PREDICTING TREE MORTALITY IN A CHANGING CLIMATE

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Using Provenance Data to Examine Height-Mortality Relationships

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ABSTRACT

Climate change has already begun to impact British Columbian forests, and the direct and indirect impacts are predicted to increase in severity and magnitude. Climate-sensitive mortality and kill selection models were developed for lodgepole pine (*Pinus contorta* var. *latifola* Douglas) in planted sites in British Columbia. Provenance data from a large trial studying populations from western North America were used to predict the number and size of trees killed annually based on temperature and precipitation variables. Seed moved from colder to warmer climates were associated with lower mortality rates compared to seed moved in the opposite direction. Precipitation had a measurable impact on the size distribution of stands at rotation; shorter trees were more likely to succumb to drought-stress conditions than tall trees. These models provide an important link between climate and mortality that can be used to examine climate-based mortality over time.

1 INTRODUCTION

Since the 1880s, global temperatures have been increasing, and the three most recent decades have each been warmer than any decade since 1850 (IPCC 2014). Depending on future greenhouse gas emission levels, this warming trend is likely to continue throughout the 21st century, which will almost certainly lead to more frequent extreme high temperatures in terrestrial ecosystems (IPCC 2014). Global climate change has already resulted in a multitude of observable changes in terrestrial ecosystems (Hoegh-Guldberg et al. 2018). Globally, forests play a large role in carbon sequestration (Dymond et al. 2016), which is crucial to offset carbon emissions. However, threats to forest productivity as a result of climate change can reduce the amount of carbon that can be sequestered in a stand (Dymond et al. 2016). Many tree species across British Columbia (BC) are predicted to experience widespread decreases in viability due to climate change. Monthly temperatures are expected to increase, which has important but varied implications for forest productivity and the range of commercial species in the Pacific Northwest (Coops and Waring 2011). The geographical and elevational ranges of many tree species are predicted to shift with changing climates, often at a faster rate than the populations can adapt.

Tree mortality has been increasing throughout much of western North America in recent years, likely due to climate warming and increased drought stress (van Mantgem et al. 2009), and these trends will likely continue, causing major changes in stand and vegetation structure (McDowell and Allen 2015), which could substantially decrease timber supply. Actions such as developing adaptive management plans are crucial in managing forests under changing climates (Spittlehouse and Stewart 2003). These plans could include managing forests to reduce climate-caused mortality, and in order to manage climate-caused mortality, we must quantify the link between climate and mortality.

The threat of climate change to BC forests necessitates methods to manage planted stands for future conditions. Other studies have aimed at introducing climate adjustments to growth models, specifically aimed at BC forests (O'Neill and Nigh 2011; Nigh 2014), in order to mitigate climate change impacts. However, many studies tend to focus on height growth and site index and how they may be affected by climate change. In this research, we aim to provide insight into tree mortality, which, alongside height, is an important factor in timber production. Along with providing a more detailed examination of climate impacts on mortality in BC, the methodology developed will be transferrable to BC's stand growth modelling program (Tree and Stand Simulator, TASS). TASS is a single tree model (Mitchell 1975) that simulates stands over time, providing annual output of stand- and tree-level variables. This will create an important link between examining climate-mortality relationships and predicting how these will impact future stands.

In this study, we will use provenance data to establish a relationship between climate and lodgepole pine (*Pinus contorta* var. *latifola* Douglas) mortality. We aim to: 1) examine how climate change will impact mortality in planted stands; 2) predict how climate change could adjust future annual mortality rates in a stand; and 3) examine how climate variables could predict the size of trees susceptible to climate-based mortality. Specifically, we will examine how the climate range of seed source origins will impact the size and number of trees susceptible to climate-based mortality.

2 METHODS

2.1 Data

The data used for this analysis come from the Illingworth lodgepole pine provenance trial (O'Neill et al. 2008). Three-year-old seedlings from 140 open-pollinated populations, ranging from California, USA, to Yukon, Canada, were planted in 1974 at 60 test sites in British Columbia and two test sites in the Yukon. Sixty of the 140 populations were planted at each test site. A randomized complete block design was used at each site, with seedlings planted at 2.5m spacing in 3x3 square tree plots, with two plots per provenance. Height was measured at 6, 10, 15, 20, and 32 years after planting.

