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Evaluating the effects of tree community species composition on *Larix occidentalis* growth

By

CHRISTIAN MICHAEL MERCADO

BS Forestry, Michigan State University, East Lansing, Michigan, 2017

Thesis

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Approved by:

Scott Whittenburg, Dean
Graduate School

David Affleck, Chair
Department of Forest Management

Andrew Larson
Department of Forest Management

Justin Crotteau
United States Forest Service

David Patterson
Department of Mathematics

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Abstract

Western larch (*Larix occidentalis*) is an important tree species exclusive to the inland northwest region of North America. It is very intolerant of shade but managed across a range of communities with both shade-tolerant and -intolerant species. Recent works have shown that tree and stand level competition in mixed-species communities can be modified depending on how the characteristics of species in a mixture interact. Such changes can alter the growth relationship of the participant species. Western larch growth has been well-characterized in empirical growth models, where growth is typically estimated from a complex of size, competition, density, and site productivity variables. Although these models have been characterized using data which span a wide-range of conditions, the effects of interspecific relationships on western larch growth dynamics have yet to be studied.

We used a network of long-term forest growth and yield research plot data to investigate (i) how mixtures modify the growth of individual western larch after accounting for other factors that influence growth and (ii) how to characterize species-mixing effects on western larch within the context of individual tree growth modelling. First, we used a generalized additive mixed model (GAMM) to estimate western larch annual basal area increment from size, competition, density, and site productivity variables, without addressing species-mixing. This model was then used in two separate analyses. In the first analysis, we identified different types of species mixtures and compared how the established western larch growth relationships in each mixture differed from those in pure larch stand conditions. In the second analysis we identified three species-informed metrics and added each to the established model. This resulted in three models which were compared to assess how each species-mixing metric affected the established growth relationship.

These analyses resulted in a GAMM that represented size, competition, density, and site variables with functional relationships similar to those identified in previous works. With this model, we showed that the way in which larch growth is characterized can differ when western larch is growing in mixtures compared to when growing in a pure stand with other western larch. When comparing species-mixing metrics in the third analysis, we showed that western larch growth may be higher in mixtures with species of higher shade-tolerance as well as in mixtures with other species in general.

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Chapter 1

Introduction

Western larch (*Larix occidentalis* Nutt.) is an important tree species in the inland northwest region of the USA because of its contribution to ecological, economic, and cultural values across the region. *L. occidentalis* is endemic and nearly exclusive to the upper Columbia river watershed within Montana, Idaho, Washington, Oregon, and southern British Columbia, and is well-adapted to the historic climate of the region (Knudsen *et al.* 1968; Schmidt *et al.* 1976; Schmidt and McDonald 1995). Additionally, its wood is characterized with desirable lumber qualities such as high specific gravity, straight grains, and tight knots (Keegan III and Wichman 1995). It is the most productive of the three North American larch species (Rehfeldt and Jaquish 2010) and its lumber is often commercially available in a mix with Douglas-fir, adding a unique and localized product value. Further, western larch and its associated forests provide important habitat to native birds, bears, and ungulates (McClelland and McClelland 1999; Schmidt *et al.* 1976). In the US northern Rocky Mountains, where fire is historically and currently prevalent, western larch is both uniquely fire resistant and a prolific pioneer species on sites following fire (Schmidt and Shearer 1995) due to its thick bark, deciduous needles, well-dispersed seeds, and germination preference for bare-mineral soil (Schmidt *et al.* 1976). *Larix* species also provide unique aesthetic characteristics throughout the year, coloring hillsides shades of green, yellow, and brown, depending on the season, adding a colorful representation of seasonality.

Western larch naturally grows across a gradient of species-mixtures (Schmidt and Seidel 1995). It is found in communities with: Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), lodgepole pine

(*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), ponderosa pine (*Pinus ponderosa*), western hemlock (*Tsuga heterophylla*), mountain hemlock (*Tsuga mertensiana*), and western redcedar (*Thuja plicata*) (Schmidt and Shearer 1995; Schmidt and Seidel 1995). It is sometimes managed in even-aged, homogeneous plantations, but more typically in mixed-conifer settings where interactions among species (or species-mixing) at tree and stand levels may occur. Additionally, western larch is classified as very intolerant of shade and one of the fastest-growing species within its communities (Baker 1949; Schmidt and Seidel 1995). Larch's prolific regeneration and rapid juvenile growth allows it to out-compete other trees and leads to high stand densities (Schmidt 1998). Thus, it responds well to density management early in stand development, which can have lasting impacts on tree and stand growth (Schaedel *et al.* 2017).

The effects that stand density has on tree and stand productivity (e.g., diameter and/or volume growth) can vary at different levels of species purity in a stand depending on community species composition (Condés *et al.* 2013; Brunner and Forrester 2020). Weiskittel *et al.* (2009a) found that the density of a stand at which self-thinning occurs for a given species was positively associated with stand purity, meaning an increase in diversity could reduce a site's maximum potential density. In contrast, Pretzsch and Biber (2016) showed that stand carrying capacity was positively impacted in more diverse stands. A similar study found that maximum density increased in shade intolerant *Pinus ponderosa* and *Pseudotsuga menziesii* stands when species-diversity was higher, but in shade-tolerant *Abies grandis* stands, the relative impact of stand purity on stand density was unimportant (Kimsey *et al.* 2019).

Density also modifies inter-tree competition and tree growth, where higher density is associated with smaller tree sizes and vice versa (Oliver and Larson 1996; Sjolte-Jørgensen 1967; Smith and Reukema 1986). However, since species-mixing may be positively, negatively, or not at all associated with stand density, the effect of species-mixing on growth can vary. Brunner & Forrester (2020) demonstrated that species mixture affected tree growth only at high densities for their studied mixture. Concurrently, in a study of *Abies grandis* and *Pinus ponderosa* mixtures in Oregon, Maguire and Mainwaring (2021) found that mixing impacted tree size only at high density at one study site. At the other site, however, the number of observations suggesting no species-mixing

effect on growth outweighed those that did (Maguire and Mainwaring 2021). A study of two European *Pinus* species showed positive growth associated with species-mixing for one species across densities, but no effect at all for the other species (Riofrío *et al.* 2019). Given these results, species-mixing effects on tree growth (albeit equivocally) may be more relevant at high densities, but the mechanisms that produce these effects must be understood for further insight.

Variation in species characteristics within mixed-species communities can modify competitive and/or complementary relationships among species (Forrester 2017). In these communities, even small differences in shade-tolerance, height growth rate, water use efficiency, tree architecture, and other characteristics can result in altered species growth rates (Riofrío *et al.* 2017; Forrester 2017). Moreover, ecological niche theory suggests that mixture effects are stronger for highly complementary species (Loreau 2010). Species shade tolerance relates to the physiological and morphological characteristics which drive growth (Reich *et al.* 1998), and thus relates to inter-tree competitive dynamics (Canham *et al.* 2006). For example, productivity in forests can be enhanced by mixing shade tolerant and intolerant species (Zhang *et al.* 2012; Williams *et al.* 2017) where different species' light requirement niches (or shade tolerances) are complementary (Thurm and Pretzsch 2016).

Furthermore, quantifying community competition for light may sufficiently capture the effects of biodiversity on productivity (Morin *et al.* 2011), provided that inter-tree competition for other resources is accounted for. For instance, Jucker *et al.* (2014) found that the degree of light-use complementarity depended on whether below-ground resources were adequate to sustain high rates of photosynthesis, and they showed that increases in competition for water negated such effects. There is also evidence indicating that below-ground competition for resources can be asymmetric among species (Rewald and Leuschner 2009), however the resulting effects on productivity may vary over time with environmental conditions, as species exploit resources differently depending on their growth strategies (del Río *et al.* 2014). Searle and Chen (2020) found that positive complementary effects on individual tree growth increase with both community shade-tolerance and phylogenetic dissimilarity. Specifically, they showed that shade-tolerance can encapsulate its effects on inter-specific competition, and that positive niche complementary effects on tree growth increase with competition intensity. Since competition modifies growth dynamics, accounting

for niche complementarity and other competitive dynamics may aid in managing mixed-species stands.

For stands in the inland northwest region of the United States, where relatively low intensity management occurs over a broad area and across tree, stand, and site conditions, managers and researchers commonly use the Forest Vegetation Simulator (FVS; Dixon 2020) to estimate future stand dynamics. FVS uses a distance-independent individual tree growth model (Stage 1973; Wykoff 1990) that does not require individual tree locations to account for competition, and projects tree growth using tree size, stand density, competition, and site variables. Its formulation is paralleled by growth models in other regions and countries, like the multiple US and Canada regional variants of FVS or PROGNAUS (Monserud and Sterba 1996) in Austria. These types of models are widely used because they provide an accurate, simple, and efficient basis for projecting tree and stand growth (Weiskittel *et al.* 2011).

Various studies have evaluated species-mixing effects on tree growth using the vetted framework of such models. One study showed that when incorporated into an individual tree growth model, and after accounting for tree, stand, and site conditions, species-mixing effects improved predictions (Riofrío *et al.* 2019). Vospernik (2021) found that individual tree basal area increment was significantly modified in mixtures after accounting for other factors. They observed species-mixing effects on *Larix decidua* in mixtures with *Picea abies*, *Pinus cembra*, *Fagus sylvatica*, and *Betulus spp.*, where it mutually benefited in mixtures with *Picea abies* (Vospernik 2021). These findings are similar to those of Zöhrer (1969) where incremental growth was increased in mixtures between shade-tolerant *Picea abies* and shade-intolerant *Larix decidua*.

Since individual tree growth models can be improved by accounting for species-mixing in addition to other variables, it may be pertinent to characterizing individual tree growth in mixed-conifer forests in the western US. Additionally, since there is evidence of this in phylogenetically similar European larch (*L. decidua*), species-mixing effects may be relevant for characterizing western larch growth, as it is a fast growing and shade-intolerant species that mixes with various other conifers across the inland northwest. The foci of the present study then are to evaluate (i) whether

community composition impacts the growth of western larch (given other variables known to impact its growth) and (ii) how to characterize species-mixing effects on western larch within the context of distance-independent, individual-tree growth modeling in the inland northwest.

The objectives of the present study were: (i) to identify a distance-independent individual tree basal area increment (BAI) model to statistically control for variations in tree size, competition, stand density, and site productivity in long-term forest inventory data, (ii) to determine if western larch BAI varies in pure larch stands versus larch-Douglas-fir mixtures or larch-lodgepole pine mixtures after accounting for other factors, and (iii) to compare generalizable species-mixing measures and identify if these improve growth estimation across a broad spectrum of mixtures. I expected that for a given size, density, and site productivity, larch growth would be greater when a larger portion of stand density was made up of more shade-tolerant species, provided that western larch has an adequate amount of overhead light to grow. This follows the idea that shade-tolerance reflects a species' resource-use (especially light-seeking) strategies, and that contrasting resource-use among species within a stand can lead to a niche complementarity effect on growth by reducing inter-tree competition for resources. For the same reason, I expected that species-mixing effects would best be captured by a measure that accounts for different species' shade tolerance, as this would address the primary mechanisms behind variations in growth, as opposed to simple measures of stand species purity or more complex measures of size-density relative to potential maximum crown area (i.e., crown competition factor, CCF).

Chapter 2

Methods

2.1 Permanent Growth Plot study

To establish a monitoring protocol for the FVS model, the USDA Forest Service Northern Rocky Mountain Region developed long-term permanent growth plot clusters (PGPs) in managed stands across the inland northwest (Montana and northern Idaho), referred herein to as the PGP program. The PGP program was primarily set up to monitor long-term treatment response to precommercial thinning relative to projections provided by FVS. The initial goal of the PGP program was to remeasure the selected stands at regular increments of 5-10 years in order to provide a robust growth increment data set. Various stand measurements were initialized and then remeasured between 1980 and 2002. The program was then paused, and was only recently revisited in 2018 and 2021, allowing for analysis of long-term effects, albeit with a wide gap between recent measurements. Stands had varying types of initialization post-disturbance; some were clearcut, burned and planted; others originated from natural seeding in a seed-tree system, for instance. Most stands were initiated between 1955 and 1970, where a handful of stands were older, with origins as early as 1910.

