Projected future suitable habitat and productivity of Douglas-fir in western North America

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Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) is one of the most common and commercially important species in western North America. The species can occupy a range of habitats, is long-lived (up to 500 years), and highly productive. However, the future of Douglas-fir in western North America is highly uncertain due to the expected changes in climate conditions. This analysis presents a summary of work that utilizes an extensive network of inventory plots to project potential future changes in Douglas-fir habitat and productivity. By 2090, the amount of potential Douglas-fir habitat is projected to change little in terms of area (–4%). However, the habitat is expected to shift from coastal areas of North America to the interior. Corresponding changes in productivity are also projected as coastal areas experience reductions, while interior areas experience modest increases in productivity. Overall, the analysis indicates a sensitivity of Douglas-fir to climate and suggests that significant changes in North America are to be expected under climate change.

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Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) is one of the most common species in western North America and is of high commercial importance throughout the region. The species consists of two varieties, namely coastal (var. *menziesii*) and Rocky Mountain (var. *glauca*). The native range of Douglas-fir in North America extends from a latitude of 19 to 44 °N and a longitude of 100 to 118 °W (Hermann & Lavender 1990). Generally, the coastal variety grows in pure stands in the maritime climate of the Pacific Northwest (Figure 1), while the Rocky Mountain variety grows in both pure and mixed species stands across a range of habitats (Franklin & Dyrness 1973). Although the coastal variety is primarily planted in pure monocultures, the species is often found in association with other species like Sitka spruce (*Picea sitchensis* [Bong.] Carr.), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), grand fir (*Abies grandis* [Douglas ex D.Don] Lindley), and western red cedar (*Thuja plicata* Donn ex.D.Don) in naturally-regenerated and old-growth stands (Franklin & Dyrness 1973).

Throughout much of its range, Douglas-fir is quite productive. For example, intensively managed plantations of coastal Douglas-fir can achieve growth rates of 17 to 22 m³/(ha × yr) and will likely increase with continued improvements in commercial tree breeding programs (Talbert & Marshall 2005). Also, due to its long-lived nature and distinct canopy structure, stands of Douglas-fir are an important source of habitat for a variety of wildlife species (Cline et al 1980). Consequently, Douglas-fir is the focus of a variety of management activities and planning efforts in western North America.

When compared to other western North America conifer species, Douglas-fir can thrive in a variety of habitat and climatic conditions (Rehfeldt et al 2008). The key climate factors controlling Douglas-fir occurrence are total as well as growing season precipitation, growing degree days, and the mean temperature of the coldest month (Rehfeldt et al 2006). This suggests that Douglas-fir should be relatively adaptable to oncoming changes in climate. However, limited knowledge on future changes in the species spatial distribution and productivity is available.

In general, the future climate in western North America is expected to become warmer and drier. In the US southwest, climate change will likely increase annual temperatures by upwards of 5 °C and greatly intensify summer droughts by decreasing spring pre-

Methods

Data

Data used in this analysis were obtained from the US Department of Agriculture (USDA) Forest Service Forest Inventory and Analysis (FIA) program and the BC Ministry of Forests, Lands, and Natural Resources Operations Vegetation Resources Inventory (VRI) program. FIA comprises a network of field plots measured periodically across the forests of the United States, while VRI has a similar program for the forests of BC. In this analysis, FIA data from eleven western US states were used, namely Arizona, California, Colorado, Idaho, Montana, New Mexico, Nevada, Oregon, Utah, Washington, and Wyoming. In addition, all VRI data from BC was included.

The FIA program uses a multi-phase sampling design in which a systematic grid of hexagons is superimposed over the country to estimate forest and nonforest conditions. One FIA field plot is established at random within each hexagon where forest lands are present. At roughly 2,400 ha per hexagon, the sampling intensity translates to approximately one field plot per 5 km of linear distance in forested regions. Each field plot consists of three 7.32 m radius subplots that are arranged in a triangular pattern around a central subplot of the same size, with the full complement of subplots covering 672.5 m². All trees are measured on each subplot and one or more trees at each plot are measured for total height and age at breast height (DBH 1.37 m) as determined from increment-core extraction and field examination of tree rings.

The VRI program uses a similar multi-phase sampling design as the FIA. The entire province of BC is divided into inventory units, which are then subdivided into polygons using aerial photographs. In the second phase, polygons are randomly selected using probability proportional to size and further subdivided into a 100 m grid for ground-based sampling. At each selected ground location, a five-point cluster is established and a variety of data is collected using fixed-area, variable-radius, and line transects. Depending on polygon conditions, an appropriate basal area factor is selected and used to measure trees with DBH ≥ 4.0 cm. A 2.50, 3.99, or 5.64 m fixed-radius (depending on project specifications) is also established and used to measure trees with DBH < 4.0 cm as well as stumps. Per site a tree of the species leading in basal area is selected and measured for height and breast-height age.

Analysis

Similar to Rehfeldt et al (2006), the presence/absence of Douglas-fir (at least 2.54 cm in DBH) was determined at each FIA and VRI plot location. Douglas-fir SI was also estimated at each FIA and VRI plot location using the 50-year base age height age model

cipitation by 10–40%, while less drastic yet significant changes are expected in the Pacific Northwest (Karl et al 2009). In the western US, Rehfeldt et al (2006) projected that the area occupied by Douglas-fir over the next 100 years would change relatively little in comparison to other species (–2 to +11%), but it would become displaced in space. In particular, the occurrence of Douglas-fir in the coastal region of Oregon and Washington was significantly decreased (Rehfeldt et al 2006). In British Columbia (BC), Hamann & Wang (2006) indicated that Douglas-fir would lose a lot of its current habitat, but significantly gain additional habitat, which would result in an overall gain for the species. The results of Coops & Waring (2011) recently supported the findings of Hamann & Wang (2006). In terms of productivity, Coops et al (2010) found Douglas-fir future site index (SI) to decrease by 10%, on average, using a hybrid growth model, but some sites could experience reductions up to 40%. In the western US, Weiskittel et al (2011) found a predominant trend of Douglas-fir SI in 2060 increasing by 0 to 5 m, with some sites experiencing reductions of up to 10 m. However, a comprehensive assessment of climate change impacts on Douglas-fir throughout western North America has yet to be presented.