2.2 Analysis

2.2.1 Transfer function

In developing transfer functions for each height group, we fit a mortality transfer function using the Illingworth provenance data to relate population mortality rate per hectare with population climate (or latitude) transfer distance (i.e., the climate distance each population was transferred in the trial - site climate minus provenance climate). Six climate variables (mean annual temperature, mean coldest month temperature (MCMT, °C), mean summer precipitation (MSP, mm), mean annual precipitation (MAP, mm), latitude, and mean warmest month temperature) were tested for their ability to predict mortality. Climate values were obtained using ClimateBC v6.21 (Wang et al. 2016). The transfer functions were fit using the nlsLM function from the minpack.lm package (Elzhov et al. 2016) in RStudio version 1.1.463 with R version 3.6.1.

The mortality transfer function was fitted with a modified Weibull function using MCMT transfer distance (td.MCMT) as the independent variable (O'Neill and Nigh 2011). The Weibull function was selected because of its ability to fit asymmetric data and its previous use in genecological research (Nigh 2014; Rehfeldt et al. 2003).

Survival (S), the dependent variable used in the mortality function, is the proportion of stems (SPH) remaining for each provenance at each site at each measurement age.

$$S_{HTxi} = \frac{{x_i}^{b_0}}{\exp({x_i}^{b_1})} + \varepsilon_i$$

Where: $x_i = a_0 + a_1 td.MCMT_i$

S_{HTxi} = mean survival rate of the *ith* provenance/site/age combination within each td.MCMT group in top height group *x*.

$td.MCMT_i$ = MCMT transfer distance for provenance *i* (site MCMT – provenance MCMT) in °C.

The data were grouped based on top height (average height of the tallest two trees in the stand), following the rationale of Nigh 2014, and mortality models were initially fit within 12 top height groups, where it was found that several groups had very similar results. Consequently, we combined the 12 groups into three distinct subsets based on the top height: Group 1, top height <= 1.5 m; Group two, 1.5 to 7.1 m; and Group three, top height > 7.1 m. In order to assess the trends in the data and reduce variability, the data were binned into 70 groups based on MCMT transfer distance. For each bin, the average value for both td.MCMT and percent survival was calculated.

The results of the above mortality transfer function provide a percent survival value for each top height group, which we converted to an annual value in order to predict mortality on a yearly basis.

$$S_{Ai} = {S_{HTxi}}^{1/t}$$

Where:

S_{Ai} = annual survival rate of seedlot *i*.

S_{HTxi} = survival rate for seedlot *i* in top height group *x*.

t = cumulative time spent in each top height group *x*.

2.3.2 Kill selection routine

The mortality transfer function predicts an annual rate of mortality, but it does not select which trees to kill. This necessitates the use of a routine to select trees to kill that is similar to how mortality will occur in a real stand. To create this routine, the data were stratified into five bins for the transfer distance of natural log of mean annual precipitation (td.lnMAP = site.lnMAP – prov.lnMAP). We chose to use five bins to classify the range in td.lnMAP. Although more bins could have been used, the use of five bins provided a balance between capturing the range of values for td.lnMAP and minimizing the computing time required to utilize this selection technique in stand simulation software.

For each td.MAP bin at each test site, we assessed the trees that died and examined trends in the relative heights of these trees (i.e., their height relative to the top height of the site recorded in the measurement taken before their death). Specifically, we determined if the relative height of the tree is related to the probability of death and how this probability is related to td.lnMAP. At each site and for each td.MAP bin, let *dti* be the *ith* dead tree and *dtt* be the total number of dead trees recorded during a survey year. We then sorted the list of dead trees by relative height in ascending order to obtain the cumulative sum of dead trees in that survey year, *cumul.dtn* (i.e., the sum of dead trees from the *ith* to the *nth* dead tree). Dividing *cumul.dtn* by *dtt* yields the cumulative annual proportion of dead trees, or *CAPDn*. Since *CAPDn* is a proportion, values range from 0 to 1. The above calculations are shown below.

$$cumul.dt_n = \sum_{i=1}^{n} dt_i$$

$$CAPD_n = cumul.dt_n/dtt$$

Where $cumul.dt_n$ = cumulative sum of dead trees in a survey year.

dt_i = the ith dead tree.

dtt = total number of dead trees in a survey year.

$CAPD_n$ = cumulative annual proportion of dead trees.

Next, we fit a model to predict CAPDn based on the relative height of a tree to the top height of the stand.

$$CAPD_i = 1 - \exp\,(-\left(\frac{relht_i}{\beta_1}\right)^{\beta_2})$$

which we fitted to the data using a mixed effects model, with a random effect for td.MAP bin on both parameters.