Each PGP stand consists of 4 plot-clusters: 1 untreated control plot cluster and 3 treatment plot clusters. The latter were treated with commercial or precommercial thinning, depending on stand age and maturity. Stand prescriptions determined target residual densities by species in the treatment areas, providing for side-by-side comparison between control and treatments under similar

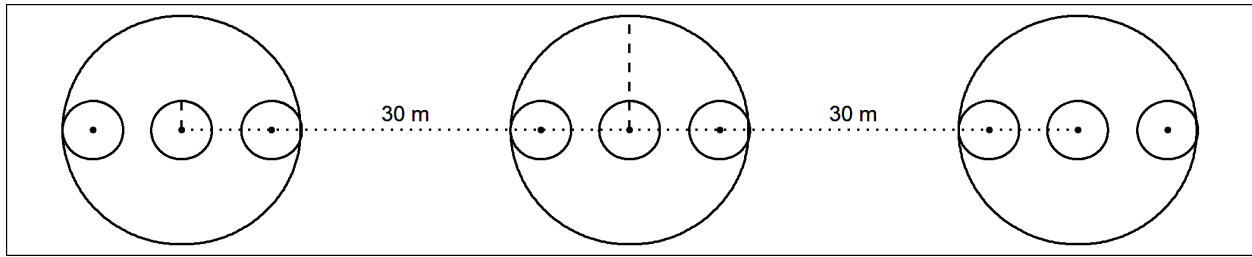


Figure 2.1: Each plot cluster consisted of three measurement plots where data was collected on large trees (large circles), each plot occupying 202 m². Each large plot contained three sub-plots where data was collected small trees, each sub-plot occupying 13.5 m². The center of each plot was approximately 30 meters from neighboring plots in the same cluster to ensure measurement trees were unique to one plot. Dashed lines from from plot centers indicate fixed radii for each type of plot, approximately 8 m and 2 m in large and small plots, respectively.

site conditions. The location of control and treatment plots were determined by random selection of coordinates on a grid laid over a map of the stand. To ensure that the control plots were not affected by nearby thinning treatments, an unthinned buffer was placed around control clusters. Every cluster is comprised of three 202 m² large-tree plots, with each plot containing three 13.5 m² small tree sub-plots (Fig. 2.1). Data for trees in large-tree plots were taken based on whether a tree was above a specified diameter threshold. The diameter thresholds varied across and within stands (across control and treatment plots), as well as within clusters over time. Yet the large trees were tagged and distance and azimuth to plot center were taken. Heights were taken on only a subset of large trees due to the operational challenges and added time of measuring tree height. Within small tree plots, tree counts by species and height class were recorded for trees greater than or equal to 15 cm in height from the ground, and up to the specified diameter threshold.

During the summer of 2018, a re-measurement campaign targeted stands with at least 3 previously recorded measurements on the Lolo National Forest. During the summer of 2021, PGP stands on the Lolo and Kootenai National Forests that were previously measured at least 3 times and that were composed of >50% overstory western larch (determined by most recent measurement) were targeted for re-measurement. Stands across the remeasured PGPs were spread between 46°N and 49°N, and between 800 and 1800 m above sea level (Fig. 2.2). Stands were primarily on north-facing aspects. Overall, species composition varied between almost pure western larch to mixed conifer forests composed of mixtures of: western larch, Douglas-fir, Engelmann spruce, grand fir, subalpine fir, western hemlock, mountain hemlock, western redcedar, cottonwood (*Populus*

balsamifera), and quaking aspen (*Populus tremuloides*).

Large-tree data recorded at each time of measurement includes: diameter at breast height (DBH), total height (as previously described), crown ratio (CR), crown class, species, whether the tree was alive or dead, and biotic and/or abiotic damage to the tree (and the intensity thereof). For small trees taller than 15 cm but shorter than 1.4 m, species, live/dead status, CR, height, and crown class were recorded. For small trees tall enough for DBH measurement (≥ 1.4 m) and with a DBH below the established threshold, DBH and height were also recorded. Small trees were tallied based on height classes: less than 1.4 m, 1.4 m to 3.7 m, 3.7 m to 5.8 m, and trees taller than 5.8 m (which were tallied individually). Both large and small tree data were used to calculate tree and stand metrics.

One such measure is the annual growth of western larch, which was quantified by basal area increment (BAI):

$$BAI_{kpm} = \frac{G_{kp(m+1)} - G_{kpm}}{t_{p,(m+1)} - t_{pm}} \quad [2.1]$$

where G_{kpm} refers to the basal area of tree k in plot p at measurement occasion m , and t_{pm} denotes the year of this measurement. The choice to annualize BAI was made because re-measurement intervals were inconsistent across the data set and annualization allows for flexibility and a finer-scale measure of stand dynamics over time (Weiskittel *et al.* 2011).

Other variables were grouped together based on the types of tree or stand attributes that they describe. These groups are variables that represent (i) tree size, (ii) individual and inter-tree density and competition (referred together as competition herein) and (iii), characteristics of the site where trees are growing. The following variables do not account for species-specific characteristics, that is, these variables describe tree size and number of trees in an area, but are insensitive to species composition.

Size variables include diameter at breast height DBH and tree basal area G .

Competition variables were:

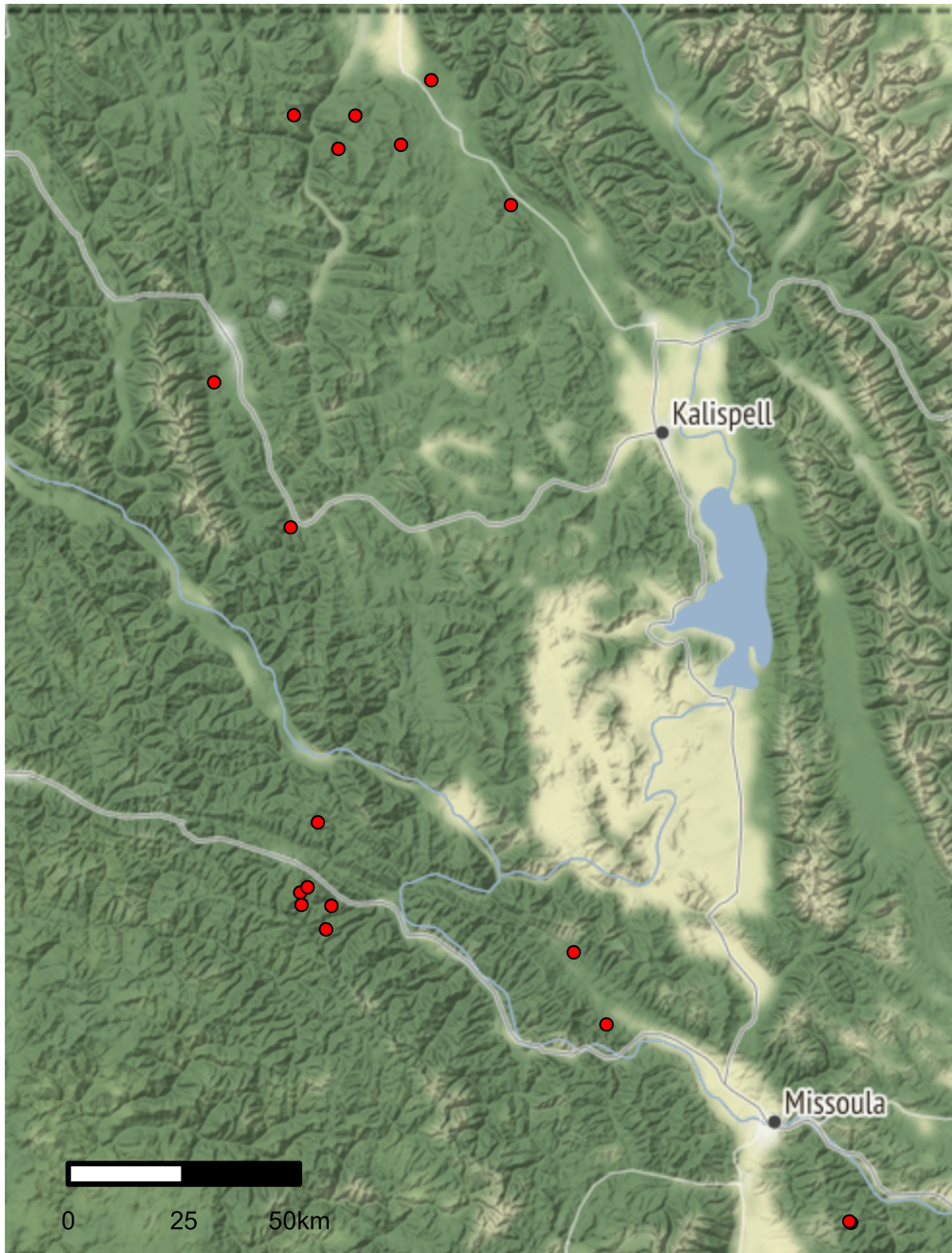


Figure 2.2: Approximate locations (indicated by red dots) of each stand remeasured during the 2018 and 2021 field seasons. Map area is within the northwestern corner of Montana, USA. Map tiles by Stamen Maps (<http://stamen.com>) provided under CC BY 3.0 (<http://creativecommons.org/licenses/by/3.0/>). Data by OpenStreetMap (<http://openstreetmap.org>), under ODbL (<http://www.openstreetmap.org/copyright>).

1. plot number of trees per hectare (TPH)

$$TPH_{pm} = \sum_k h_{kpm} C_{kpm} \quad [2.2]$$

where h_{kpm} is the tree expansion factor and C_{kpm} is the number of trees represented,

2. plot basal area per hectare (BAH)

$$BAH_{pm} = \sum_k h_{kpm} G_{kpm} \quad [2.3]$$

3. the ratio of plot BAH in trees that are larger than the subject tree (BAL)

$$BAL_{kpm} = \frac{\sum_{k'} h_{k'pm} G_{k'pm}}{BAH_{pm}} \quad [2.4]$$

where the sum is over trees k' with DBH larger than the subject tree,

4. plot quadratic mean diameter (QMD)

$$QMD_{pm} = \sqrt{\frac{BAH_{pm} \cdot 40,000}{TPH_{pm} \cdot \pi}} \quad [2.5]$$

and

5. the ratio of tree DBH to QMD (Dq)

$$Dq_{kpm} = \frac{DBH_{kpm}}{QMD_{pm}} \quad [2.6]$$

In this study, CR was considered a tree-level competition metric instead of a tree size variable. This is because CR reflects the cumulative effects of past management and competition and, thus,

it is responsive to stand density and light-availability (Wykoff 1990; Monserud and Sterba 1996; Hasenauer and Monserud 1996). The same is true for DBH growth, however, CR reflects a tree's photosynthetic capacity and competitive status (Leites *et al.* 2009) more readily than DBH, justifying its selection as a C variable.

Topographic site variables, measured at the cluster-level, were percent slope, aspect (between 0 and 360 degrees), and elevation (in meters). Western larch site index (base age 50, year at breast height, with height in meters) was calculated at the stand-level as an average value over dominant, undamaged trees between 25 and 100 years of age (Milner 1992). Continuous heat insulation load index (heatload, herein), for each cluster was estimated as described by Theobald *et al.* (2015), relating solar insulation and topographic shading to site productivity. Slope, aspect, elevation, and heatload were measured and/or calculated using GPS data points taken at a point in each cluster using Google Earth Engine (Gorelick *et al.* 2017). Additionally, a stand-specific offset was considered as a site variable (as a dummy variable).

The effects of different combinations of these variables on BAI of western larch trees were evaluated throughout the PGP data. These data were split into a model training data set, and a data set that was withheld from model training, which was used to validate and assess models. The withheld data consisted of tree data from two randomly selected measurement plots out of each stand. An overview of the amount of data in the training data set may be viewed in Table 2.1.