In this analysis, the projected habitat and productivity of Douglas-fir in western North America will be examined. Specific objectives are to: 1) relate current occurrence and productivity to climate variables; 2) project habitat and productivity under climate change; and 3) map changes in both habitat and productivity. The working hypothesis is that Douglas-fir will see significant shifts in its distribution, while productivity will moderately decrease for areas occupied by the coastal variety and increase for areas occupied by the Rocky Mountain variety.

Variable name	Definition	Mean	Minimum	Maximum
adi	sqrt(dd5)/map	0.0827	0.0069	1.3256
adimindd0	adi*mmindd0	121.5473	0.8836	510.4495
d100	Julian date the sum of degree-days > 5 °C reaches 100°	120.1	13.0	200.0
dd0	Annual degree-days < 0 °C (based on monthly mean temperatures)	605.3	0.0	2549.0
dd5	Annual degree-days > 5 °C (based on monthly mean temperatures)	1737.0	256.0	6755.0
dd5mtcm	(dd5 × mtcm)/1000	−2.46	−26.37	83.61
fday	Julian date of the first freezing date of autumn	261.8	216.0	363.0
ffp	Length of the frost-free period	106.0	13.0	363.0
gsdd5	Degree-days > 5 °C accumulating within the frost-free period	1228.8	44.0	6559.0
gsp	Growing season precipitation, April–September	264.9	21.0	1808.0
gspdd5	(gsp × dd5)/1000	420.73	61.82	1787.67
gspmtcm	(gsp × mtcm)/1000	−0.96	−9.87	3.33
gsptd	(gsp × tdiff)/100	54.16	2.59	300.12
map	Mean annual precipitation	693.0	62.0	4306.0
mapdd5	(map × dd5)/1000	1138.9	160.4	6636.6
mapmtcm	(map × mtcm)/1000	−1.71	−23.95	17.72
maptd	(map × tdiff)/100	133.09	14.35	714.80
mat	Mean annual temperature	6.57	−3.80	23.50
mmax	Maximum temperature in the warmest month	26.33	12.30	44.90
mmin	Minimum temperature in the coldest month	−9.59	−25.40	6.10
mmindd0	Annual degree-days < 0 °C based on monthly minimum temperatures	1596.0	7.0	4361.0
mtcm	Mean temperature in the coldest month	−3.40	−20.2	12.90
mtcmgsp	mtcm/gsp	−0.0121	−0.1058	0.5120
mtcmmap	mtcm/map	−0.0069	−0.0500	0.1855
Mtwm	Mean temperature in the warmest month	17.69	8.20	37.10
pratio	gsp/map	0.4474	0.0947	0.8216
prdd5	pratio × dd5	769.32	84.51	3326.96
prmtcm	pratio × mtcm	−1.82	−9.78	6.43
sday	Julian date of the last freezing date of spring	156.6	8.0	203.0
sdi	Summer dryness index = sqrt(gsdd5)/gsp	0.1614	0.0145	3.8395
sdimindd0	sdi × mmindd0	201.83	5.14	801.48
tdgsp	tdiff/gsp	0.0968	0.0074	1.2905
tdiff	Mtwm−mtcm	21.10	5.40	34.70
tdmap	tdiff/map	0.0436	0.0029	0.4371

Tab 1 *Climate variables from the US Forest Service Moscow Laboratory climate model (http://forest.moscowfsl.wsu.edu/climate) used for modeling Douglas-fir occurrence and productivity. Temperature-related variables are defined in units of °C and precipitation values in mm.*

of Monserud (1984), similar to Weiskittel et al (2011). Justification for using the Monserud (1984) equation is given in Weiskittel et al (2011). In short, the equation was found to be rather flexible, developed using data from a broad geographic region, and provided an unbiased estimate for the majority of the species in the database (Weiskittel et al 2011).

Thirty-year (1961–1990) averaged monthly values for maximum, mean, and minimum daily temperatures, along with monthly total precipitation were obtained from a spline surface model developed from numerous climate stations throughout western North America (Rehfeldt 2006). Climate values for each FIA and VRI plot location were generated from the spline surface based on longitude, latitude, and elevation (Rehfeldt 2006). A suite of derived variables were computed from the monthly climate data (Table 1) based on the expectation that some of the variables would be relevant for predicting or explaining relationships between climate and Douglas-fir occurrence and potential productivity.

All computations were done using R (R Development Core Team 2009), including several freely-available packages that extend the software's basic capabilities. The R packages used were 'randomForest' and 'maps'. The nonparametric regression tool, Random Forests (RF, Breiman 2001), as implemented in R by Liaw & Wiener (2002), was used to predict presence-absence or SI from climate. To determine the number of variables to use, the RF regression procedure was sequentially repeated, dropping the least influential variable at each step until there were only two predictors left. The fit statistics (e.g. R^2, RMSE, error rate) were then plotted over the number of var-

Location	Current	2030	2060	2090
British Columbia	180,357	355,286	533,979	487,183
United States	789,101	713,534	639,467	446,854
Total	969,458	1,068,820	1,173,446	934,037