3 RESULTS

3.1 Mortality Transfer Function

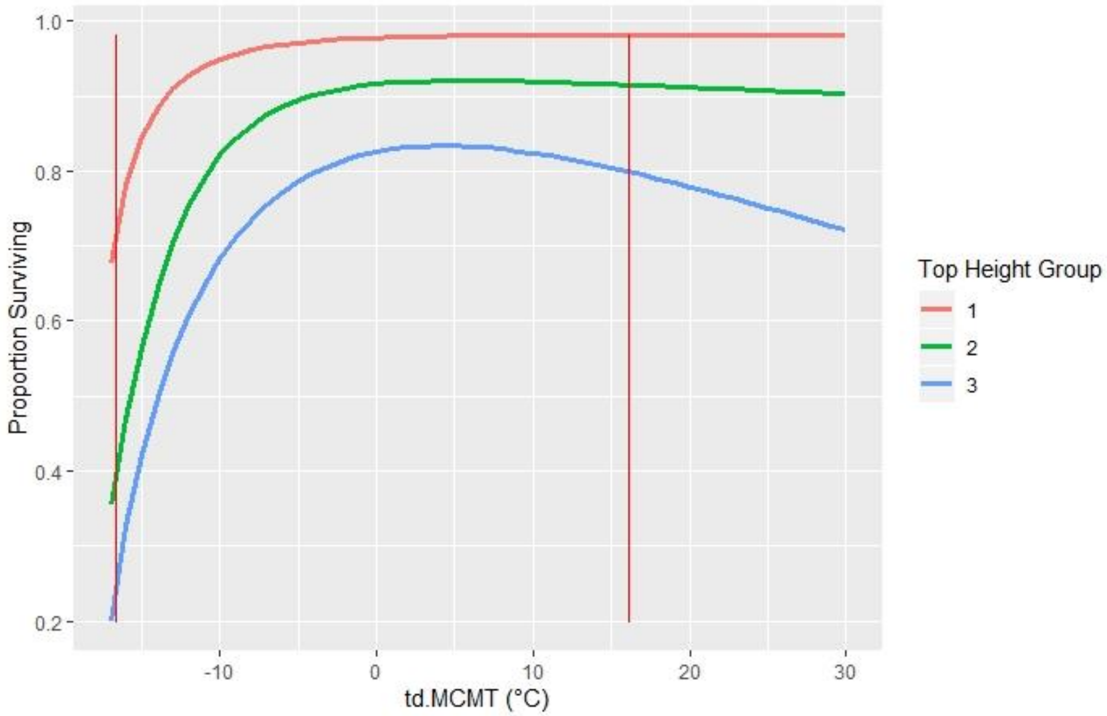

Figure 1. Results of mortality transfer function, the vertical red lines indicate the td.MCMT range of the observed data. Top height groups are based on site top height, group 1 is ≤1.5m, group 2 is >1.5m and ≤7.1m, and group 3 is >7.1m.

We found that S_{HTx} was related to the top height of the stand. Figure 1 represents survival rate of trees if the stand spent the entirety of the time in each top height group at that transfer distance. Based on the model fits, we chose to group the data into three distinct top height groups, as this allowed for the most thorough examination of the climate/mortality relationship while also allowing the models to remain simple enough to implement in a stand simulating program.

While the proportion of surviving trees is greater in the first top height group compared with the second and third groups, annual mortality rates decline with increases in top height (Figure 2). Negative transfer distances have a greater impact on mortality in this study compared with positive transfer distances. In other words, seedlot transfer from a warmer climate to a colder climate was associated with increases in mortality, particularly for strongly negative transfers. In contrast, positive transfer distances have a much smaller negative relationship with mortality. Within the observed range of the data, a positive transfer distance of ~16°C (the maximum transfer distance in the data) leads to a maximum annual mortality rate of only 0.006, compared to 0.033 at ~-16°C (Figure 2).