2.2 Overview of additive modeling approach

Using these data, generalized additive mixed models (GAMMs) were developed to relate the BAI of western larch trees to the variables described above. Generalized additive models (GAMs; Hastie and Tibshirani 1990) allow for flexibility in model fitting and an allowance for non-linear relationships across variables (Zhao *et al.* 2005; Wood 2006). Contrary to traditional parametric modeling approaches, GAMs let the data determine the shape of the functional relationships by fitting predictor effects with a sum of smooth functions of covariates instead of fitting them with specified parameters (Wood 2006; Robinson *et al.* 2011). The choice to use a mixed-model approach was made owing to the dependence structure that arises from repeat measurements on the

Table 2.1: Distribution of numbers of unique western larch trees and growth increments across the PGP stands evaluated in this study for model training. Two plots were selected from each stand at random for the validation data set, so only 10 of 12 plots are shown for each stand. Stands 1609, 1614, and 1618 had plots that either did not have any western larch growth data or simply did not have any data at all, so only 9 plots are shown for these stands.

Stand	Measurements	Unique trees	Increments	Plots
1401	4	53	150	10
1402	5	188	631	10
1403	5	113	313	10
1404	5	146	465	10
1405	5	188	676	10
1406	5	99	304	10
1407	4	74	108	19
1408	4	77	212	10
1609	5	37	139	9
1610	5	129	416	10
1611	5	77	222	10
1612	4	211	548	10
1614	5	49	181	9
1615	4	133	379	10
1616	4	106	291	10
1617	4	131	355	10
1618	4	30	66	9
1619	4	134	338	10
Totals		1975	5794	186

same trees that were within plots within clusters over time, and thus random effects were specified at the individual tree-level.

GAMMs were fit using the *mgcv* package (Wood 2011) in R (R Core Team 2021). Smoothers are composed of a sum of fitted basis functions which characterize the conditional relationship between a predictor and an independent variable. They are penalized by a smoothing parameter, which constrains a smoother as its complexity (or ‘wigginess’) grows higher, as indicated by a smoother’s effective degrees of freedom (EDF) (Pedersen *et al.* 2019). The thin-plate regression spline (TPRS) is the default smoother in *mgcv* owing to its simple and effective behavior (Wood 2003), and was used for all model terms fit in the present study.

The *mgcv* package allows smoothing parameters to be estimated via likelihood, information the-

oretical methods, or cross-validation-based methods (Wood 2006). The maximum likelihood method was used in this study where comparison across models with different fixed terms and smoothing parameters was necessary. Otherwise models were fit using the restricted maximum likelihood criteria (REML) approach because it reduces computation time and typically renders comparable results. Since smoothing parameters are estimated during model fitting, there is a level of uncertainty associated with them. This may be accounted for when plotting partial effects, resulting in wider confidence bands associated with a smooth. Additionally, random effects may also be coded as penalized smooths in this format (Pedersen *et al.* 2019), allowing for simple specification of random intercepts for individual trees. Using this method, random effects are modeled as independent and identically distributed (Gaussian) random deviates while preserving overall model distribution assumptions (Wood 2008).

Furthermore, the `mgcv` package allows for smooth functions that vary across different groups. This works by fitting a smoother with its own smoothing parameter for each level of a categorical variable (Pedersen *et al.* 2019). Specifically, one level may be specified as the ‘reference’ level and fit with a reference smooth to represent reference conditions. Each of the remaining levels are then fit with respective smooths that each characterize how the relationship for that level deviates from the reference smooth (Pedersen *et al.* 2019; Wood 2006; Zuur *et al.* 2009).

In this study it was of interest to compare GAMs on the basis of predictive accuracy, which was estimated by two different definitions of root mean squared error (RMSE). One definition was evaluated as within sample error using the model training data and model number of residual degrees of freedom (RMSE_{int}). The other evaluated error using the withheld data and number of observations therein (RMSE_{ext}):

$$\text{RMSE}_{\text{int}} = \sqrt{\frac{\sum_m \sum_p \sum_k (\widehat{BAI}_{kpm} - BAI_{kpm})^2}{n_{df}}} \quad [2.7]$$

$$\text{RMSE}_{\text{ext}} = \sqrt{\frac{\sum_m \sum_p \sum_k (\widehat{BAI}_{kpm} - BAI_{kpm})^2}{n}} \quad [2.8]$$

where \widehat{BAI}_{kpm} and BAI_{kpm} are the predicted and observed values of BAI, n_{df} is the model residual degrees of freedom (number of increments less model effective degrees of freedom) and n is the number of increments in the withheld data. $RMSE_{int}$ was used for comparing model accuracy across models during model selection, and $RMSE_{ext}$ was used to assess model validity and predictive accuracy.

In addition to model accuracy, model fit was also of interest. Model fit for GAMs may be evaluated through visual examination of residual structure as well as through assessing the proportion of null deviance explained by the model, simply referred to as deviance explained (Wood 2006). A combination of these assessments were made to evaluate fit in the present study. Additionally, model concurvity (Hastie and Tibshirani 1990) may be used to measure dependence among predictors in a GAM. It determines whether one covariate smooth function in a model is associated with a different covariate smooth function in the same model (Wood 2006), and thus is analogous to collinearity in linear models. Concurvity estimates may be calculated pair-wise between functions, or between each smooth and the rest of the model in which it is embedded. The latter of these two options was chosen for simplicity, and a model with any estimated concurvity value > 0.8 was not considered.

A sequence of three different analyses was conducted to accomplish the objectives of this study, each using the model training data set. The first involved identifying an initial model by selecting size (S), competition (C), and site productivity (P) predictors that effectively estimate western larch growth but that carry no information about community species composition. This initial model and its formulation will be referred to herein as SCPt (t refers to the inclusion of tree-level random effects). Once identified, SCPt was then used as a foundation for subsequent analyses. The second analysis utilized a subset of the training data incorporating only three specific stand species combinations, and evaluated differences of SCPt smooths across these combinations. The third analysis involved augmenting SCPt using three different species-mixing measures (each in its own respective model and trained with the full training data set) in order to evaluate whether they could effectively contribute to differences in the growth of western larch more broadly. The following three sections will describe each of these analyses in more detail.

2.3 Model selection

Selecting which predictors to include within the initial model (SCPt) followed the logic of Wykoff (1990), Monserud and Sterba (1996), and Vospernik (2021) where predictors were grouped together based on the categories described above (i.e., S, C, and P). Prior to testing predictors within a GAM, a colinearity assessment was performed within each group of variables to avoid including highly correlated variables together in candidate models. Any predictors with an absolute Pearson correlation of 0.65 or higher were not considered in a model together. Additionally, variables known to represent the same processes, even if not highly linearly correlated (such as heatload and aspect, for instance), were not considered together to avoid redundancies and reduce model complexity. Furthermore, since BAI is a positive continuous response variable with uneven dispersion across predictor values, it was modeled with a natural log link and Gamma distribution.

GAMs were fit in iterations to select predictors and visually examine predictor partial effects on BAI. Iterations were in order of the established predictor grouping as stated previously (Wykoff 1990; Monserud and Sterba 1996). Highly correlated variables in the same group were compared in alternative models to determine which contributed the most to estimating BAI. For example, alternative models were fit for both tree DBH and BA, selecting whichever best predicted BAI. Then, with the selected S variable(s) present in the model, C variables were evaluated and selected based on maximizing model accuracy and reducing overlap between variables. A model formulation with the lowest $RMSE_{int}$ was selected over alternatives. If estimated concavity was greater than 0.8 for a particular term, then alternative predictors were assessed in its place. The same process was used for P variables thereafter. Once a parsimonious GAM was identified with variables for each group, random intercepts for individual trees were then included. This resulted in model SCPt, taking the following form:

$$\ln[E(BAI)] = B + \sum_j f_{1j}(x_{1j}) + \sum_j f_{2j}(x_{2j}) + \sum_j f_{3j}(x_{3j}) \quad [2.9]$$

where \ln represents the natural logarithmic link function, $E(BAI)$ represents the expected value of BAI, B represents an estimated tree-level random intercept (t), x_{ij} represents a predictor variable in group i (S, C, or P), and f_{ij} is the smooth function thereof.

2.4 Assessing western larch growth across different communities

In order to test for differences in larch growth between different species mixtures, distinct species combinations were determined based on species' proportional shares of plot basal area. To qualify as a specific mixture-type, a minimum of 20% of the total plot basal area had to be in western larch trees and a minimum of 20% in either Douglas-fir or lodgepole pine. This was to ensure that there was minimal representation by both western larch and its counter-species in a mixture. To ensure that neither species was over-represented in a plot, neither larch nor the other species could exceed 65% of plot basal area. Also, both species combined basal area had to occupy at least 70% of plot basal area. For reference, a pure larch condition was defined as at least 70% of plot basal area in western larch.

Model SCPt was then fit with the species-mixture data, allowing each mixture an offset for the intercept and for each smooth term. This resulted in a model containing a reference smooth for each predictor corresponding to the pure larch condition, and a difference smooth (Wood 2006) for each identified species-mixture:

$$\ln[E(BAI)] = B + \sum_i \sum_j f_{ij}(x_{ij}) + \sum_s \delta_s [\alpha_s + \sum_i \sum_j g_{ij,s}(x_{ij})] \quad [2.10]$$

where δ_s is a species-mix indicator ($\delta_s = 0$ if the observation is in a pure larch condition or $\delta_s = 1$ if the observation is in mixture s), α_s is an offset on the intercept, and $g_{ij,s}()$ is an offset smooth for species s and predictor j in group i . This means that the reference smooth is centered around zero, and then a difference (offset) smooth is centered about the reference smooth. In other words, a difference smooth characterizes how a smooth function for a given condition differs from that of the corresponding reference condition. Given this, a hypothesis test may be used to evaluate whether a difference smooth does indeed represent a departure between a mixture and the pure conditions. In this test the null hypothesis states that the predictor effect in the mixture condition is no different from the reference smooth (i.e., that a difference smooth is a flat, no-effect function). The alternative hypothesis states that the predictor effect for the mixture does indeed deviate from the corresponding reference smooth (i.e., the difference smooth function is not a flat function). P-values were calculated using the F-test described by Wood (2013).

2.5 Comparing species-mixing measures

In addition to comparing growth across mixtures, it was of interest to capture species-mixing effects by using measures that are easy to estimate or readily available. Three different species-mixing measures were identified and each added as an additional predictor in the SCPt model: crown competition factor, the proportion of plot basal area occupied by larch, and proportion of plot basal area weighted by species-shade tolerance values. They were compared in alternative models to assess their contributions to model prediction (after accounting for other factors) and evaluated to further determine how species-mixing might impact the growth of larch.

Crown competition factor (CCF) is a species-informed density measure that is based on tree crown allometry (Krajicek *et al.* 1961). In this measure, each species has an identified maximum crown area (MCA) that would be achieved in open-grown conditions for a given DBH and are estimated using species-specific coefficients in polynomial equations of DBH. MCA values are summed within a plot to express overall competition for crown space, or CCF:

$$CCF_{pm} = \sum_k h_{kpm} C_{kpm} w_s(DBH_{kpm}) \quad [2.11]$$

where $w_s()$ is a function of DBH for a species (s), returning a MCA density (MCA per unit land area) in percent. This study used the species-specific equations and coefficient values identified by the FVS-IE variant (Keyser 2015). This measure is normalized such that a CCF value of 100 means that if all trees in a stand achieved their respective MCAs then 100% canopy cover is achieved. Thus, a value of 100 describes the onset of competition for crown space. CCF is typically used to describe competition, but since it varies depending on species-specific allometries, it is considered a species-mixing metric here. Figure 2.3 displays an example of how CCF varies depending on species composition.