Tab 2 Predicted current and future area (km²) of potential Douglas-fir habitat by location using the developed random forest model and the Canadian Center for Climate Modeling and Analysis general circulation model under the A2 emissions scenario.
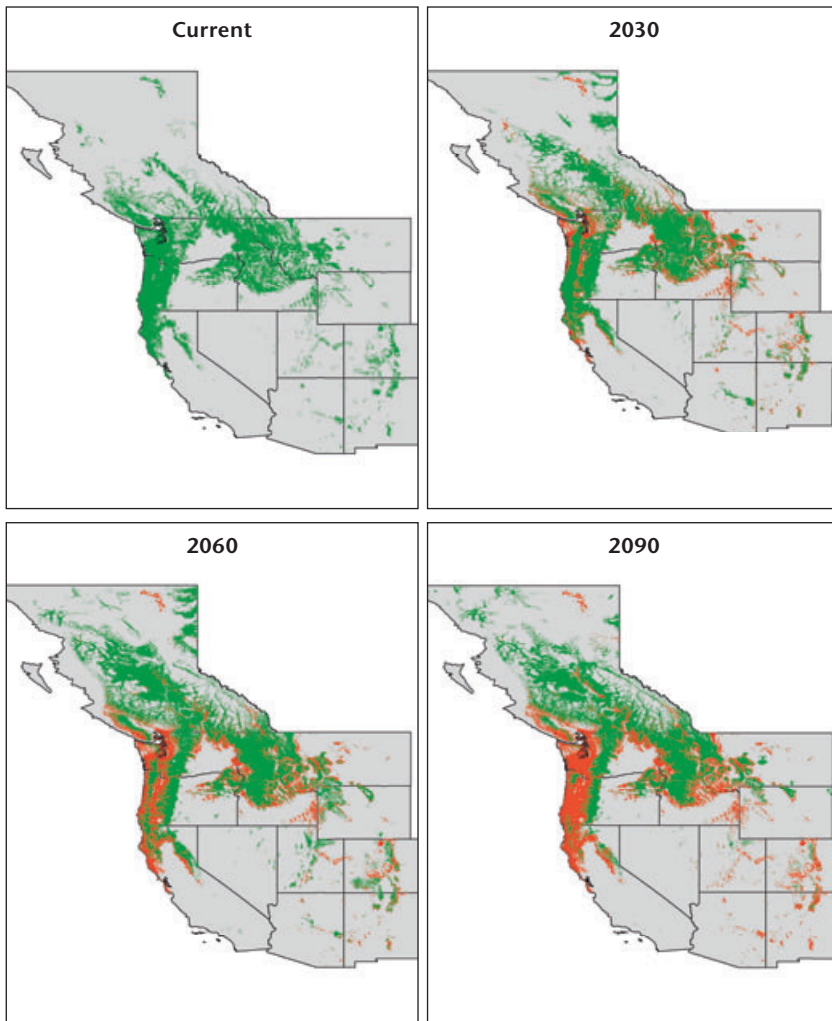
Fig 2 Predicted current and future distribution of Douglas-fir potential habitat based on the developed random forest model and the Canadian Center for Climate Modeling and Analysis general circulation model under the A2 emissions scenario. Green: current and predicted habitat, red: losses in habitat.

iables in the sequentially-fitted regression analyses and the optimal number of variables was identified by finding the point, where the curve's rate of increase slowed to near zero. This approach was assumed to balance model parsimony with overfitting. The RF algorithm builds a set of regression trees (100 in our case), each based on a separate boot-strap sample of the data. The observations that are left out of the sample are called out-of-bag (OOB) samples. Once the set of regression trees are created a value of mean square error (MSE) is computed for each tree using the OOB samples that correspond to the tree. The MSE from all the trees is averaged and reported as overall MSE (the same observations are used to compute an estimate of R^2).

RF models having the strongest ability to predict both occurrence and productivity were subsequently used to forecast changes in productivity in western North America forest lands under forecast climate change scenarios for 2030, 2060, and 2090. Monthly downscaled predictions from the Canadian Center for Climate Modeling and Analysis general circulation models (CGCM) were used to demonstrate potential climate-change effects on changes in species occurrence and productivity. Climate predictions were based on the A2 greenhouse gas emissions scenario as defined by Nakicenovic & Swart (2000). Downscaled GCM data from the Moscow Forestry Sciences Laboratory[1] were used, which were produced by adapting spline surfaces from contemporary climate data to future GCM outputs (Rehfeldt 2006). To accomplish this, downscaling from the GCM grids to the point locations of the weather stations used a weighted average of the monthly change for the GCM cell centers lying within 400 km of a weather station. The inverse of the square of the distance from the station to the cell center was used for weighting. Monthly climate surfaces for average, minimum, and maximum temperature and precipitation were then fit anew for each GCM and each scenario for each of three 10-year periods, nominally, 2030, 2060, and 2090.

For the occurrence analysis, a total of 55,184 observations were available, while 38,235 observations were available for the productivity analysis.

Results

Potential habitat

Douglas-fir occurred on 18,338 or 33% of the plots examined. In comparing models with a different number of covariates, the error rate did not change substantially among the different models. Consequently, a model with five climatic variables was selected as the final model. The overall OOB estimate of error rate for the final model was 14% with errors of commission (presence = no, but prediction = yes; 21%) being higher than errors of omission (presence = yes, but prediction = no; 10%). The most influential variables were (in order of importance) annual dryness index (adi), maximum temperature in the warmest month (mmax), ratio of growing season to total precipitation multiplied by annual degree days > 5°C (prdd5), mean temperature of the warmest month (mtwm), and summer dryness index multiplied by the annual degree days < 0°C (sdimindd0).