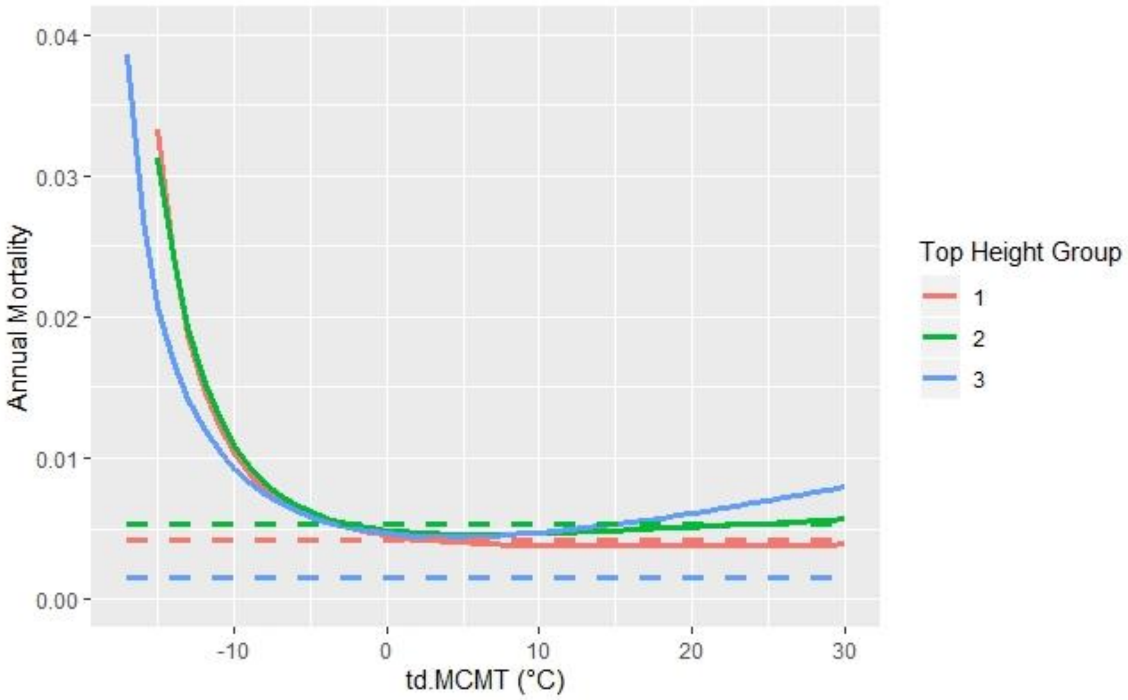

Figure 2. Annual mortality rates for each top height group expressed as a proportion of total stems. Solid lines indicated model results, while dashed lines indicate mean simulated mortality rates for a stand with no climate-based mortality adjustments.

Compared to mortality rates without adjustments for maladaption due to climate change, the results of the mortality transfer functions show that climate change could negatively impact survival (Figure 2). For comparison purposes, we examined a simulated stand with characteristics similar to sites in the Illingworth trial (with an assumed site index of 20m) and calculated the mean annual mortality values over time, without adjusting mortality with climate change. The results of this comparison show that climatically adjusted mortality rates for stands are similar to the non-adjusted stand when td.MCMT is slightly above 0°C and the top height is less than 7.1m (top height groups one and two). However, non-climate-based mortality could underestimate mortality at td.MCMT = 0 when the stand top height is greater than 7.1m (Figure 2). Figure 2 shows that the results of the climate-based mortality transfer function would allow for estimates of stand mortality that would differ from scenarios with no climate integration, especially at negative transfer distances.

3.2 Kill Selection Routine

The trends from the Illingworth provenance trial indicate that among the trees that die, the relative size of the dead trees differs between provenances moved to a site with less MSP and provenances moved to a site with more MSP (Figure 3). Specifically, when populations are moved to environments drier than that of their provenance, mortality is greater in short trees than in tall trees. Conversely, when populations are moved to environments wetter than their provenance, larger trees contribute a greater proportion to the overall number of dead trees (the curves increase slowly at first, and then rapidly as relative height increases). Compared to randomly selecting trees to kill in the mortality function, using an MAP-based kill selection routine results in smaller trees being selected first, even when the MAP values are similar to the local values at the site (Figure 3).