One alternative to CCF involves a weighted proportion of plot basal area in a given target species. It follows from the simple logic that if a high proportion of basal area in a plot is in western larch trees, then species-mixing effects simply cannot occur. However, if the proportion of western larch

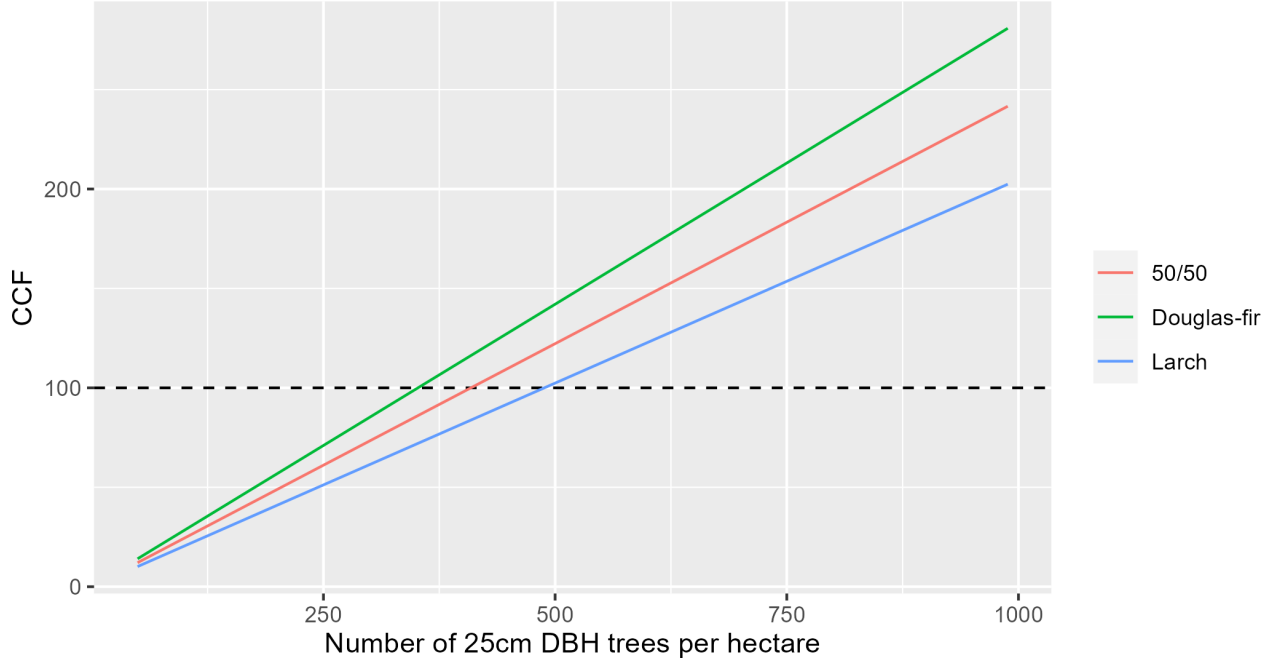


Figure 2.3: Plot of CCF and number of equally sized (DBH 25 cm) trees in a theoretical sample from: a pure larch stand (blue), a pure Douglas-fir stand (green), and one consisting of a 50/50 mix between both species. CCF increases with number of trees, however the onset of intertree competition varies by species composition, as displayed by the trend lines.

in a plot is low, then species-mixing effects may be present. Therefore, as an alternative to CCF, the proportion of basal area occupied by larch (purity, herein) was used to evaluate species mixing effects. It is simply calculated as the proportion of plot basal area occupied by western larch:

$$L_{pm} = \frac{\sum_k \alpha_{kpm} G_{kpm}}{\sum_k G_{kpm}} \quad \text{where} \quad \begin{cases} \text{if tree } k \text{ is western larch } \alpha_{kpm} = 1 \\ \text{else } \alpha = 0 \end{cases} \quad [2.12]$$

and L_{pm} denotes the plot larch purity value at measurement m .

The third species-informed measure makes use of a shade-tolerance index (Lienard *et al.* 2015) where different species are assigned with values ranging between 0 and 1, 0 being very shade-tolerant, and 1 being very shade-intolerant (as shown in Table 2.2). Shade intolerance values were multiplied by individual tree basal area values, and then summed:

$$T_{pm} = \sum_k \rho_{kpm} G_{kpm} \quad [2.13]$$

Table 2.2: Shade intolerance values for the PGP species, based on the inverse of the shade tolerance values identified by Lienard *et al.* (2015).

Genus	Species	Shade intolerance
<i>Larix</i>	<i>occidentalis</i>	1.00
<i>Pinus</i>	<i>contorta</i>	1.00
<i>Pinus</i>	<i>ponderosa</i>	0.75
<i>Pinus</i>	<i>monticola</i>	0.50
<i>Pseudotsuga</i>	<i>menziesii</i>	0.50
<i>Abies</i>	<i>grandis</i>	0.25
<i>Abies</i>	<i>lasiocarpa</i>	0.25
<i>Picea</i>	<i>engelmannii</i>	0.25
<i>Thuja</i>	<i>plicata</i>	0
<i>Tsuga</i>	<i>heterophylla</i>	0

where T_{pm} represents plot shade intolerance at a given measurement and ρ_{kpm} represents the shade intolerance value associated with the species of tree k (Lienard *et al.* 2015). A T_{pm} value of 1 means that a plot at a given measurement is composed completely of shade intolerant species, and a value of 0 means a plot is composed completely of shade tolerant species.

To evaluate and compare these measures, each was added as an additional predictor to the SCPt model formulation:

$$\ln[E(BAI)] = B + \sum_j f_{1j}(x_{1j}) + \sum_j f_{2j}(x_{2j}) + \sum_j f_{3j}(x_{3j}) + f_{4j}(x_{4j}) \quad [2.14]$$

where x_{4j} is one of CCF , L , or T . Each resulting model was then compared in terms of predictive accuracy ($RMSE_{\text{ext}}$). Model fit was also evaluated for each respective model with deviance explained.

Chapter 3

Results

3.1 Trends in western larch growth data

Tree size was positively associated with the growth of western larch but this relationship was modified by other variables, as shown in Fig. 3.1. Growth was the lowest in smaller trees, but increases rapidly at DBH less than 20 cm (at low densities) and then tapers as tree size and density increase. The occurrence of large-diameter trees raise plot basal area, so larger diameter trees appear at higher densities in each mixture. High-density growth data was limited in the lodgepole-pine mixture type. The range in shade-intolerance was limited such that there were few data with values below 0.4. Pure larch and lodgepole pine mixtures were more shade intolerant than those of Douglas-fir and other mixtures.

Site attributes for different mixtures are displayed in Fig. 3.2. These data mostly lie on north-facing aspects, which are typically cooler and wetter, and are distributed from west to east. Higher heatload values indicate that a site may be hotter and/or drier than others, and appeared in these data on west and south facing aspects. Lower heatload values are shown more abundantly on north-northeast aspects. Few data were evaluated on southern aspects. Elevation ranged from 800 m to 1800 m, but much of these data appear at sites above 1200 m (Fig. 3.2).

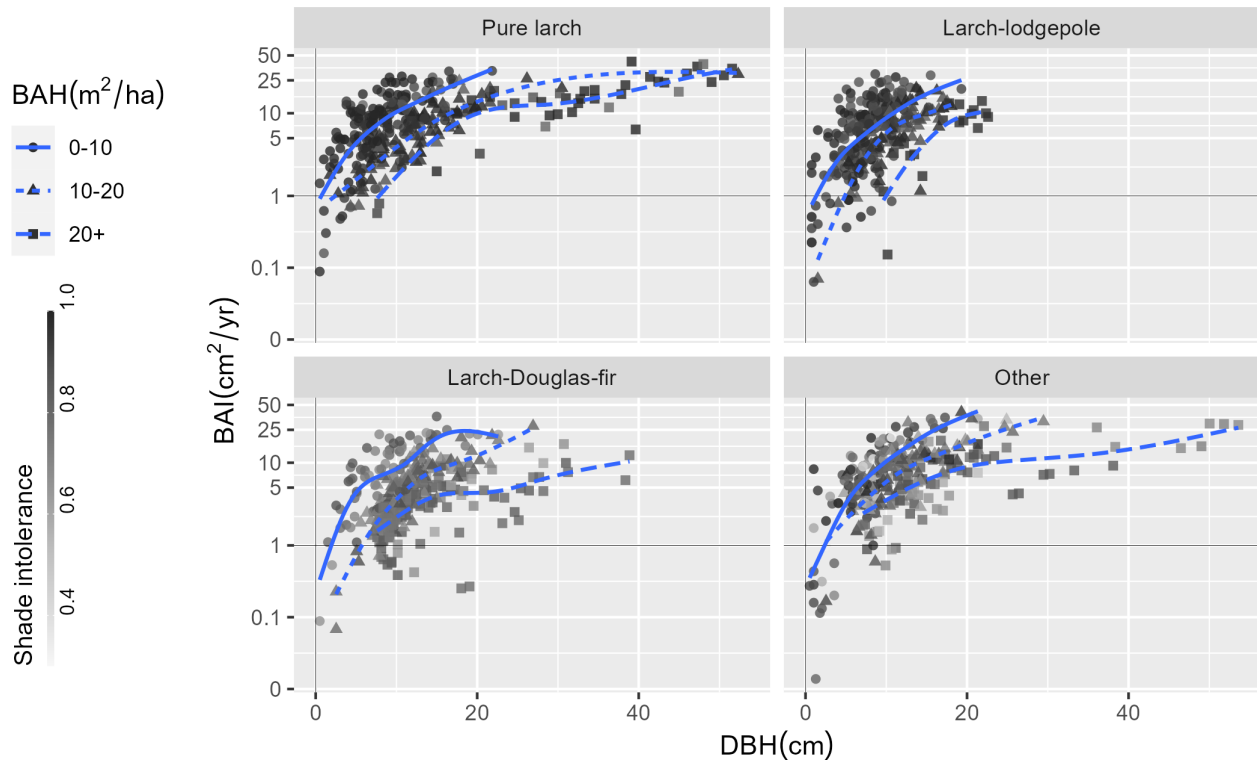


Figure 3.1: Relationship between western larch BAI (plotted with natural logarithm transformation) and DBH. Each line type (solid, long-dashed, short-dashed) represent different levels of plot basal area (BAH m²/ha) and each panel represents different species mixtures. Shades of grey from white to black represent plot shade intolerance values. 300 observations were randomly sampled for each displayed mixture type from the training data set to avoid over-plotting.