Based on CGCM projections, the total potential Douglas-fir habitat is expected to increase by 10% and 21% in the decade surrounding 2030 and

1 further information: http://forest.moscowfsl.wsu.edu/climate (7.12.2011)

Attribute	2030	2060	2090
Mean	0.29	1.52	2.03
Median	0.09	0.69	0.73
Standard Deviation	3.11	4.54	4.85
25% percentile	−1.72	−2.36	−2.28
75% percentile	1.98	3.82	4.85

Tab 3 Predicted changes in Douglas-fir site index (m; base age 50 years) from current conditions based on the developed random forest model and the Canadian Center for Climate Modeling and Analysis general circulation model under the A2 emissions scenario.

2060, respectively, when compared to the amount of current habitat (Table 2). However, the amount of total potential Douglas-fir habitat should decrease by 4% in 2090 when compared to the amount of current habitat. Overall, only 40% of the potential Douglas-fir habitat in 2090 will overlap with current habitat. Spatially, Douglas-fir potential habitat would shift from the coastal areas of North America to the interior mountains (Figure 2).
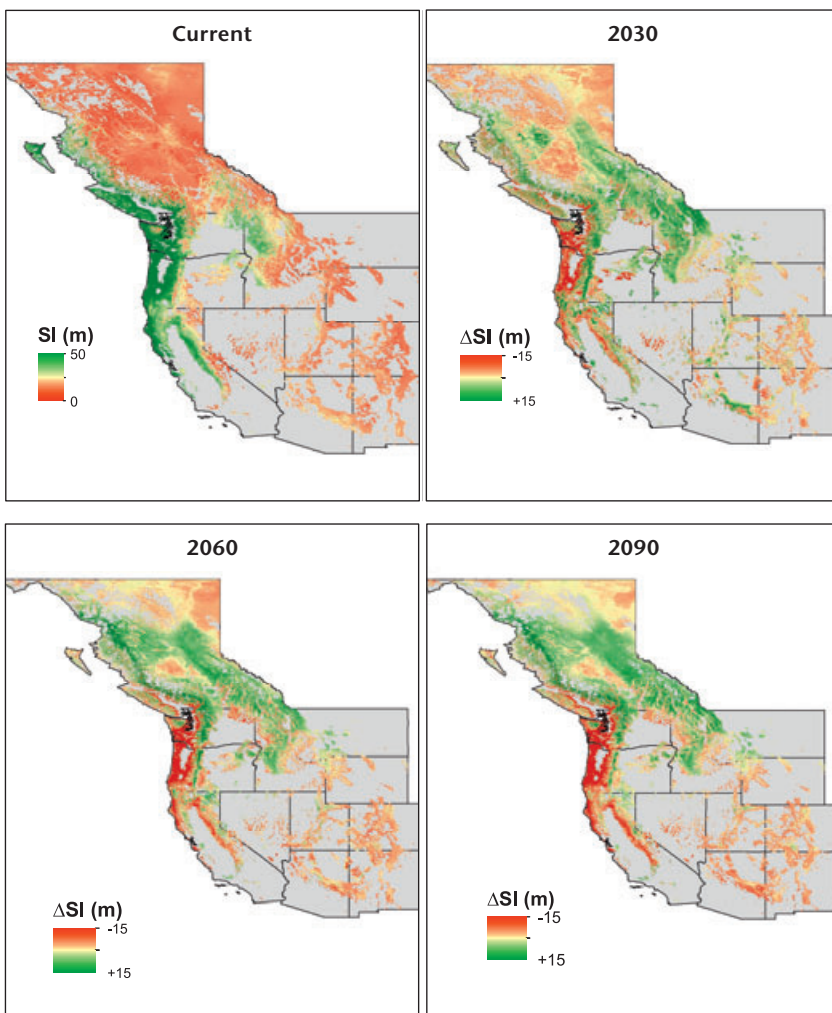
Productivity

Like the potential habitat analysis, the most parsimonious model for estimating SI also had 5 climate variables. The model had an R^2, mean bias, and RMSE of 71%, −0.01 m, and 4.74 m, respectively. The most influential variables were (in order of importance) maximum temperature in the warmest month (mmax), mean annual precipitation multiplied by annual growing degree days > 5 °C (mapdd5), Julian date the sum of degree-days of > 5 °C exceeds 100 (d100), ratio of growing season to total precipitation (pratio), and growing season precipitation multiplied by the mean temperature of the coldest month (gspmtcm). The median observed SI was 35.4 ± 15.2 m (mean ± SD), while the median predicted SI was 36.5 ± 13.1 m. Although this indicates a slight bias in the predictions (~4%), there were no obvious trends in the residuals (not shown). The highest observed and predicted values were along the coasts of Oregon and Washington as well as on Vancouver Island (BC), that is, sites with long growing season, high summer precipitation combined with warm summers and warm winters and early spring had the highest SI. Those with short growing seasons, low precipitation in the growing seasons, and cold winters had the lowest SI.