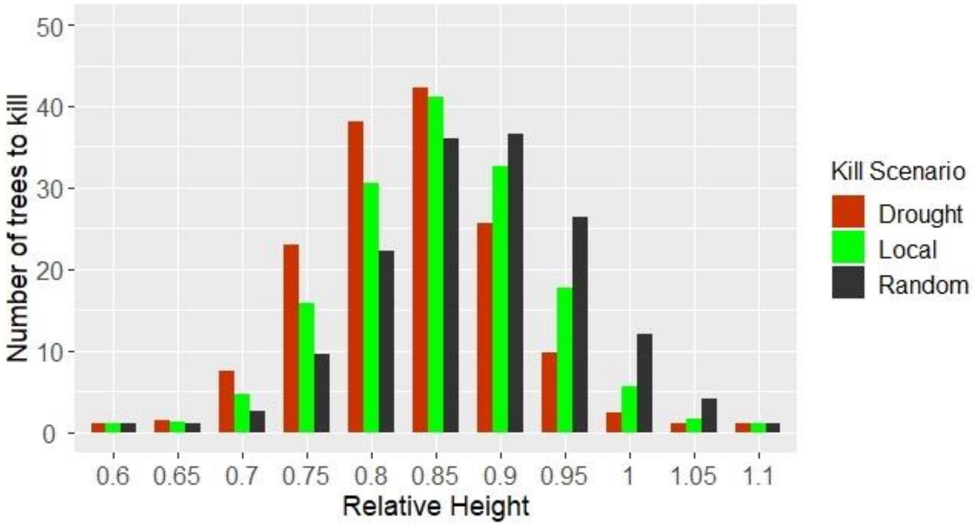

Figure 3. Number of trees selected to kill per year by their height relative to the top height of the stand. *Drought* denotes a movement of a seed source to a site having an MAP value less than the provenance; *local* denotes seed sources having an MAP equal to that of the site; *random* is a random selection of the trees in the plot.

4 DISCUSSION

4.1 Mortality Response to Seedlot Transfer

The results of this study suggest that the lowest mortality rates occur when transfer distance is slightly greater than 0°C (Figure 1) (i.e., sites are planted with populations from climates that are slightly colder than the site). Consistent with this study, the greatest survival in Scots pine (*Pinus sylvestris* L.) provenance trials was observed among populations moved from the north than from the south. However, the opposite was true of height; the tallest populations at a given site were those transferred from the south. (Berlin et al. 2016). Northern populations of several conifer species are expected to benefit from at least some degree of climate warming, which southern populations are expected to decline (Pedlar and McKenney 2017). The mortality transfer function demonstrates that climate-based mortality transfer functions are important for finding seedlots that may experience survival rates better than local seedlots. For younger stands (top height ≤ 7.1m), seedlots with td.MCMT values between +2 and +8°C had lower mortality rates than the mean rates that do not account for climate change (Figure 2). This is in contrast with other literature, which suggests that the optimal seed source transfer should be pre-emptive of warming, thus an optimal seed source would be adapted to a warmer climate than the planting site. Specifically, Nigh (2014) found that the optimal MCMT of a seed source for this plantation would originate from locations between -4.9 and -5.7°C, which are slightly warmer than the test site. This does not align with the results of this study, however that could likely be attributed to the fact that this study is examining mortality as well as height growth, whereas the focus of Nigh's (2014) study is strictly height growth. It is possible that increased height growth could be the result of decreased light and nutrient competition caused by an increase in mortality, as competition for light and nutrients are often associated with reductions in tree growth (Coomes and Allen 2007). Given these results, it is possible that optimal conditions for survival are not equivalent to optimal conditions for height growth, and proper management of stands for climate change must consider both criteria.

4.2 Climate-based Kill Selection

In order to estimate the effects of climate change on tree mortality, we cannot only examine how many trees may be killed due to adverse growing conditions, but also which trees in a stand would be more likely to succumb. Our results showed that tall trees fare better under drought stress conditions, making up a smaller proportion of overall stand mortality compared to small trees (Figure 3). This climate-mortality relationship has been observed in both coniferous and deciduous trees (Pile et al. 2019; Colangelo et al. 2017), where small trees are disproportionately impacted by drought-caused mortality. While other literature suggests that in many cases, larger trees are susceptible to mortality due to drought conditions, this relationship was most apparent when bark beetles were present (Bennett et al. 2015). The interaction between multiple disturbances could impact the size of trees susceptible to drought-associated mortality.

The results of our climate-based mortality selection techniques clearly demonstrate that it is necessary to incorporate selection techniques in stand simulations. When comparing results between stands that are under normal precipitation conditions to a random selection of trees to kill (Figure 3), we found that when using random selection, taller trees were over-selected compared to what was observed in the dataset. This suggests that stand volume and differences in yield due to climate-based mortality could be underestimated using random mortality selection.