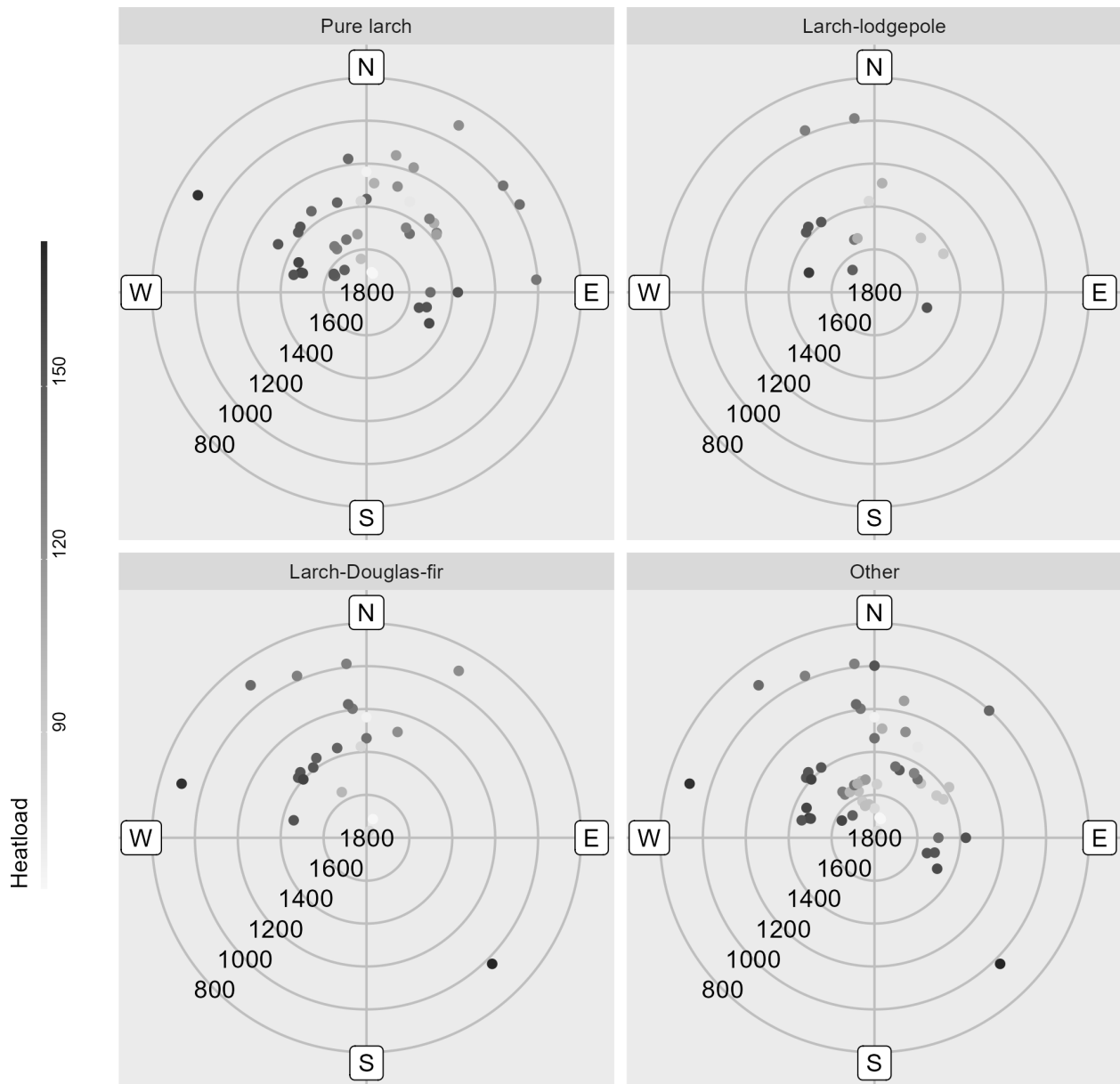


Figure 3.2: Plot of aspect and elevations for different species mixtures. Each point represents an individual cluster within a PGP stand.

3.2 SCPt model determination

The SCPt model training data set consisted of 5,792 basal area increments across 1,975 individual western larch trees. Predictors were determined through a sequential selection from within each group (S, C, and P), considering S variables first, and then considering C variables in addition to S variables, and P variables in addition to S and C. This is visualized in Table 3.1 and results are described below.

Table 3.1: Table of effective degrees of freedom (EDF) for each variable in each model (Size = S, Size + Competition = SC, Size + Competition + Site Productivity = SCP, Size + Competition + Site Productivity + tree random intercept = SCPt). $RMSE_{ext}$ was not used for selection, but is included here .

Smooth	EDF	Deviance explained (%)	$RMSE_{int}$ (cm ² /yr)	$RMSE_{ext}$ (cm ² /yr)
S		30.82	5.64	5.68
DBH	7.1			
SC		62.87	4.31	4.68
DBH	7.7			
CR	2.0			
BAL	5.9			
BAH	8.6			
SCP		67.39	4.01	4.45
DBH	7.6			
CR	4.5			
BAL	7.1			
BAH	8.5			
Aspect	27.2			
SCPt		84.91	3.32	4.81
DBH	8.0			
CR	1.6			
BAL	7.8			
BAH	8.7			
Aspect	25.7			
t	1337.0			

S variables were tree DBH and tree basal area (G). DBH and G were highly correlated (0.938) and were evaluated as predictors of BAI in separate models. DBH as a predictor yielded slightly higher

accuracy in predicting BAI than G, with model RMSE_{int} values of $5.64 \text{ cm}^2/\text{yr}$ and $5.70 \text{ cm}^2/\text{yr}$, respectively.

C variables were partitioned into two sub-groups: variables representing a tree's competitive position in a stand (BAL, Dq, and CR), and variables that represent the overall competitive environment (QMD, TPH, and BAH). Highly collinear variable combinations were TPH-Dq (0.732) and BAH-QMD (0.684). With DBH effects included, adding BAL and CR to the model reduced RMSE_{int} to $4.50 \text{ cm}^2/\text{yr}$, and then to $4.31 \text{ cm}^2/\text{yr}$ with plot BAH included.

Topographic variables (slope, aspect, elevation) were evaluated as potential predictors separately from site index, heatload, and the stand-specific offset. Since aspect is a circular measure, both sine (easting) and cosine (northing) transformations were applied as in previous works (e.g., Stage 1976) using an isotropic smooth. Aspect was best accounted for as an interaction of the sine and cosine transformations. Slope and elevation contributed little to prediction accuracy when included with aspect and were associated with concurvity values beyond the established threshold. The stand offsets contributed to high concurvity, and were excluded from evaluation. Thus, building on the model and comparing aspect, site index, and heatload, aspect was selected as the best (and only) site term, further reducing model RMSE_{int} to $4.01 \text{ cm}^2/\text{yr}$.

Given this information, the SCPt basal area increment model was specified with the following predictors: DBH, CR, BAL, BAH, and aspect. Upon the addition of tree-level random effects, SCPt RMSE_{int} was $3.34 \text{ cm}^2/\text{yr}$. Fixed effects terms used 53 degrees of freedom, and percent model null deviance explained was 84.9%. Tree-level effects were accounted for using a spline basis (Wood 2006), and had an associated effective degrees of freedom of 1337. Model statistics are reported in Table 3.1.

Partial response curves on the log-link scale are shown in Fig. 3.3. On this scale DBH had a positive, but nonlinear effect on BAI, eventually tapering at values larger than 30 cm. Crown ratio was penalized to a near-linear increasing effect that was small relative to DBH. BAL appeared to have a negligible (negative) effect on BAI until a threshold of approximately 0.9 (where 90% of plot basal area is in trees larger than the subject tree) after which it produced a strong negative effect. BAH was characterized by a sharp negative effect, tapering at values above $20 \text{ m}^2/\text{ha}$,

where little change is seen at values in excess of 30 m²/ha. Positive partial effects of aspect on BAI were associated with N-NW, N-NE, and NE aspects. NW and SE aspects were associated with negative effects on growth. Data were insufficient for estimating effects for southwest-facing aspects and therefore do not appear in Fig. 3.3.

Model term complexity, overall fit, and predictive accuracy (respective of the iterative group-wise selection) are shown Table 3.1. Improvements in RMSE_{int} and deviance explained were seen with the addition of predictors from each group. The final SCPt model residuals as well as model estimation error are shown in Fig. 3.4. Residuals are roughly centered about zero across the range of fitted values except as fitted values approach their lower limit (data are sparse at this range). The estimation errors showed four unusually high predicted values of BAI with large negative errors (predicted BAI > 30 cm²/yr. and errors < -20). All four of these points represent predictions on one relatively large tree that is surrounded by comparably small trees. This created a combination of DBH (> 45 cm) and BAH (11 m²/ha) that was not well-represented in the training data, resulting in very large predictions and estimation errors. Otherwise, errors appear centered around zero and don't show any other notable patterns.

3.3 Assessing growth differences across communities

Distinct distributions of conditions were observed over the identified mixtures and the pure larch (reference) plots (Table 3.2). The reference conditions had the most growth observations over the broadest range of BAI and DBH (Table 3.2) and sat on aspects spanning northwest to northeast (Fig. 3.2). Lodgepole pine mixtures had the narrowest range of BAI and BAH as well as the lowest mean value of BAH. The Douglas-fir mixture data had the widest range of BAH values and the highest average of BAH. Both mixtures evaluated were more abundant on northwest-facing slopes (Fig. 3.2).

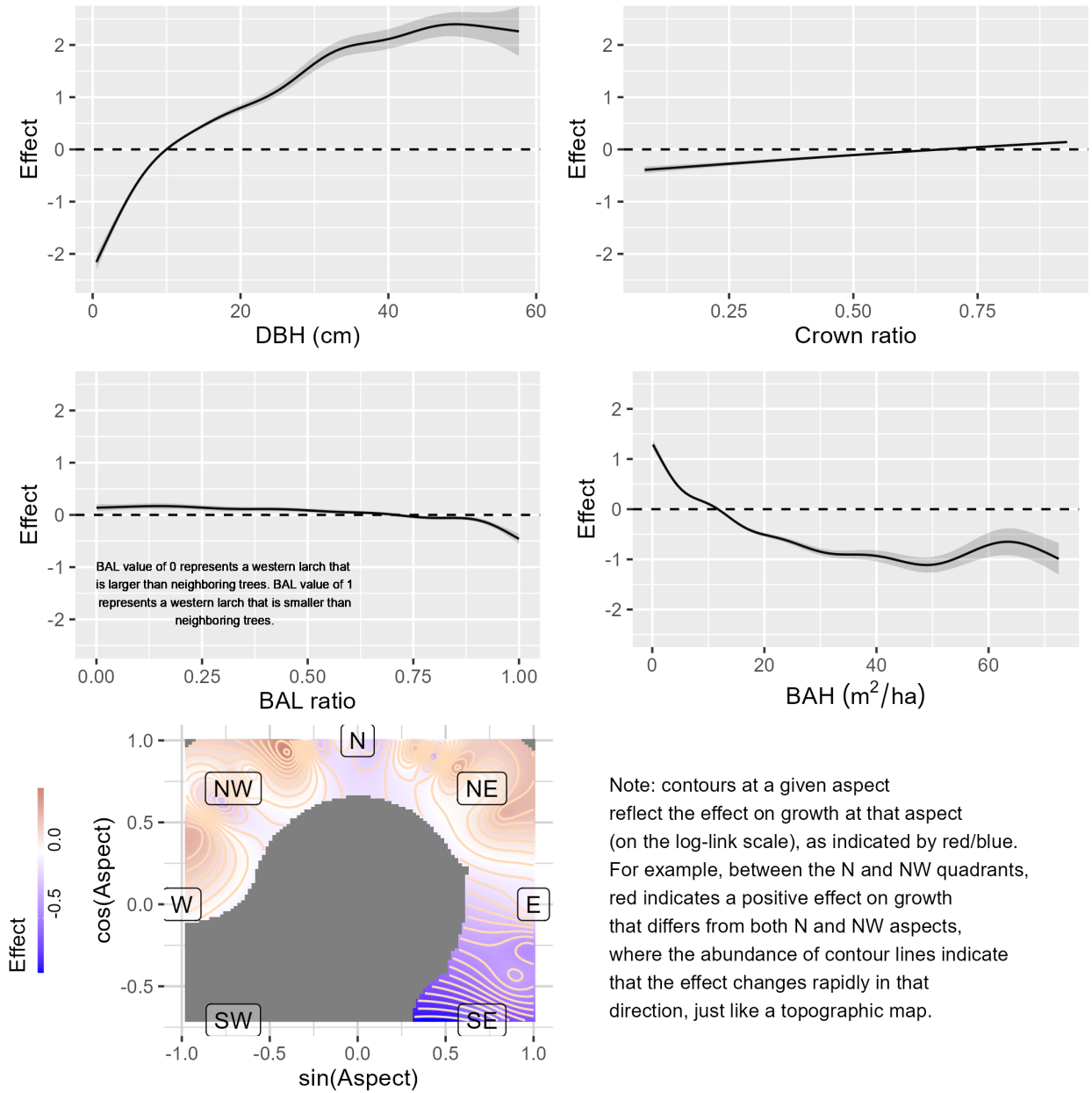


Figure 3.3: Partial effects of each predictor after accounting for the effects of other predictors in the selected base model, shown on the log-link scale. Error bands represent ± 2 standard errors and account for uncertainty in smoothing parameter estimation.