Overall, a slight increase in the mean SI was projected for the coming century (Table 3), but reductions up to 15 m were observed at some sites (Fig-
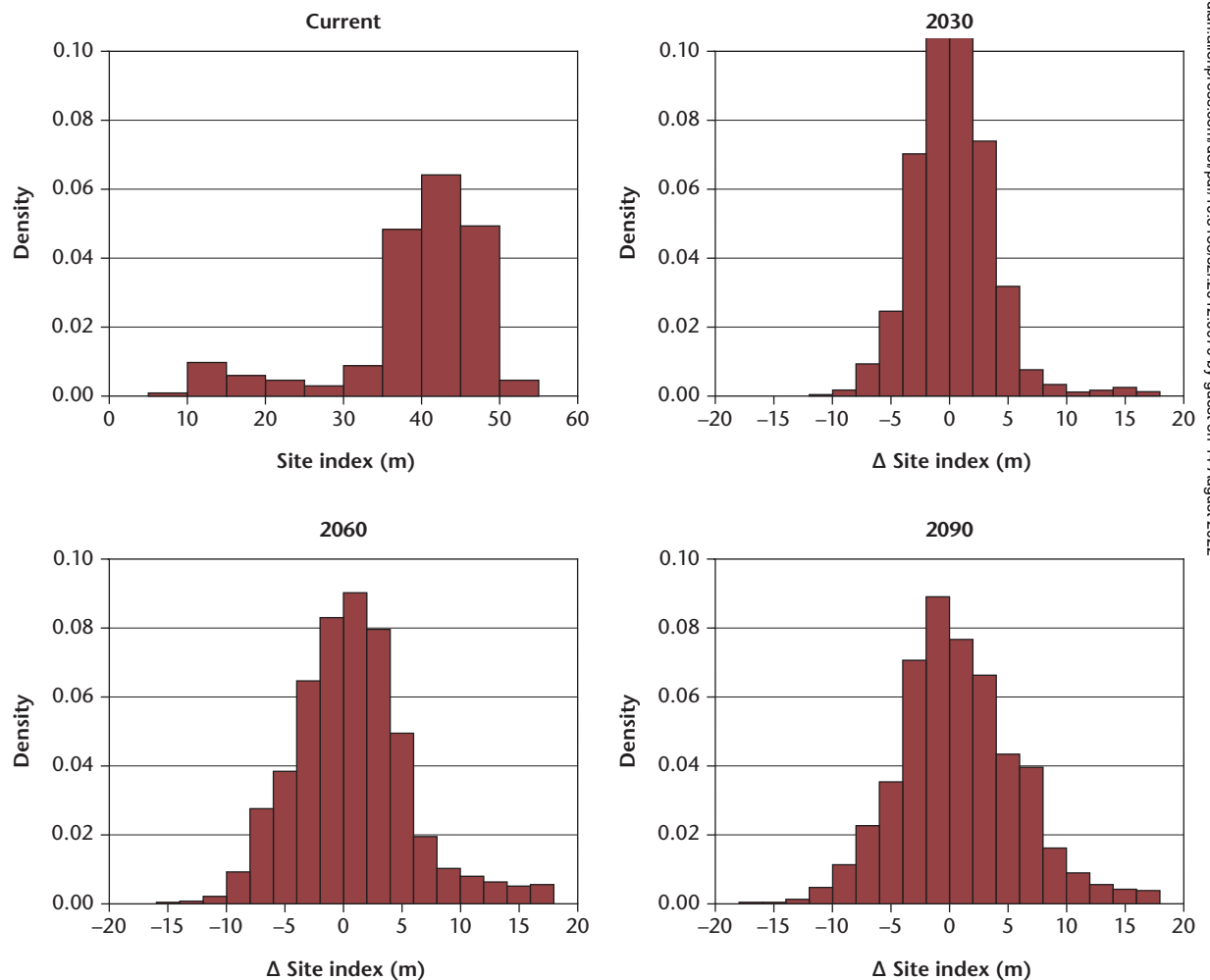
Fig 3 Distribution of current and predicted changes in Douglas-fir site index (m; base age 50 years) based on the developed random forest model and the Canadian Center for Climate Modeling and Analysis general circulation model under the A2 emissions scenario.

Fig 4 Predicted current and future changes in productivity of Douglas-fir in terms of base-age 50 years site index (m) based on the developed random forest model and the Canadian Center for Climate Modeling and Analysis general circulation model under the A2 emissions scenario.

ure 3). The reductions were most severe in the coastal areas, whereas the increases were most significant in interior BC as well as central Idaho and western Montana (Figure 4). Although changes in mean SI were relatively small, the distribution of SI became less uniform through time, suggesting higher variability in future productivity.

Sensitivity analysis

A sensitivity analysis was conducted by changing the input climate variables by ± 25% and comparing the predictions to the average predicted value. Overall, the probability of occurrence was more sensitive to changes in the input variables than SI (Figure 5). However, SI was particularly sensitive to changes in maximum temperature in the warmest month (mmax; –15%). Douglas-fir probability of occurrence was most sensitive to growing season precipitation (gsp), annual degree-days < 0 °C (dd0), and mean annual precipitation (map). Douglas-fir SI was most sensitive to mmax, map, and annual degree-days > 5 °C (dd5). All percent changes were less than 15% indicating moderate model sensitivity.

Discussion

This analysis combined datasets from the US and Canada to assess the potential influence of climate and climate change on Douglas-fir habitat and productivity. A nonparametric regression technique was used to relate current Douglas-fir occurrence and productivity to contemporary climate. This model was then utilized to project for Douglas-fir the occurrence of suitable climates and their productivity into the future climate space described by downscaled CGCM A2 scenario climate information. Overall, it was found that for the examined scenario both Douglas-fir habitat as well as productivity are expected to change drastically over the next 100 years. Although the total potential Douglas-fir habitat would decrease only slightly by 2090, the spatial distribution of the habitat should shift away from coastal areas. Similar changes in productivity are expected, decreasing in coastal area and increasing slightly in the interior. The results highlight the sensitivity of Douglas-fir to climate and the significant implications of expected climate change in North America. However, the analysis only examined the influence of climate factors, while other management, biotic, and abiotic factors may be more influential in the future.

Potential habitat

Douglas-fir can thrive in a variety of habitats and climatic conditions when compared to other western North American conifers (Rehfeldt et al 2008). Although Douglas-fir consists of two varieties, they were not differentiated in this analysis, similar to Rehfeldt et al (2006), as the US FIA only distinguishes between Douglas-fir strictly speaking and bigcone Douglas-fir (*Pseudotsuga macrocarpa* [Vasey] Mayr). Likely, future improvements in predicting the species occurrence could be achieved by differentiating between the two varieties.