4.3 Limitations

This study provides valuable insight into the impacts of climate change on the mortality of lodgepole pine stands. While provenance trials are important and powerful tools for examining tree responses to climate conditions (Matyas 1994), there are limitations associated with the use of provenance data. Provenance trials can be costly and time-intensive, and are often created using small plots with few trees. Along with these practical barriers, provenance trials may not allow us to observe the full effect of climate on tree growth response. If the site climate is suboptimal for the species in question, climate-provenance growth responses could be masked by adverse effects, which could lead to results that do not capture the impacts of seedlot transfer (Klisz et al. 2019). Consequently, seedlot transfer guidelines based on provenance planting sites with suboptimal growing conditions could lead to unintended results. In addition, many provenance trials encompass a narrow range, lacking sites with extreme conditions that would result in almost complete mortality. The lack of extreme transfers could lead to an underestimation of mortality at the transfer limits of the provenance trial (Leites et al. 2012).

4.4 Recommendations and Next Steps

This project provides valuable information about the adaptability of lodgepole pine under changing climatic conditions. The development of the methodology in this study is an important step towards understanding the impact of climate change on timber production in BC. There are several other economically important BC tree species that would benefit from a similar analysis, such as hybrid spruce and western hemlock. These results are an important first step, however more research is needed in order to create guidelines and recommendations for forest managers to plan planting strategies that will allow our forests to survive and flourish under changing conditions.

Transfer functions developed based on provenance common garden experiments are extremely valuable in examining the effects of climate change on timber supply. While transfer and response functions give us crucial insight into growth responses to climate change, they do not provide exact quantifications of climate change impacts on forest yield (Pukkala 2017). In order to understand how climate change will affect future stands, it is necessary to examine how these functions look on the landscape. Using these transfer functions in simulation software, such as TASS, can allow for a more complete picture of how climate change will impact forests, providing information for management decisions. Applying these models throughout the life cycle of a stand is a crucial next step in this process.

5 CONCLUSIONS

The mortality transfer function for lodgepole pine developed in this study allows us to examine methods to account for the impacts of climate change mortality in lodgepole pine plantations. Climate change has a clear and demonstrable impact on mortality that must be considered when managing stands to maximize both timber yield and carbon storage. In comparison to mortality estimates that do not incorporate climate change impacts, the climate-based mortality functions outlined in this report show that moving seedlots to colder climates could substantially increase mortality rates. Future moisture levels will also impact stand size distributions, smaller trees are disproportionately killed when stands are facing drought stress. Integrating this transfer function into stand simulations along with a climate-sensitive height model will be beneficial for forest managers, researchers, and other decision and policy makers. The methodology developed in this project is an important precursor to being able to predict and manage for the impact of climate change on British Columbia’s forests.

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REFERENCES

Bennett, A. C., McDowell, N. G., Allen, C. D., and Anderson-Teixeira, K. J. 2015. Larger trees suffer most during drought in forests worldwide. Nature Plants, 1: 1–5. https://doi.org/10.1038/nplants.2015.139

Berlin, M., Persson, T., Jansson, G., Haapanen, M., Ruotsalainen, S., Bärring, L., and Gull, B. A. 2016. Scots pine transfer effect models for growth and survival in Sweden and Finland. Silvia Fennica 50(3): 1-21.

Colangelo, M., Camarero, J. J., Borghetti, M., Gazol, A., Gentilesca, T., and Ripullone, F. 2017. Size matters a lot: Drought-affected Italian oaks are smaller and show lower growth prior to tree death. Frontiers in Plant Science 8: 1–14. https://doi.org/10.3389/fpls.2017.00135

Coomes, D. A., and Allen, R. B. 2007. Effects of size, competition and altitude on tree growth. Journal of Ecology 95: 1084–1097. https://doi.org/10.1111/j.1365-2745.2007.01280.x

Coops, N. C., and Waring, R. H. 2011. Estimating the vulnerability of fifteen tree species under changing climate in Northwest North America. Ecological Modelling 222: 2119–2129. https://doi.org/10.1016/j.ecolmodel.2011.03.033

Dymond, C. C., Beukema, S., Nitschke, C. R., Coates, K. D., and Scheller, R. M. 2016. Carbon sequestration in managed temperate coniferous forests under climate change. Biogeosciences 13: 1933–1947. https://doi.org/10.5194/bgd-12-20283-2015

