Climatic Change (2011) 105:313–328
DOI 10.1007/s10584-010-9861-2

A process-based approach to estimate lodgepole pine (*Pinus contorta* Dougl.) distribution in the Pacific Northwest under climate change

Nicholas C. Coops · Richard H. Waring

Received: 12 December 2008 / Accepted: 10 March 2010 / Published online: 19 August 2010

Abstract Lodgepole pine (*Pinus contorta* Dougl.) is a widely distributed species in the Pacific Northwest of North America. The extent that the current distribution of this species may be altered under a changing climate is an important question for managers of wood supply as well as those interested in conservation of subalpine ecosystems. In this paper, we address the question, how much might the current range of the species shift under a changing climate? We first assessed the extent that suboptimal temperature, frost, drought, and humidity deficits affect photosynthesis and growth of the species across the Pacific Northwest with a process-based model (3-PG). We then entered the same set of climatic variables into a decision-tree model, which creates a suite of rules that differentially rank the variables, to provide a basis for predicting presence or absence of the species under current climatic conditions. The derived decision-tree model successfully predicted weighted presence and absence recorded on 12,660 field survey plots with an accuracy of $\sim$70%. The analysis indicated that sites with significant spring frost, summer temperatures averaging $<$15°C and soils that fully recharged from snowmelt were most likely to support lodgepole pine. Based on these criteria, we projected climatic conditions through the twenty-first century as they might develop without additional efforts to reduce carbon emissions using the Canadian Climate Centre model (CGCM2). In the 30-year period centered around 2020, the area suitable for lodgepole pine in the Pacific Northwest was projected to be reduced only slightly (8%). Thereafter, however, the projected climatic conditions appear to progressively favor other species, so that by the last 30 years of twenty-first century, lodgepole pine could be nearly absent from much of its current range. We conclude that process-based models, because

---

N. C. Coops (✉)
Department of Forest Resource Management, University of British Columbia,
2424 Main Mall, Vancouver, BC, V6T 1Z4, Canada
e-mail: nicholas.coops@ubc.ca

R. H. Waring
College of Forestry, Oregon State University, Corvallis, OR, 97331, USA

they are highly sensitive to seasonal variation in solar radiation, are well adapted to identify the importance of different climatic variables on photosynthesis and growth. These same variables, once indentified, and run through a decision-tree model, provide a reasonable approach to predict current and future patterns in a species' distribution.

1 Introduction

Lodgepole pine (*Pinus contorta* Dougl.) is widely distributed in western North America. Within the Pacific Northwest, the species, or one of its subspecies, occurs on sandy soils along the coast, and inland over much of the subalpine zone, which extends to east of the Rocky Mountains and north into the Yukon Territory. Ecologically, lodgepole pine is a pioneer following fire, or an early seral-stage species, with low shade tolerance and relatively rapid juvenile growth. As a result of these attributes, it is often planted following clearfelling in large areas of British Columbia and Alberta. The widespread distribution of the species, combined with its commercial value, has resulted in a great deal of attention to its environmental adaptations and growth potential (Wang et al. 2004).

In the Pacific Northwest, considerable variation in climatic conditions have been observed over the past three decades, in particular, a reduction in the amount and duration of snow cover (Mote et al. 2005a; Knowles et al. 2006). Substantial evidence has amassed that we are in a period of rapid climate change (IPCC 2001; Parmesan and Yohe 2003). The most notable warming in the region has occurred, and will likely continue, in the northern portion of the ranges of Northwest tree species (Easterling et al. 2000; Berry et al. 2002; Root et al. 2003; Barrow and Yu 2005).

Based on these trends and those projected, there is an urgency to understand the relationship between climatic factors and the response of forests. Such knowledge, if it were available, would be most valuable to those charged with designing and implementing sustainable forestry operations under shifting climatic conditions (Green et al. 1989; Monserud et al. 2008).