Similar to Rehfeldt et al (2006), this analysis found Douglas-fir to be sensitive to both temperature and moisture. However, the overall classification error in this analysis was nearly three times as high as in comparison to Rehfeldt et al (2006; 14% vs. 5%). This likely reflects the wider geographic area covered in this analysis as Rehfeldt et al (2006) analyzed data only from the western US and southwestern Canada (up to 51 °N). On the other hand, the classification error was significantly better than one recently observed for predicting Douglas-fir occurrence in western North America by Coops et al (2011; 14% vs. 27%), which might be partially attributed to differences in the statistical technique and climate data used. One other important factor influencing the error rate in this analysis and likely Coops et al (2011) is that only forested plots were used, while Rehfeldt et al (2006) used both forested and nonforested plots. Future analyses should evaluate
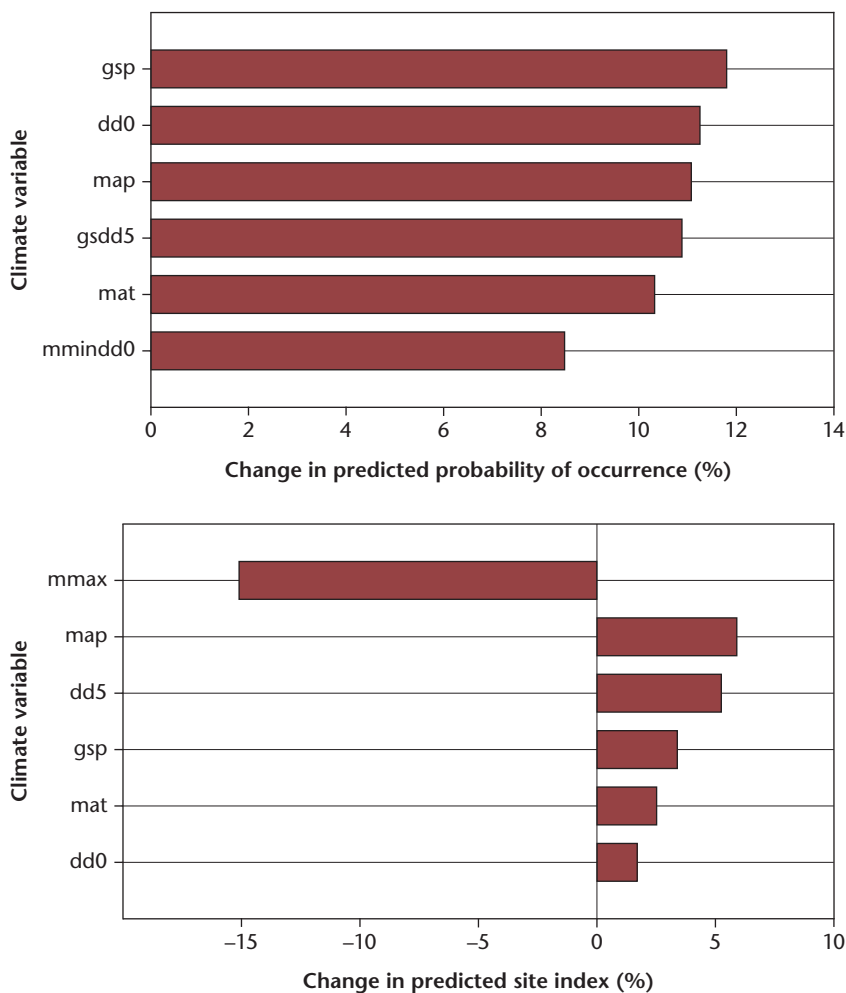
Fig 5 Sensitivity of Douglas-fir probability of occurrence (above) and site index (below) to ± 25% change in climate variables. Only the top 6 variables are shown based on their average sensitivity. For abbreviations, see table 1.

the consequences of including forested and nonforested plots on their predictions.

Using two different GCMs, Rehfeldt et al (2006) indicated that Douglas-fir habitat would increase by 11, 7, and 2% in 2030, 2060, and 2090, respectively, when compared to the current habitat. These values are different to the values found in this analysis, except 2030 where Douglas-fir habitat was expected to increase by 10%. These differences are likely attributed to the inclusion of projections north of 51°N, where large increases in Douglas-fir potential habitat were predicted. In general, the amount of Douglas-fir habitat is in relative agreement with Coops & Waring (2011) as they estimated the habitat to increase from 800,000 to 1,200,000 km² from current to 2080 for approximately the same study area (except Colorado and New Mexico). Two important differences between this study and Coops & Waring (2011) are: 1) they predict Douglas-fir habitat to continue to increase from current to 2080, whereas this analysis indicates Douglas-fir habitat availability will peak in 2060 and then begin to decline and 2) they indicate Douglas-fir habitat to be much larger than current and this analysis suggests a smaller future habitat than today. This difference could be due to

the GCM used, as Coops & Waring (2011) used both the A2 and B1 scenarios from the CGCM, whereas this analysis only used the A2 scenario. In addition, Coops & Waring (2011) used regression decision trees, which can have lower prediction accuracy when compared to the random forest techniques utilized in this analysis (e.g. Prasad et al 2006).

This analysis indicates that Douglas-fir habitat becomes displaced spatially, despite no drastic change in the absolute amount available. In general, Douglas-fir habitat shifts eastward particularly along the coastal areas due primarily to increased temperatures and decreased precipitation. This is in general agreement with Rehfeldt et al (2006). In addition, the general spatial pattern of Douglas-fir habitat in interior BC corresponds to Hamann & Wang (2006) as this area is predicted to become much more amendable to Douglas-fir than it is currently. However, Hamann & Wang (2006) suggest that Douglas-fir will remain a strong component throughout forests on Vancouver Island, whereas this analysis suggests the habitat would primarily be on the eastern half of the island. These important differences highlight the inherent assumptions associated with any statistical technique and dataset used for calibration. For example, Hamann & Wang (2006) used data only from BC, a first generation GCM, and canonical discriminant analysis.