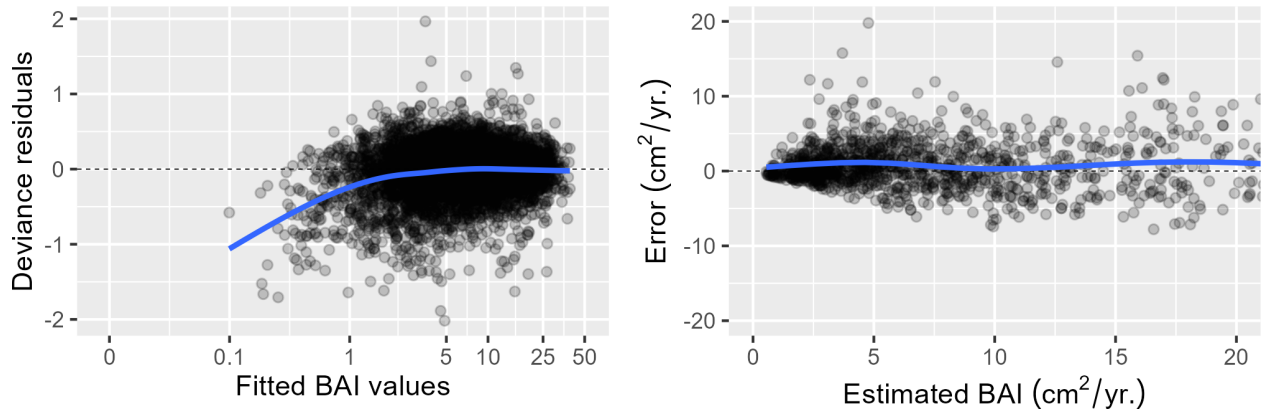


Figure 3.4: Deviance residuals vs. fitted BAI values (plotted on the log-link scale; left) and estimation error (right) vs. estimated BAI values for the SCPT model. Deviance residuals are from the training data and estimation errors are derived from BAI predictions using the withheld data set. The estimation error plot is used to evaluate model predictive bias. Errors for BAI values > 20 $\text{cm}^2/\text{yr.}$ are not shown due to sparse data and because one exceptionally large tree in the withheld data produced exceptionally low error values.

Table 3.2: Summary table of BAI, DBH, CR, BAL, and BAH for different species-mixture data subsets.

Variable		Pure larch	Larch-lodgepole	Larch-Douglas-fir	Other
BAI(cm^2/yr)	min	0.05	0.03	0.10	0.00
	max	53.3	29.7	36.2	47.8
	sd	7.69	5.76	5.48	7.16
	mean	8.94	7.53	6.05	8.90
DBH(cm)	min	0.5	0.8	0.5	0.5
	max	57.7	22.6	38.9	53.6
	sd	11.7	4.3	6.2	6.6
	mean	13.6	9.2	12.4	11.79
Crown ratio	min	0.08	0.20	0.08	0.08
	max	0.93	0.93	0.93	0.93
	sd	0.25	0.18	0.24	0.19
	mean	0.61	0.78	0.53	0.72
BAL (ratio)	min	0.00	0.00	0.00	0.00
	max	1.00	1.00	1.00	1.00
	sd	0.30	0.27	0.29	0.291
	mean	0.59	0.64	0.58	0.59
BAH(m^2/ha)	min	0.23	0.13	0.67	0.35
	max	55.9	23.4	69.1	66.4
	sd	11.5	5.4	16.0	11.3
	mean	12.8	9.2	21.7	15.2
Observations		2932	366	638	1858
Unique trees		1064	207	320	384

Table 3.3: Table of effective degrees of freedom for reference (pure larch) and difference smooths (Larch-lodgepole, larch-Douglas-fir; see Fig. 3.5) and associated p-values. Higher EDF values indicate more complexity in the fitted smooth. P-values are associated with the corresponding smooth.

Smooth	Pure larch		Larch-lodgepole		Larch-Douglas-fir	
	EDF	p-value	EDF	p-value	EDF	p-value
Intercept	1	0.018	1	0.694	1	0.778
DBH	7.89	< 0.001	2.75	< 0.001	2.14	0.398
Crown ratio	1.00	< 0.001	2.78	0.031	3.74	0.004
BAL ratio	3.12	< 0.001	3.12	< 0.001	2.11	0.122
BA	8.65	< 0.001	4.69	< 0.001	2.23	0.001
Aspect	17.02	< 0.001	6.61	0.014	10.7	< 0.001

The difference-of-smooths model (see Equation 2.10) was fit to the SCPt model formula using the data described above. This resulted in a reference smooth function for each predictor for the pure western larch conditions as well as corresponding difference smooths for the lodgepole pine and Douglas-fir mixtures. Each reference smooth was visually indistinguishable from those fit in the SCPt model (shown in Fig. 3.3), and thus these are not shown. Model outputs indicate that each reference smooth holds some association with BAI (see p-values in Table 3.3). Results for each mixture are reported in the following two sub-sections.

3.3.1 Western larch-lodgepole pine mixtures

There was strong evidence indicating a departure of growth response from pure western larch conditions as DBH, BAL, and BAH varied when western larch was mixed with lodgepole pine, and modest evidence for such in crown ratio and aspect (Table 3.3). In this mixture, growth was less in smaller western larch trees, but became greater when larch diameters exceeded 12 cm, compared to pure stands. A similarly-shaped difference effect is displayed as BAL increases from zero (Fig. 3.5). This means that a western larch tree would grow less when in a dominant position ($BAL < 0.5$) when growing in a mixture with lodgepole pine compared to a western larch in a dominant position in the pure-larch conditions, holding everything else constant. Conversely, a western larch in a subordinate position ($BAL > 0.75$) would grow more than a subordinate western larch growing in a pure stand, holding everything else constant. The BAI-BAH difference smooth

showed a positive difference at low densities and a negative difference at high densities but was within two standard errors of zero across most of its range. This is also true for the smoothed effect of CR.

3.3.2 Western larch-Douglas-fir mixtures

For larch-Douglas-fir mixtures, growth deviated from the pure stands as CR, BAH, and aspect varied, but little to no variation was observed in response to different levels of DBH or BAL. The growth differences in response to CR were slightly elevated for larch-Douglas-fir mixtures, but only in mid-range values of CR (Fig. 3.5). BAH impacts on western larch growth in larch-Douglas-fir mixtures were negative and more pronounced at higher densities.

3.4 Comparing growth estimation across different species-mixing measures

The utility of using CCF, L (purity of western larch), and T (shade intolerance) for estimating the BAI of western larch was compared by fitting separate models. Both L and T were incorporated as additional predictors in their own respective calibrations of the SCPT model formula. CCF and BAH were found to be highly correlated with one-another, so CCF was included in place of BAH in the SCPT formula.

Model accuracy was best improved by the addition of L, followed by T and then CCF (Table 3.4). Inclusion of all three terms was supported by p-values below 0.001, suggesting that each was an important predictor in its respective model. Changes in $RMSE_{ext}$ were modest, all of which were at the sub- square centimeter per year- level. Model deviance explained increased in concert with improvements to accuracy except in the case of CCF, where deviance explained decreased when CCF replaced BAH in the model (Table 3.4).

In the absence of BAH in the model, CCF displayed a larger partial effect on tree growth than purity or shade intolerance (Fig. 3.6). However, since CCF is a size-weighted measure of stand density, it appears very similar to the BAH smooth in the SCPT model (in Fig. 3.3), showing a negative

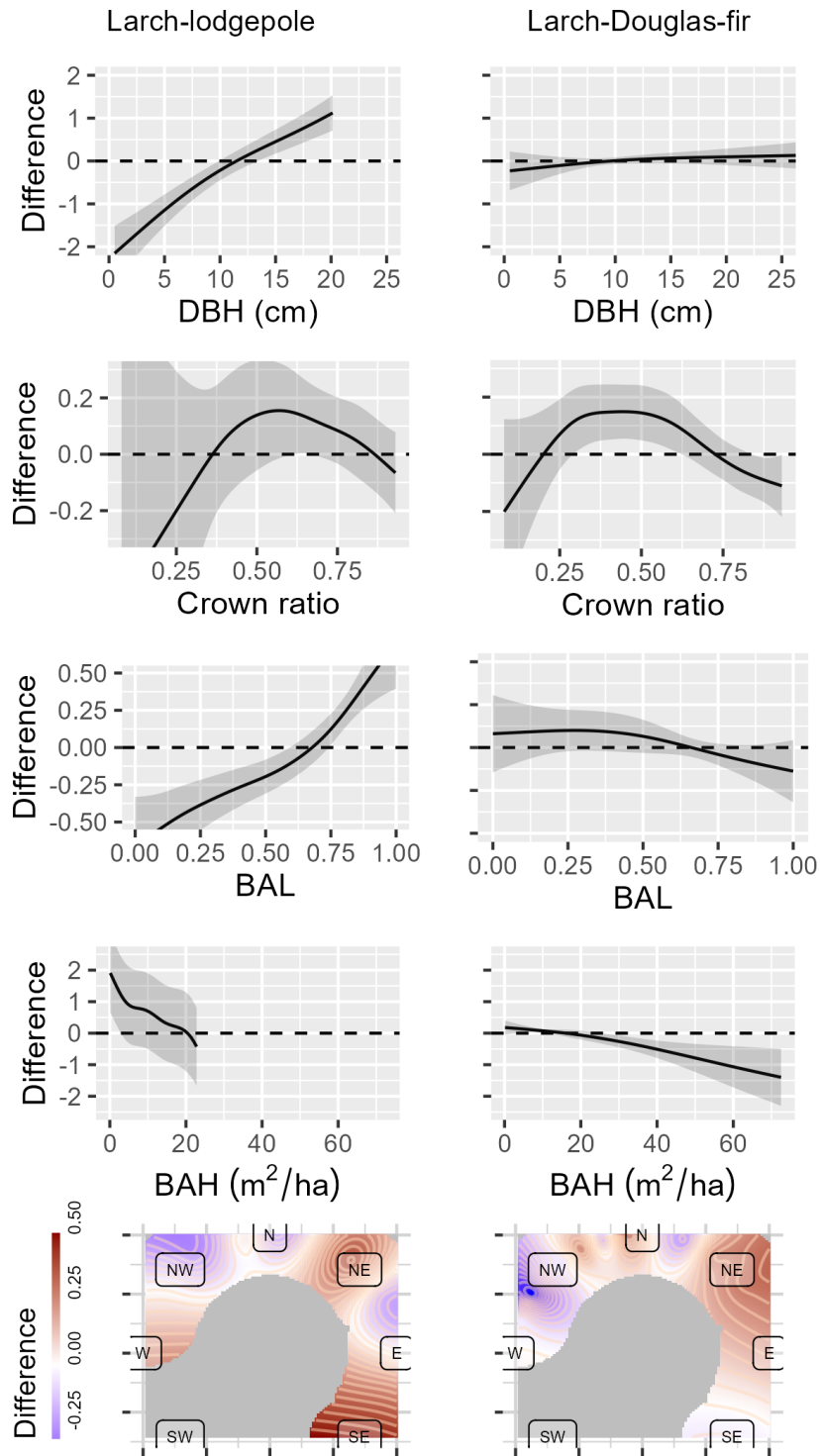


Figure 3.5: Difference smooths for each SCPT predictor displaying the differences between Larch-lodgepole pine (left) mixtures and the pure larch (reference) conditions as well as between the Larch-Douglas-fir mixtures (right) and the reference smooths. Differences from the 0 (dashed) line indicate values at which the partial response for larch growth when fitted for the given mixture differ from the that of the pure larch condition, holding everything else constant. Error bands represent ± 2 standard errors and account for uncertainty in smoothing parameter estimation. Y-axes are scaled differently across predictors. Reference smooths not shown - compare to the smooths in Fig. 3.3. This figure corresponds to the p-values and EDFs in Table 3.3.