There are a number of approaches available to predict how climate affects the distribution of vegetation. Based on their prevalence in the literature, the most common is an empirical approach that defines a "bioclimatic envelope" (Austin 1985; Iverson and Prasad 1998; McKenzie et al. 2003; Hijmans and Graham 2006; Thuiller et al. 2008). Although such models usually relate the presence or absence of a species, or its growth, to climatic variables; at times, topographic relief and soil properties are also included. The statistical methods employed vary; they include multiple regression techniques, neutral networks, and decision-tree analysis (Guisan and Zimmermann 2000; Iverson and Prasad 2001; Pearson et al. 2002; Elith et al. 2006). Whether empirical models provide a sound basis for predicting shifts in a species' distribution is unclear, particularly in a region where the day length varies substantially with latitude, novel climatic conditions may emerge, and the floristic elements may sort in new ways (Williams et al. 2007).

Process-based models offer some advantages over purely empirical approaches, but to date they have been mainly applied to predict the growth of individual species under an array of environments, including those outside the natural distribution of a species (Waring 2000; Sands et al. 2000; Rodriguez et al. 2002; Almeida et al. 2004;

Dye et al. 2004). These models take into account seasonal variation in solar radiation, humidity, and temperature as well as how soil properties and management might influence photosynthesis and the partitioning of growth above- and below-ground. An advantage of process-based models is that they are able to identify the relative importance of various environmental constraints directly on growth. The obvious disadvantage of such models is that they generally require detailed knowledge of a species' physiological attributes and generally do not consider constraints imposed by competition with other species (plants and animals), pollination or seed dispersal.

There has been an attempt to expand the utility of process-based models by including more empirical, statistically sophisticated analyses (Coops et al. 2009). This hybrid approach permitted the authors to contrast the environmental distributions of a half dozen native tree species to one with well documented physiological attributes. Rather than correlate the presence or absence of a species directly with climatic data, the relative importance of four variables on photosynthesis and growth were assessed via an automated decision-tree analysis. This analysis provided a suite of rules to predict a species' presence or absence on survey plots with a combined weighted accuracy averaging 87%.

In this paper, we first apply the hybrid-modelling approach to lodgepole pine to calibrate its distribution with observations made on thousands of field survey plots throughout much of the Pacific Northwest, including British Columbia. We then go on, using one of many available global climate models, to assess the probable shifts in the species' distribution between now and the end of twenty-first century.

2 Methods

2.1 Hybrid model

The 3-PG model (Physiological Principles Predicting Growth) provides a reasonable compromise between highly complex, fine-temporal scale, process models, and those applied at annual time-steps. The model calculates rates of photosynthesis, transpiration, growth allocation and litter production at monthly intervals. It is based on a number of established biophysical relationships and constants and incorporates simplifications that have emerged from studies conducted over a wide range of forests (Landsberg et al. 2003).

These simplifications include the following assumptions: (1) that climatic data are adequate when averaged at monthly time steps, (2) that each month, knowledge of the most limiting variable constraining photosynthesis is effective, (3) that autotrophic respiration (R_a) and net primary production (NPP) are approximately equal fractions of gross photosynthesis (GPP), (4) that canopy conductance approaches a constant as leaf area indices (LAI) > 3.0, and (5) that the proportion of photosynthate allocated to roots increases with drought and decreases with nutrient availability.

Previous to this study, we parameterized the 3-PG model for lodgepole pine using available data from both conventional forestry yield tables and other literature. Within the Pacific Northwest, a large amount of forest inventory data is available for lodgepole pine. These tables provided information on the allometric relationship between stem diameter and stem biomass required by the model (Whitehead and

Russo 2005). In addition, reasonable estimates of physiological parameters were available from studies on lodgepole and related pine species (Landsberg et al. 2003; Law et al. 2001; Hall et al. 2006). Model parameters used in this analysis are listed in Table 1.