Elzhov, Timur V., Mullen, K. M., Spiess, A-J., and Bolker, B. 2016. minpack.lm: R Interface to the Levenberg-Marquardt Nonlinear Least-Squares Algorithm Found in MINPACK, Plus Support for Bounds. R package version 1.2-1. https://CRAN.R-project.org/package=minpack.lm

Hoegh-Guldberg, O., Jacob, D., Taylor, M., Bindi, M., Brown, S., Camilloni, I., Diedhiou, A., Djalante, R., Ebi, K., Engelbrecht, F., Guiot, J., Hijioka, Y., Mehrotra, S., Payne, A., Seneviratne, S. I., Thomas, A., Warren, R., and Zhou, G. 2018. Impacts of 1.5°C Global Warming on Natural and Human Systems. In: Global Warming of 1.5°C. An IPCC Special Report on the Impacts of Global Warming of 1.5°C above Pre-Industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty [V. Masson- Delmotte, P. Zhai, H. O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J. B. R. Matthews, Y. Chen, X. Zhou, M. I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, T. Waterfield (eds.)]. In Press.

International Panel on Climate Change (IPCC). 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the

Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp

Klisz, M., Buras, A., Sass-Klaassen, U., Puchałka, R., Koprowski, M., and Ukalska, J. 2019. Limitations at the limit? Diminishing of genetic effects in norway spruce provenance trials. Frontiers in Plant Science 10: 1–15. https://doi.org/10.3389/fpls.2019.00306

Leites, L. P., Rehfeldt, G. E., Robinson, A. P., Crookston, N. L., and Jaquish, B. 2012. Possibilities and limitations of using historic provenance tests to infer forest species growth responses to climate change. Natural Resource Modeling 25(3): 409–433.

Matyas, C. 1994. Modeling climate change effects with provenance test data. Tree Physiology 14: 797–804. https://doi.org/10.1093/treephys/14.7-8-9.797

McDowell, N. G., and Allen, C. D. 2015. Darcy's law predicts widespread forest mortality under climate warming. Nature Climate Change 5: 669–672. https://doi.org/10.1038/nclimate2641

Nigh, G. 2014. Mitigating the effects of climate change on lodgepole pine site height in British Columbia, Canada, with a transfer function. Forestry 87(3): 377–388. https://doi.org/10.1093/forestry/cpu009

O'Neill, G.A., Hamann, A., and Wang, T. 2008. Accounting for population variation improves estimates of the impact of climate change on species growth and distribution. J. Appl. Ecol. 45(4): 1040–1049. doi:10.1111/j.1365-2664.2008.01472.x.

O'Neill, G. A., and Nigh, G. 2011. Linking population genetics and tree height growth models to predict impacts of climate change on forest production. Global Change Biology 17(10): 3208–3217. https://doi.org/10.1111/j.1365-2486.2011.02467.x

Pedlar, J. H., and McKenney, D. W. 2017. Assessing the anticipated growth response of northern conifer populations to a warming climate. Scientific Reports 7: 1–10. https://doi.org/10.1038/srep43881

Pile, L. S., Meyer, M. D., Rojas, R., Roe, O., and Smith, M. T. 2019. Drought impacts and compounding mortality on forest trees in the Southern Sierra Nevada. Forests 10(3). https://doi.org/10.3390/f10030237

Pukkala, T. 2017. Transfer and response functions as a means to predict the effect of climate change on timber supply. Forestry 90: 573–580. https://doi.org/10.1093/forestry/cpx017

Rehfeldt, G.E., Tchebakova, N., Milyutin, L., Parfenova, E., Wykoff, W., and Kouzmina, N. 2003. Assessing Population Responses to Climate in Pinus sylvestris and Larix spp. of Eurasia with Climate-Transfer Models. Eurasian J. For. Res. 6(2): 83–98.

Spittlehouse, D. L., and Stewart, R. B. 2003. Adaptation to climate change in forest management. BC Journal of Ecosystems and Management 4(1): 1–11. https://doi.org/10.1109/lsp.2009.2014096

van Mantgem, P. J., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fulé, P. Z., Harmon, M. E., Larson, A. J., Smith, J. M., Taylor, A. H., and Veblen, T. T. 2009. Widespread increase of tree mortality rates in the Western United States. Science, 323: 521–524. https://doi.org/10.1126/science.1165000

Wang T., Hamann A., Spittlehouse D., and Carroll C. 2016. Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America. PLoS ONE 11(6): e0156720. doi:10.1371/journal.pone.0156720