Table 3.4: $RMSE_{\text{ext}}$ calculated with the withheld data and percent of the training data null deviance explained by the model for model SCPt and models including each species-mixing metric (CCF, L, T).

Metric	$RMSE_{\text{ext}}$ (cm ² /yr)	Deviance explained (%)
None	4.814	84.91
CCF	4.801	84.42
Purity (L)	4.595	85.07
Shade intol. (T)	4.627	85.02

effect that is very pronounced at low values ($CCF < 50$) but that tapers to a near constant effect at high values ($CCF > 150$). Both purity and shade intolerance were also characterized by negative effects on growth, but since stand density is already accounted for by BAH in each of these models, both of these measures have a smaller effect on growth compared to CCF (Fig. 3.6). In addition, the partial effects smooths for purity and shade intolerance were fit with complex non-monotonic functions whose confidence bands (± 2 standard errors) are wider at low values (especially those of shade-intolerance).

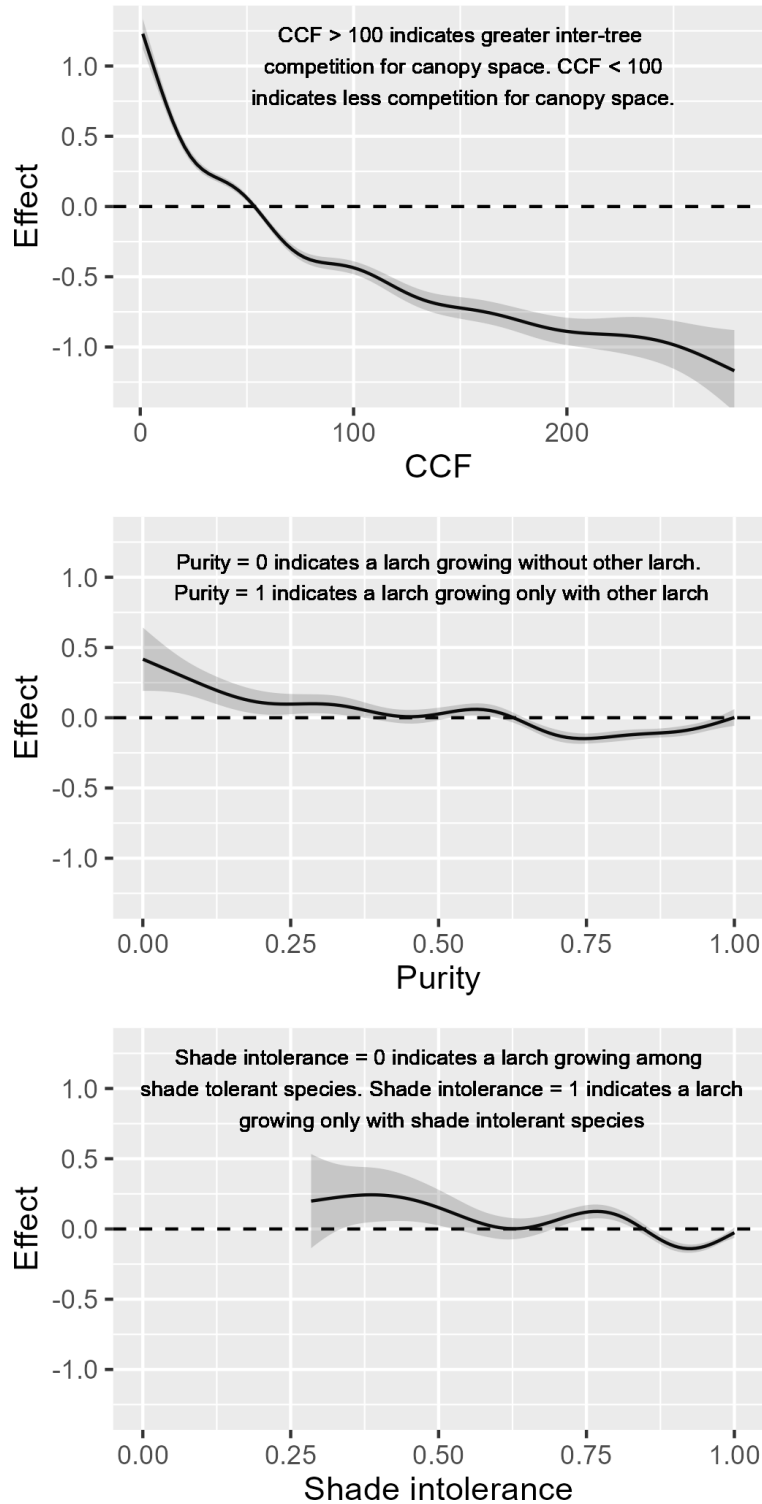


Figure 3.6: Fitted partial effects for crown competition factor (CCF), plot purity (of larch; L), and plot shade intolerance (T), shown on the log-link scale. Error bands represent ± 2 standard errors and account for uncertainty in smoothing parameter estimation. Shade intolerance is truncated below 0.3 due to lack of data.

Chapter 4

Discussion

4.1 Model selection

The model selection approach applied in this study produced a BAI model consistent with other empirical individual tree growth models. The effect of tree size (diameter) on growth (shown in Fig. 3.3) resembled the findings of Wykoff (1990), Monserud and Sterba (1996), and Vospernik (2021) such that BAI increases rapidly at lower values of DBH and then tapers at high values. The effects of crown ratio were similar to those shown by Hann *et al.* (2003) and Wykoff (1990), as it is represented by a near-linear increasing effect (Fig. 3.3) such that trees with longer crowns have enhanced growth. The density effect of BAH was characterized as a decreasing effect approaching a negative limit (Fig. 3.3), which is similar to that of Hann *et al.* (2003) (displayed by Weiskittel *et al.* 2011). The agreement of these results is somewhat unsurprising given these studies strongly motivated the choice of variables considered here and that the PGP program is in the same region studied by Wykoff (1990).

The way that site conditions were represented in the selected model contrast from previous formulations, with the latter often including information about slope, aspect, elevation, habitat, site index, and/or climatic data (Weiskittel *et al.* 2009b). In this study, site effects on growth were only represented by a multi-dimensional smooth of aspect, potentially failing to account for other site differences. By only accounting for aspect differences, an implicit assumption is made that the effect of site on growth is constant regardless of slope or elevation. However, aspect was selected

because it outperformed alternative measures, including a more comprehensive heatload metric based on a combination of slope, aspect, elevation, and incoming solar radiation (Theobald *et al.* 2015). Climate-based metrics (such as heatload) derived at varying cartographic scales rely on their own set of assumptions. Of particular relevance is the cartographic scale at which a metric is calculated, where one must assume that microclimates and biophysical conditions are constant at smaller scales. Stage and Salas (2007) suggested that using a combination of slope, aspect, and elevation should improve prediction accuracy, which was observed here. However, the realized improvements were marginal and were associated with high concavity values (> 0.8) among topographic variables as well as with BAH. Furthermore, the relative improvements to prediction accuracy realized by adding site variables was minimal, which is in line with previous findings (Weiskittel *et al.* 2011). Clearly there are tradeoffs associated with accounting for different site effects in this format, and future growth modelling efforts should consider these tradeoffs and how they may interact with modelling objectives.

In contrast to the effects of BAL that were estimated in this study (Fig. 3.3), others have identified BAL with a concave-shaped decreasing effect on growth (Monserud and Sterba 1996; Hann *et al.* 2003; Vospernik 2021). Of note, however, is that the present study implemented BAL as a ratio of plot BAH, similar to Stage (1973), but dissimilar to Monserud and Sterba (1996) and Vospernik (2021), who implemented BAL as an absolute quantity instead of a ratio (see Kiernan *et al.* (2008) for comparisons of BAL metrics). In the SPCt model presented in section 3.2, BAL appears to have a marginal effect on BAI until it is in excess of 0.8 (Fig. 3.3), meaning that western larch growth may not be particularly adversely affected by the presence of larger trees until there is a very large abundance of them. Such instances may arise when larch regenerates after a mixed-severity fire or variable retention harvest, allowing favorable conditions for seedling establishment, but unfavorable light-availability for long-term development. Vospernik (2021) found that only including BAL as a competition measure was sufficient in capturing competitive effects across species. That option was excluded here because it was thought important to consider tree-level competitive effects (e.g., BAL) in addition to community crowding effects (e.g., BAH), especially since both have been shown to interact with species composition (Brunner and Forrester 2020). Contreras *et al.* (2011) identified BAL to have a closer relationship with growth in western larch than other

distance-independent measures, partially justifying its use within the SCPT model. Additionally, this study identified important effects of BAL and BAH within the same model, which is consistent with Wykoff (1990), Monserud and Sterba (1996), and more recently Riofrío *et al.* (2019) and Vospernik (2021).

4.2 Assessing species-mixing impacts on growth

Competition for resources among species has been used to explain forest development (Oliver and Larson 1996), and more recently has been applied to explain how species interactions can modify how different species grow and develop in mixtures. Competition among tree species in a community occurs when two or more species access or use the same resource(s) (Connell 1983; Callaway and Walker 1997). Thus competitive dynamics among species can modify productivity depending on how each species in a mixture competes for shared resources, and whether their resource use and/or acquisition methods are complementary, conflicting, or even neutral (Pretzsch *et al.* 2017). Niche complementarity arises from complementary resource-use, resulting in competitive reduction, explaining increases in productivity among species with complementing attributes.

Since western larch is known for its high growth efficiency and shade-intolerance (Schmidt *et al.* 1976), it was posited that limitations in light availability in mixtures with other light demanding species would increase competition and result in lower growth compared to pure larch conditions. Similarly, it was believed that western larch growth would be increased in mixtures with species that don't require as much light to grow, reducing competition for light through niche complementarity. This study did not specifically evaluate competition for light, but rather identified stand conditions where it might be different, such as when larch is growing in a pure stand or when growing with other species with similar or different tolerances for shade. So whether competition itself varied and led to modified growth of western larch when mixed with either lodgepole pine or Douglas-fir was unclear. However, the results provide evidence that the way that larch growth related to each predictor was different in each mixture (Table 3.3 and Fig. 3.5).

The results for DBH in Fig. 3.5 suggest that larch in mixtures with lodgepole pine would have higher expected growth than larch growing with other larch at DBH values between 12-23cm,

holding all else constant. This directly contradicts the expectations for these conditions provided in Chapter 1 since lodgepole pine is also intolerant of shade. Such results may suggest that western larch with DBH values greater than 12cm may out-compete neighboring lodgepole pine owing to species-specific attributes unrelated to intolerance of shade (e.g., nutrient uptake efficiency, water, etc.). There must be an empirical basis for the positive difference displayed, but it also may be partially due to the average and maximum tree sizes in this mixture being substantially smaller than those of the reference level, in addition to lower average stand densities (see DBH and BAH in Table 3.2). A visual comparison between the trends of pure larch and larch-lodgepole mixtures in Fig. 3.1 (top two panels) shows few observations of DBH greater than 20 cm in lodgepole-pine mixtures. As a result, the trend lines in the lodgepole pine mixtures in the second row of Fig. 3.1 do not display the same reduced growth shown in the relationships of other mixtures at higher diameters. Thus growth at larger values of DBH in Fig. 3.5, which show positive differences between the lodgepole pine mixtures and the pure larch smooths, should be questioned, and interpretation at values larger than 20 cm is withheld completely.

Additionally, the results for DBH in Fig. 3.5 suggest that smaller-diameter western larch trees mixed with shade intolerant lodgepole pine experience lower rates of growth than the same size trees growing primarily with other western larch. Although not explicitly stated, this agrees with the expectations. However, given that western larch and lodgepole pine have the same shade-intolerance value (of 1), the expectation was that there would not be any difference in growth between the corresponding mixtures. This may indicate that the competition for some resource other than light impacts the growth of smaller western larch trees in this mixture. Further research evaluating whether these small-tree negative growth effects are modulated by different proportions of each species in this mixture could help explain the presently observed effects.