Following procedures outlined in Coops et al. (2009), we assessed the implications of the seasonal limitations of water availability, deviations from the optimum temperature (15°C), frost frequency, and atmospheric humidity deficits (VPD) on photosynthesis and growth. The link to photosynthesis is critical because the potential varies seasonally. The upper limits are set by the amount of light absorbed by the canopy's foliage. Thus a day of subfreezing temperatures in the winter when the day length is short (in the Northern Hemisphere) has much less effect than in May when

Table 1 Summary of the 3-PG lodgepole pine model parameters used in this study

3PG parameter	Units	Lodgepole pine
Biomass partitioning and turnover		
Allometric relationships and partitioning		
Foliage:stem partitioning ratio at $D = 2$ cm	–	1.53
Foliage:stem partitioning ratio at $D = 20$ cm	–	0.55
Constant in the stem mass v. diam. relationship	–	0.0073
Power in the stem mass vs. diameter relationship	–	3.282
Maximum fraction of NPP to roots	–	0.8
Minimum fraction of NPP to roots	–	0.25
Litterfall and root turnover		
Maximum litterfall rate	1/month	0.015
Litterfall rate at $t = 0$	1/month	0.01
Age at which litterfall rate has median value	Months	120
Average monthly root turnover rate	1/month	0.015
NPP and conductance modifiers		
Temperature modifier (fT)		
Minimum temperature for growth	°C	−7
Optimum temperature for growth	°C	15
Maximum temperature for growth	°C	30
Soil water modifier (fSW)		
Moisture ratio deficit for $f_q = 0.5$	–	0.7
Power of moisture ratio deficit	–	9
Age modifier (fAge)		
Maximum stand age used in age modifier	Years	150
Power of relative age in function for fAge	–	4
Relative age to give $fAge = 0.5$	–	0.95
Stem mortality and self-thinning		
Max. stem mass per tree at 1,000 trees/ha	kg/tree	220
Canopy structure and processes		
Specific leaf area		
Specific leaf area for mature leaves	m^2/kg	3.1
Production and respiration		
Canopy quantum efficiency	molC/molPAR	0.035
Ratio NPP/GPP	–	0.47
Conductance		
Maximum canopy conductance	m/s	0.012
Canopy boundary layer conductance	m/s	0.2

the day length is much longer. The effect of any limitation in monthly precipitation is realized through a monthly water balance that takes into account evaporation, transpiration, and partial, to complete, recharge of the soil water storage capacity (Nightingale et al. 2007).

Although we recognize that soil fertility and soil water storage capacity vary considerably across the region (Swenson et al. 2005), in this paper, we chose to keep soil properties constant to simplify the analysis of the effects of climatic variation on tree distribution. We did this by setting the maximum available soil water storage capacity at 200 mm and assigning a moderately high rank to a soil fertility index (0.7), which generates a maximum photosynthetic quantum efficiency of 0.05 mol C mol photon^{-1} (2.75 g C MJ^{-1} of absorbed photosynthetically active radiation). The relative low value set for soil water storage assures that if drought occurs that it will be recognized (Nightingale et al. 2007). We recognize that lodgepole pine competes well on infertile soils, but following disturbance, it also can thrive on better soils. By choosing a moderate high level of soil fertility we minimize site differences in this property and accentuate limitations imposed by climatic variables.

2.2 Climate data, current and projected

Long term climate observations for stations throughout the region were interpolated across British Columbia using CLIMATE-BC, which includes a bilinear interpolation of the PRISM (Parameter-elevation Regressions on Independent Slopes Model) records, along with elevation corrections to temperature records for mountainous terrain (see Hamann and Wang 2005 for details of climate surface fitting approaches and use of PRISM). In order to undertake the predictions, information on elevation is required. To provide this, a 90 m Digital Elevation Model (DEM) was obtained from the Shuttle Radar Topography Mission (SRTM), resampled to 250 m for plot assessment (discussed later), and then expanded to a 1-km for this analysis. Mean monthly atmospheric VPD for daylight periods was estimated by assuming saturation at the average monthly minimum temperature would be equivalent to water vapor concentrations present throughout the day (Kimball et al. 1997). The maximum VPD is calculated each month as the difference between the saturated vapor pressure at the mean maximum and minimum temperatures. Mean daytime VPD was assumed to be two thirds of the maximum (Waring 2000). The number of days per month with subfreezing temperatures was estimated from empirical equations with mean minimum temperature (Coops et al. 1998). Monthly global solar radiation was derived using a topographic solar radiation model based on a regionally defined cloudless index, which was used to downscale the North American Regional Reanalysis (NARR, http://stommel.tamu.edu/~baum/narr.html). This reanalysis consists of a three-hourly radiation budget for North America from 1979 to 2008. We averaged the three-hourly observations into spatial coverages of monthly observations following methods of Schroeder et al. (2009).