An important assumption not tested to date in the analyses mentioned above is the role of genetics. When compared to other species, Douglas-fir is considered a genetic specialist (Rehfeldt 1994). This means that Douglas-fir growth and mortality at any given site is highly dependent on its seed source, as the local population is often highly attuned to their growing environment. This is well illustrated in the work of Leites et al (in press)[2] who showed that Douglas-fir seed sources had relatively narrow ranges in climate where potential height growth were achieved. As suggested by Crookston et al (2010), this indicates that potential habitat should be considered at the population rather than species level. The implications for this analysis are in assuming that Douglas-fir trees have the same ability to grow anywhere in its range, that is, that SI is dependent on only the growing environment. This assumption, however, is false for a genetic specialist like Douglas-fir (Monserud & Rehfeldt 1990). Consequently, the impact of a changing climate on Douglas-fir occurrence may be much less optimistic than depicted in this analysis, as the potential of genetic maladaptation for sub-populations of this species is relatively high (St. Clair & Howe 2007) and was not accounted for in any of the analyses discussed above. In addition, other factors

2 LEITES LP, ROBINSON AP, REHFELDT GE, MARSHALL JD, CROOKSTON NL (IN PRESS) Height-growth response to climatic changes differs among populations of Douglas-fir: a novel analysis of historic data. Ecol Appl.

like management activities, pests, and local soil conditions may also be important determinants of Douglas-fir occurrence not considered in this analysis.

Productivity

Similar to Weiskittel et al (2011) and Coops et al (2010), this analysis suggests significant future changes in Douglas-fir productivity as measured by SI throughout its entire range. In the western US, Weiskittel et al (2011) observed an overall mean increase in SI of 1.6 m with some sites experiencing reductions of up to 10 m. This analysis suggests a similar increase (0.29 to 2.03 m), but greater reductions in SI (up to 15 m). This could be related to the wider range of growing conditions in the SI calibration dataset in this analysis and the fact that the predictions were not averaged between different GCMs as done in Weiskittel et al (2011).

In BC, Coops et al (2010) found that SI may increase up to 10% on average in the interior, but decrease between 10 to 30% along the coast. For Douglas-fir along the coast, Coops et al (2010) indicated reductions upwards to 30% with an average reduction near 17%. In this analysis, the overall mean increase by 2090 was 17% with reductions upwards to 55%, which is more severe than the 40% reduction found by Coops et al (2010). However, an important difference between this analysis and Coops et al (2010) is that this analysis assessed changes in SI for all forested areas, while Coops et al (2010) only assessed areas where Douglas-fir is currently present.

In general, the overall spatial pattern was that coastal areas showed the highest reductions in SI, while interior areas showed increased potential productivity. This parallels the findings presented for Douglas-fir habitat. This is likely because coastal areas will generally become warmer and drier than currently, while the growing season length will increase in interior areas. However, as indicated by Coops et al (2010), there can be relatively high variation in predicted changes in SI within a local climate zone. For example, this analysis suggested that some areas along Vancouver Island's western coast may experience a modest increase in SI, unlike predictions for the general surrounding area. This highlights the importance of improved downscaling of current and future climate.

As noted with predictions of Douglas-fir future suitable habitat, forest management and genetics will play a significant role in determining the future productivity of any given site. An important assumption used in this analysis is that species at any given site is well adapted and indicative of site potential productivity. However, actual site productivity is a complex by-product of genetics, current environmental conditionals, and their interaction. For example, Monserud & Rehfeldt (1990) indicated that Douglas-fir genotype was over 30% more important than contemporary environment in determining phenotypic variation in dominant height of natural stands. Therefore, the changes in SI projected by this analysis assume that the species that are adapted to new climatic environments will be growing at those locations. This means that the trees that are currently present at any given site might not display the predicted change in SI as their genetic makeup is adapted to the current environmental conditions. Consequently, seed source and future climate would be needed to be matched in order to realize the expected increases in SI predicted in certain areas.

Conclusions

Douglas-fir is a commercially and ecologically important species in western North America, but a changing climate should have a tremendous impact on its future habitat, largely because it is a genetic specialist needing to cope with rapidly changing climatic conditions. Thus, this analysis indicates that Douglas-fir will experience significant changes under a future climate throughout its current native range and not just at its edges, which was also suggested by Chen et al (2010). In general, Douglas-fir prime habitat will likely shift eastward from the coast to the interior and the species will not be as productive as it is currently. However, it is important to note that several factors not accounted for in this analysis may ultimately control these potential changes, particularly genetics, CO_2 concentration, and alternations in the disturbance rate and severity (Weiskittel et al 2011). Regardless, the predicted changes in Douglas-fir habitat and productivity have significant implications for the projection of future growth and yield as demonstrated by Crookston et al (2010). Future work needs to better consider the role of genetics influencing Douglas-fir habitat and productivity.

Acknowledgements

Literature

BREIMAN L (2001) Random forests. Machine Learning 45: 5–32.

CHEN PY, WELSH C, HAMANN A (2010) Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. Glob Chang Biol 16: 3374–3385.

CLINE SP, BERG AB, WIGHT HM (1980) Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J Wildl Manage 44: 773–786.

COOPS NC, HEMBER RA, WARING RH (2010) Assessing the impact of current and projected climates on Douglas-fir productivity in British Columbia, Canada, using a process-based model (3-PG). Can J For Res 40: 511–524.

COOPS NC, WARING RH (2011) Estimating the vulnerability of fifteen tree species under changing climate in Northwest North America. Ecol Model 222: 2119–2129.

COOPS NC, WARING RH, BEIER C, ROY-JAUVIN R, WANG T (2011) Modeling the occurrence of 15 coniferous tree species throughout the Pacific Northwest of North America using a hybrid approach of a generic process-based growth model and decision tree analysis. Appl Veg Sci 14: 402–414.