The results described in section 3.3.1 suggest that competitively dominant larch trees grow less when mixed with lodgepole pine and that non-competitively dominant larch trees in the same mixtures grow more compared to larch growing in pure stands with the same values of BAL. Yet, since BAL was calculated as the proportion of plot basal area in larger trees as opposed to the absolute amount of the former, an issue of scale was created when comparing across mixtures. For example, if comparing a BAL value of 0.25 in a pure larch plot where the BAH is 40 m²/ha, to

a larch-lodgepole pine mixed plot where the BAH is $10 \text{ m}^2/\text{ha}$, the tree of interest is facing $10 \text{ m}^2/\text{ha}$ and $2.5 \text{ m}^2/\text{ha}$ worth of area occupied by larger trees, respectively. Thus, in this example the relative social position, although being proportionally equal, does not imply the same quantity of competition in larger trees, confounding the interpretation of BAL. This scaling issue is a known weakness of accounting for BAL as a proportion of plot basal area, but studies of alternative forms provide mixed results (Weiskittel *et al.* 2011). A related issue arises when considering the relative ranges of DBH values for both lodgepole pine mixtures and pure larch mixtures. Table 3.2 shows that the western larch in mixtures with lodgepole pine are smaller (based on average and maximum DBH) than those in the pure data (as noted above). Therefore a competitively dominant larch (i.e., one with a low BAL) in a lodgepole mixture is likely smaller than one growing with other larch. Thus, BAL is also confounded with tree size in this comparison across conditions. However, BAL is still a useful measure of social competitive position within the model for estimating growth, given that all other variables (including BAH and DBH) are accounted for.

In Douglas-fir mixtures, the differences from the reference conditions (see Fig. 3.5) were generally smaller than those of the lodgepole pine mixtures. The difference shown for BAH effects in Figure 3.5 indicates that larch growth is impacted the same way when mixed with Douglas-fir as it is in pure larch conditions at densities below $25 \text{ m}^2/\text{ha}$. At BAH values greater than $25 \text{ m}^2/\text{ha}$, however, there is an increasingly negative effect on growth. Both lodgepole pine and Douglas-fir mixtures show a change from positive difference to negative difference near $25 \text{ m}^2/\text{ha}$. Considering that the primary BAH effect (for the SCPT model, shown in Fig. 3.3) is near its lower limit at $25 \text{ m}^2/\text{ha}$, the negative growth differences for each mixture may simply imply that resources are generally scarce, leading to lower rates of growth. Thus there don't appear to be any complementary effects between western larch and Douglas-fir that lead to enhanced growth in western larch.

4.3 Comparing CCF, purity, and shade intolerance

Despite the lack of conclusive results in lodgepole pine and Douglas-fir mixtures, the addition of species-information proved useful in estimating the growth of western larch in this study. The relationships fit with both plot purity and shade intolerance metrics indicate that after accounting for other influential factors, western larch growth may be better characterized with a simple

measure of proportional basal area than with CCF (Table 3.4). These findings are in line with those of Dirnberger *et al.* (2017), which found that species-proportional measures of composition were more reliable than crown-area based measures. Furthermore, assessing and characterizing species-mixing impacts is simpler if they aren't tied into a density-based measure like CCF. CCF simply does not provide any straight-forward interpretation of whether different species dynamics are at play, as it only represents potential crown area. A comparison of CCF effects on western larch growth between specific mixtures could show how the CCF effect changes with mixture, however, that is beyond the scope of this study. Consequently, using measures which directly indicate specific mixing-characteristics (e.g., shade tolerance, species-specific weighted densities) is particularly useful, given the interplay among species-composition, density, and site productivity (Kimsey *et al.* 2019; Weiskittel *et al.* 2009a; Huber *et al.* 2014).

Both shade intolerance and purity displayed relationships indicating that individual western larch growth may be positively impacted when growing with other species (Fig. 3.6; Table 3.4), holding all other variables constant. Considering this, and in addition to the differences of smooths identified across mixtures in the competition variables (Table 3.3), competitive dynamics and species composition together likely play an important role in characterizing how western larch grows. The results in Table 3.4 and Fig. 3.6 are similar to Searle and Chen (2020), who showed that increasing dissimilarity in shade tolerance led to higher individual tree growth, depending on the level of competition, demonstrating positive effects of niche complementarity. The findings in this study lack adequate data and design to determine whether niche complementarity specifically impacts western larch growth. However, the models fit do suggest that a relationship between larch growth and both purity of larch and relative abundance of shade-intolerant species exists. Others have attributed differences in productivity to shade-tolerance heterogeneity (Weiskittel *et al.* 2009b; Maguire and Mainwaring 2021), but few have evaluated the use of a shade-tolerance metric in the estimation of tree growth. This study provides additional support for the use of a shade-tolerance metric in growth modeling, given its ease of use, availability, and relevance, as suggested also by Russell *et al.* (2013).

4.4 Management and other implications

The information provided here may be useful when managing western larch in a multi-species setting. Crotteau *et al.* (2019) discuss initiating climate adaptation in western larch forests through various silvicultural treatments, all of which involve managing larch with other species. Understanding the mixing dynamics on larch growth may assist in developing such adaptive strategies to aid in selecting species-mixtures which promote the growth of western larch. In the case of managing jointly for biodiversity and timber value, increasing relative shade tolerance and/or diversity may maximize growth in western larch. However, evaluating how much more western larch growth is in diverse/shade tolerant mixtures in addition to the growth of other species in the presence of fast-growing larch requires further investigation. Thus, in order to recommend optimal mixtures which promote the growth of western larch as well as other species while also maintaining favorable climate adaptive conditions, further investigation into western larch and the potential for an over-yielding effect (Pretzsch and Schütze 2009) is required.

The *Larix*-specific findings of this research add to the limited knowledge base that exists for species-mixing effects on larch worldwide. Vospernik (2021) showed that *L. decidua* mutually benefited in mixtures with shade-tolerant *Picea abies*, and was negatively impacted by shade-intolerant *Pinus cembra*, shade-tolerant *Fagus sylvatica*, and intolerant *Betula spp.*. Pretzsch and Biber (2016) observed a positive mixture effect on stand density, where maximum stand density was increased when *L. decidua* was growing with spruce. Zhang *et al.* (1999) showed that larch and *Fraxinus spp.* heights mutually increased in mixtures together compared to pure stands of either. However, Xie *et al.* (2020) assessed the height-diameter relationship of *L. olgensis* when mixed with *Fraxinus spp.*, and found results inconsistent with Zhang *et al.* (1999). Given the limited information on species-mixing dynamics for *Larix*, a literature review covering each *Larix* species may be useful to identify next-steps to elucidate *Larix occidentalis* (as well other species') growth and yield dynamics in mixed-species forests.

4.5 Additive model considerations

To realize the benefits of using a (non-parametric) smoother-based approach, one must ensure that a smooth has enough flexibility to capture complex functional forms, but that it does not capture *too much* variability in observed scatter around those forms. The former requires setting a sufficiently large limit of a smooth's EDF, which is defined by $k-1$, where k is the basis size, and one degree of freedom is used to ensure identifiability (Wood 2006). The latter requires that variability is penalized appropriately, which is modulated by the estimated smoothing parameter (see section 2.2; Wood 2006; Pedersen *et al.* 2019). In this study the choice of k was 10 for DBH, BAL, and BAH (10 is the default value provided by `mgcv`), which appeared appropriate given how each estimated smooth compared to previous studies (as discussed above). However, the variability shown at high values of BAH ($> 50 \text{ m}^2/\text{ha}$) and the irregularities in aspect in Fig. 3.3 highlight an instance where smoothing complexity could complicate interpretation. Although the BAH smooth was fit with high confidence as a non-zero effect, it also had a relatively high complexity (EDF > 8 ; Table 3.1; Fig. 3.3), given the basis dimension. In this case it doesn't challenge the interpretability of the BAH effect on growth, as there clearly is an overall decreasing effect, and it is known that growth tends to be limited in densely packed stands (Reukema 1979). However, in other cases, such as the shade intolerance smooth in Fig. 3.6, further constraints may be necessary for more accurate characterization and clearer interpretation. An additional consideration is the range and relative abundance of data informing each of these smooths. There were few data at both high densities and low shade-intolerance values, respectively, compared to the overall range of each. Given this, the adequacy of basis dimension choice should be further evaluated and more careful consideration should focus on determining whether variations in the smooth are a function of sample size, the range of conditions in the data, penalization, or some other influencing factor.

Beyond basis dimension and penalization, complexity in GAMs may be introduced with interacting effects. Although GAMs are additive, implying no interactions, interactions may still be specified between covariates using `mgcv`. The only type of interaction considered in this study was a TPRS-based interaction among the sine and cosine transformations of aspect. The resulting smooth (Fig. 3.3) was represented by surface that was somewhat challenging to interpret, perhaps

stemming from little diversity in sites sampled or perhaps due to the lack of other interacting site effects within the model. Beyond isotropic interactions like the aspect effect, the `mgcv` package allows for the specification of interactions among continuous variables with differing units by applying a tensor product smooth in a way that is analogous to a multiplicative interaction in a linear model (Wood 2006; Pedersen *et al.* 2019; Johnston *et al.* 2019). While using tensor products would be useful in this study, for example, by examining how species-mixing variables interact with competition variables, it would add further complexity to this model, perhaps through inflating concurvity or introducing results that are more difficult to interpret. Since this study was focused on evaluating species-mixing effects on tree growth after accounting for other factors, we refrained from examining these types of interactions. Future studies covering these topics should evaluate how species-mixing variables like shade-tolerance and purity interact with competition and/or density effects in western larch growth models.

Chapter 5

Conclusions

In this study we showed evidence indicating that the growth of western larch is characterized differently across different types of species-mixtures. The results did not indicate any complementarity arising from the differences in shade-tolerance between western larch and Douglas-fir. However, in indistinct mixtures with shade-tolerant species as well as when larch simply is growing with other non-larch species, there was evidence suggestive that western larch can achieve higher rates of growth. Furthermore, there was evidence suggestive that smaller western larch trees are more negatively impacted when in mixtures with shade-intolerant lodgepole pine. This information may benefit managers who are interested in managing western larch in a mixed-species setting or simply who want to enhance the growth of western larch. Across-species analysis to determine which type of mixture optimizes the growth and yield of western larch and the other incumbent species through mutual or competitive relationships is necessary. Additionally, future work will aid in determining if and how the site productivity, competition, and density dynamics of a stand interact with species composition for stands in the inland northwest.

When accounting for species-mixing in empirical growth models, one should be aware of the tradeoffs associated with different options to account for site and/or competition effects on growth. Although we showed an effective way to capture competitive effects in a growth model as a whole, the same effects were difficult to disentangle when the model was subset for different species-mixtures. These issues could be resolved by (i) ensuring that the range of data across mixtures is comparable, (ii) implementing a competition index that accounts for observed differences in

attributes across different mixtures (e.g., using BAL as a quantity instead of a ratio), or (iii) doing both.

Despite the shortcomings of our data and/or design, we demonstrated a means of model selection that can be used to create a useful individual tree growth model using a flexible and non-linear data-driven approach. Furthermore, we demonstrated methods by which non-linear functional relationships can be compared across different conditions. When applying these types of methods, it is of critical importance to ensure that (i) there is ample data across the range of conditions being evaluated and (ii) the person(s) fitting and evaluating GA(M)Ms has a good sense of how smooths are penalized and how to balance the inevitable bias-variance tradeoffs that they will face when fitting GA(M)Ms.

In conclusion, GA(M)Ms can effectively capture empirical relationships consistent with previously identified growth models for western larch in addition to uncovering unique patterns in growth relationships that differ from previous models. Further assessment of western larch and its counterparts is necessary to determine and characterize how species-mixing can impact growth dynamics in inland northwest forests. This study provided a necessary initial step in exploring these dynamics within this region, and has positively identified the presence of species-mixing effects on western larch growth within the context of distance-independent empirical growth modelling.

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