codes are western hemlock (Hw), western redcedar (Cw), lodgepole pine (Pl), western larch (Lw), and black spruce (Sb) [continued]

Paper	Type of mixture	Site conditions	Yield	Explanation
Lindén & Agestam 2002	Scots pine and Norway spruce in pure and mixed stands after 20 years	Medium fertility	• Pine diameters were 7% greater in mixture than monoculture, but differences in volume increment were insignificant.	Species with patterns in growth that are more different than Scots pine and Norway spruce may be better candidates for higher yields in mixed stands, but these pine-spruce mixtures may have higher yields at an older stand age.
Pretzsch et al. 2010	Differing proportions of Norway spruce and European beech in pure and mixed stands	Poor, medium, and rich	• An 8% increase was noted in above-ground dry mass in mixed stands. • Higher over-yielding was noted on poorer sites.	The positive effects of beech litter on spruce growth increased on poorer sites, high intra-specific competition in beech was broken up by spruce on rich sites.
Sayyad et al. 2006	Replacement series of eastern cottonwood and Caucasian alder	Not considered	• No change was evident in basal area for mixtures or monocultures, but cottonwood height and diameter were higher in 50:50 mixtures. • Alder was not affected by differing amounts of cottonwood.	Improved growth in cottonwood was attributed to higher nutrients due to alder and less intraspecific competition in mixtures.
Vogel & Gower 1998	Jack pine with and without a green alder understorey	Two study areas, one northern and one southern, both with degraded dystric brunisols	• Southern study had 18% higher above-ground net primary productivity (NPP) in stands with alder. • Northern study had 41% higher NPP in stands with alder.	Contribution of a nitrogen fixer to nitrogen cycling was noted and availability of the stands increased productivity.
Wierman & Oliver 1979	35–80-year-old natural Douglas-fir and western hemlock mixed stands	Not considered	Mixed stands were compared to volume table for pure stands and had higher basal area on average.	By 20 years, canopy stratification became evident in mixed stands, but it was unclear if planted stands would have had the same timing until dominance by Douglas-fir. There were positive effects of mixtures on Douglas-fir bole characteristics.
Wipfli et al. 2003	Sitka spruce with red alder	Not considered	Live tree basal area of spruce decreased with increasing alder.	Alder stands had a more open canopy structure, and alder grows quickly initially and then slows down, so alder diluted the Sitka spruce volume in these stands.