To simulate the forest distribution under future climate, we utilized the Special Report on Emission Scenarios (SRES) climate scenarios developed by the IPCC (IPCC 2001). These scenarios include “a business as usual” prediction that permits atmospheric CO_2 to continue to increase unabated. We applied, similar to other researchers (Monserud et al. 2008), the Canadian Climate Centre (CGCM2; Flato et al. 2000) predictions based on the A2 scenario, which is close to the upper bound of the SRES scenarios (IPCC 2001; Monserud et al. 2008). We used three 30-year periods, the 2020s (2011–2040), 2050s (2041–2070) and the 2080s (2071–2100). This scenario is referenced in terms of deviations from the baseline period, and was thus easily integrated with the CLIMATE-BC layers described above. As average irradiance from CGCM2 under future scenarios does not differ substantially from twentieth century estimates, the NARR baseline data were used. Any change in the simulated distribution of lodgepole pine over the rest of the twenty-first century ignores therefore changes in cloud cover that would be associated with variation in the intensity, duration, or amount of monthly precipitation.

2.3 Species occurrence data

Across the Pacific Northwest, tree species presence/absence data were assembled from a number of sources. In Alberta, permanent sample plots and plots measured as part of the Province's ecological land classification were combined to form a baseline reference for the simulations. In British Columbia, presence/absence data were extracted from inventories of protected forested areas. The spatial accuracy of the Canadian plot coordinates was estimated at ±1 km. For the United States, we utilised data available from the US Forest Service, Forest Inventory and Analysis (FIA) plots. FIA data are recorded on a permanent sampling grid (approximately 1 plot per 2,400 ha) established across the conterminous USA (Bechtold and Patterson 2005). The publically available FIA plot locations, which we used, have similar spatial accuracy as the Canadian data (i.e., ±1 km). A detailed discussion of the FIA data sets is provided elsewhere (Schroeder et al. 2010).

The presence/absence data from both Canada and the USA were combined into one database. To verify plot locations, we compared the elevation recorded at each plot with the corresponding elevation from the 250 m DEM for the same location. Plots differing by more than ±150 m were discarded from the database. After this filtering procedure, 12,600 plots were available for modelling.

2.4 Delineating limiting climatic factors and decision-tree analysis

Across the region where field survey data were available, we applied the 3-PG model to predict stand growth and LAI when stands reached an age of 50 years. We set the initial stocking density of tree seedlings at 1,000 ha^{-1}, a value low enough to assure no stagnation and normal rates of self-thinning. At the end of the 50th year, by which time maximum LAI had been reached, the simulations were stopped and the monthly modifiers extracted. The degree that available soil water, suboptimal temperature, frost and VPD restricted photosynthesis was then determined for winter (December to February), spring (March to May), summer (June to August) and fall (September to November), as well as annually.

A decision-tree analysis was applied to assess the extent that 3-PG environmental modifiers might serve to predict the distribution of lodgepole pine. This type of analysis is increasingly advocated for ecological research because it is not dependent on the assumption of a normalized distribution, is well suited to dealing with collinear datasets, and excludes variables that are insignificant (De'ath 2002; Schwalm et al. 2006; Melendez et al. 2006). The technique automatically separates the dependent variables (presence or absence of the species) into a series of choices that not only identifies the importance of each constraining variable, but also establishes thresholds that best separate one species from another. The decision-tree analysis was undertaken with a 10-fold cross validation technique, similar to a "jackknifing" procedure, which starts by using all available data (the reference tree). The total dataset is partitioned randomly into 10 equally sized groups (or folds). One set is held in reserve, while the other nine are pooled and a model generated. The accuracy of the model is assessed using the remaining 10% of the data not used in model development. This process is then repeated 10 times, resulting in 10 different test trees and ten different accuracy assessments. The decision rules of the 10 models are then merged to produce a final decision tree with an overall accuracy assessed by averaging the independent results of the 10 simulations (Breiman et al. 1984).