CROOKSTON NL, REHFELDT GE, DIXON GE, WEISKITTEL AR (2010) Addressing climate change in the Forest Vegetation Simulator to assess impacts on landscape forest dynamics. For Ecol Manage 260: 1198–1211.

FRANKLIN JF, DYRNESS CT (1973) Natural vegetation of Oregon and Washington. Portland: USDA Forest Service, General Technical Report GTR-PNW-8. 427 p.

HAMANN A, WANG T (2006) Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87: 2773–2786.

HERMANN RK, LAVENDER DP (1990) Pseudotsuga menziesii (Mirb.) Franco. In: Burns RM, Honkala BH, editors. Washington DC.: USDA Forest Service, Agriculture Handbook 654. pp. 527–540.

KARL TR, MELILLO JM, PETERSON TC (2009) Global climate change impacts in the United States. New York: Cambridge Univ Press. 188 p.

LIAW A, WIENER M (2002) Classification and regression by random-forest. R News 2: 18–22.

MONSERUD RA (1984) Height growth and site index curves for inland Douglas-fir based on stem analysis data and forest habitat type. For Sci 30: 943–965.

MONSERUD RA, REHFELDT GE (1990) Genetic and environmental components of variation of site index in inland Douglas-fir. For Sci 36: 1–9.

NAKICENOVIC N, SWART RE (2000) Emissions scenarios: A special report of working group III of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge Univ Press. 599 p.

PRASAD A, IVERSON LR, LIAW A (2006) Newer classification and regression tree techniques: Bagging and random forests for ecological prediction. Ecostwes 9: 181–199.

R DEVELOPMENT CORE TEAM (2009) R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

REHFELDT GE (1994) Evolutionary genetics, the biological species, and the ecology of the interior cedar-hemlock forests. In: Baumgartner DM, Lotan JE, Tonn JR, editors. Proc Conference "Interior Cedar-Hemlock-White Pine Forests: Ecology and Management", Spokane, 2–4 Mar 1993. Pullman: Washington State Univ Extension. pp. 91–100.

REHFELDT GE (2006) A spline model of climate for the Western United States. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-165. 21 p.

REHFELDT GE, CROOKSTON NL, WARWELL MV, EVANS JS (2006) Empirical analysis of plant-climate relationships for the Western United States. Int J Plant Sci 167: 1123–1150.

REHFELDT GE, FERGUSON DE, CROOKSTON NL (2008) Quantifying the abundance of co-occurring conifers along Inland Northwest (USA) climate gradients. Ecology 89: 2127–2139.

ST. CLAIR JB, HOWE GT (2007) Genetic maladaptation of coastal Douglas-fir seedlings to future climates. Glob Chang Biol 13: 1441–1454.

TALBERT C, MARSHALL D (2005) Plantation productivity in the Douglas-fir region under intensive silviculture practices: results from research and operations. J For 103: 65–70.

WEISKITTEL AR, CROOKSTON NL, RADTKE PJ (2011) Linking climate, gross primary productivity, and site index across forests of the western United States. Can J For Res 41: 1710–1721.

Prognostizierte Veränderung von Lebensraum und Produktivität der Douglasie im Westen Nordamerikas

Die Douglasie (*Pseudotsuga menziesii* [Mirb.] Franco) zählt zu den häufigsten und wirtschaftlich bedeutendsten Baumarten im Westen Nordamerikas. Sie besiedelt eine grosse Bandbreite an Lebensräumen, erreicht ein hohes Alter (~500 Jahre) und ist ausserordentlich wuchskräftig. Angesichts der erwarteten klimatischen Veränderungen ist die Zukunft der Douglasie im Verbreitungsgebiet ungewiss. Der vorliegende Artikel präsentiert eine Zusammenfassung von Arbeiten, die mithilfe eines umfangreichen Netzes von Inventurflächen Veränderungen des Verbreitungsgebiets und der Produktivität der Douglasie abzuschätzen versuchen. Es wird erwartet, dass sich die Douglasie in Nordamerika in Bezug auf ihre Fläche bis ins Jahr 2090 nicht stark verändern wird. Jedoch wird sich das Verbreitungsgebiet von der Küste ins Landesinnere verlagern. Gleichzeitig werden Änderungen in der Produktivität vorausgesagt, indem diese in den Küstengebieten abnehmen und im Landesinnern leicht zunehmen wird. Über alles gesehen zeigt die Untersuchung die Abhängigkeit der Douglasie vom Klima, und sie erwartet im Zuge des Klimawandels erhebliche Veränderungen für diese Baumart in Nordamerika.

Pronostique sur les changements de l'aire de répartition et de la productivité du douglas dans l'ouest de l'Amérique du Nord

Le douglas (*Pseudotsuga menziesii* [Mirb.] Franco) est une des essences les plus fréquentes et productives de l'Ouest américain. Il est présent sur une grande diversité de stations, atteint un âge respectable (~500 ans) et est extrêmement productif. L'avenir de cette essence dans son aire d'origine est incertain en regard des changements climatiques attendus. Le présent article résume les résultats de travaux qui, à l'aide d'un réseau étendu de surfaces d'inventaire, tentent de décrire les changements de l'aire de répartition et la productivité du douglas. On estime que la surface totale occupée par des peuplements de douglas ne variera pas significativement d'ici à l'an 2090. Toutefois, sa présence se déplacera des côtes vers l'intérieur du pays. Simultanément, sa productivité dans les régions côtières devrait diminuer, alors que celle des régions intérieures devrait légèrement augmenter. Sur un plan global, l'étude démontre que le douglas est sensible au climat et que les changements climatiques affecteront considérablement cette essence en Amérique du Nord.