2.5 Spatial validation of current species distribution

To provide a visual comparison of model accuracy with referenced sources, we applied the decision-tree rules over the Pacific Northwest region to produce maps of predicted lodgepole pine distribution that could be compared with field plot surveys and more general range maps (Critchfield and Little 1966; Little 1971).

2.6 Future lodgepole pine distribution

Using the validated decision rules developed using the current climate, we ran the 3PG simulations for lodgepole pine using the 2020s, 2050s and 2080s projected climate datasets. Again, modifiers defined at the end of 50 years of simulations were extracted, and the decision rules applied to draft maps of the species' distributions in the three future periods.

3 Results

Spatial variation in the climatic modifiers as they constrain photosynthesis on lodgepole pine during the most unfavourable month is shown in Fig. 1a–d. Optimum conditions for photosynthesis are indicated by the number 1; whereas 0 indicates complete shutdown for at least one month out of each year. According to model predictions, when the maximum available water supply is set at 200 mm, late summer drought could restrict growth throughout most of the interior regions (Fig. 1a; Hu et al. 2009).

High evaporative demand during the summer is typical throughout much of the southern interior, in particular for areas on the eastern sides of the Cascade and the prairies boundary in Alberta. The coastal mountains throughout the PNW are buffered from extremes in temperature and humidity deficits by their proximity to marine air masses. Mountainous areas toward the interior and throughout the northern regions of the Pacific Northwest also remain sufficiently cool to reduce evaporative demand (Fig. 1b). Deviations from optimum temperature (Fig. 1c) and limitations imposed by frequent frost (Fig. 1d) exhibit similar seasonal patterns.

The temporal trajectories of the modifiers on a monthly time-step provide additional information on seasonal variation (Fig. 2a–d)). It is evident that growth is limited by temperature throughout the winter (Fig. 2a) with values in January and

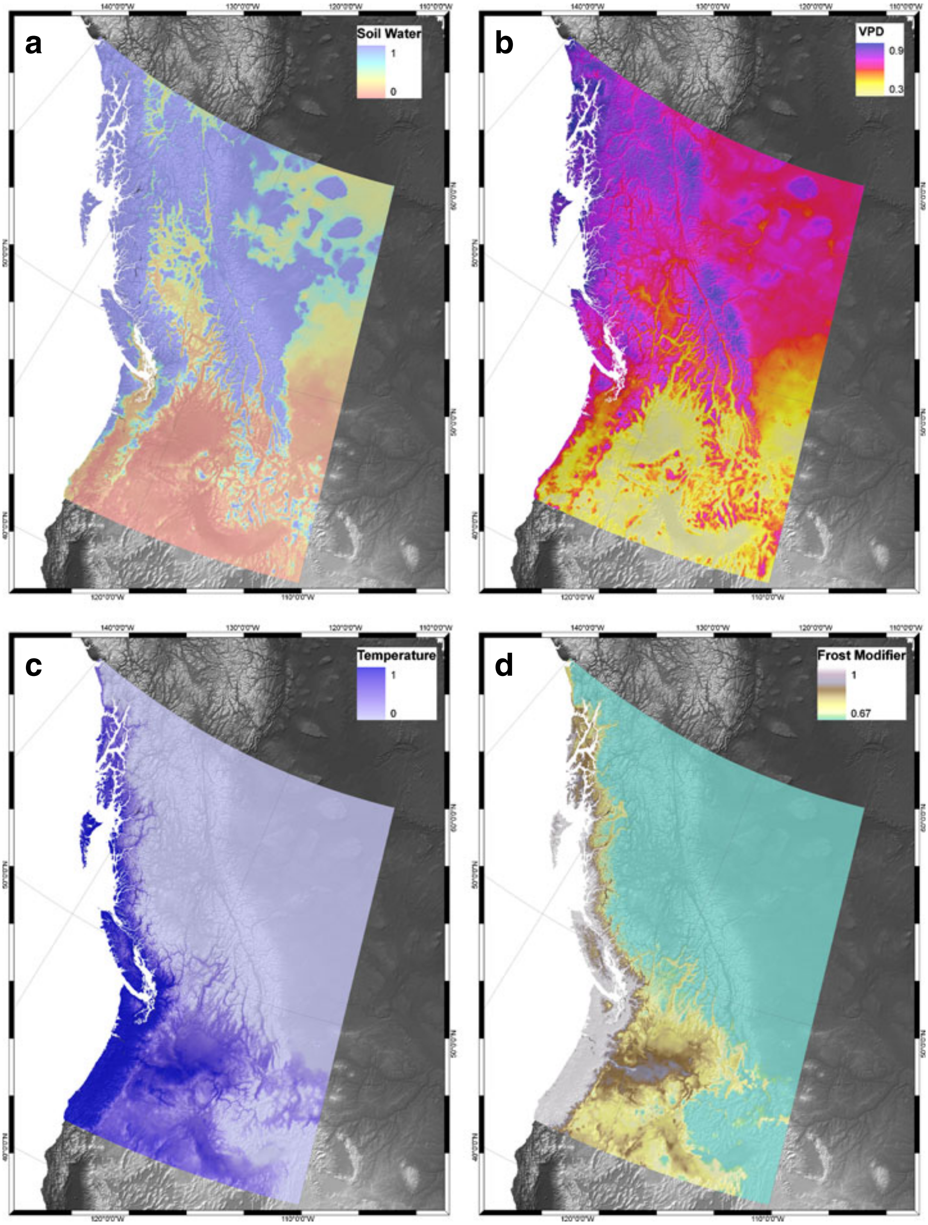
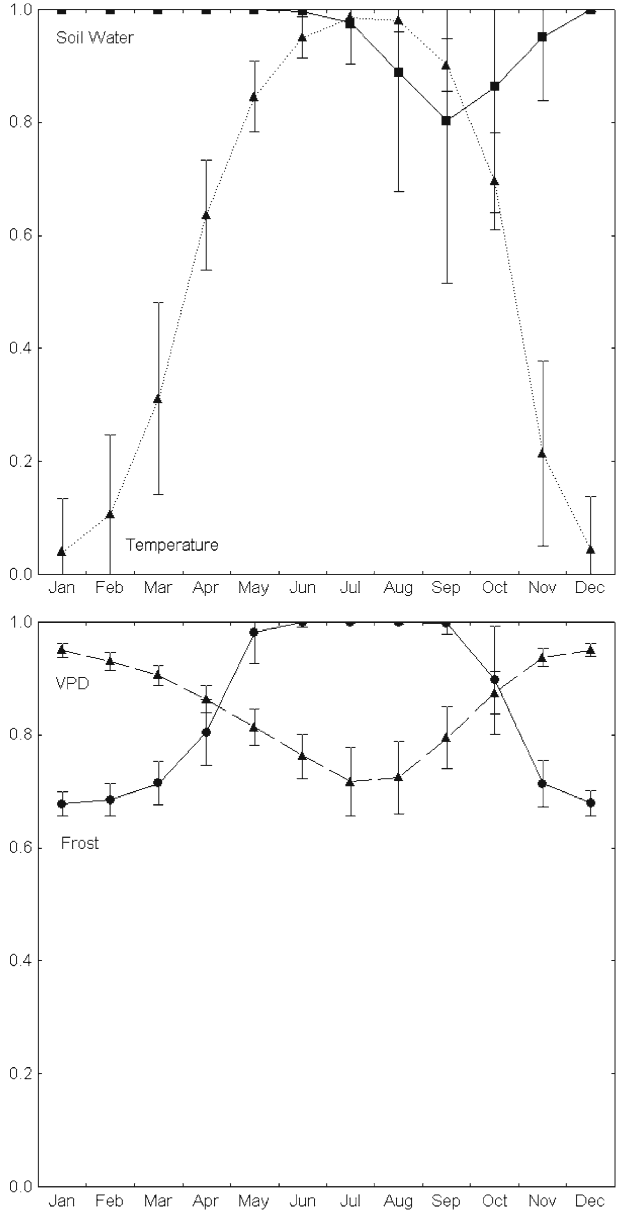


Fig. 1 **a**–**d** Spatial variation in the climatic modifiers as they constrain photosynthesis on lodgepole pine. All the modifiers are scaled between 0 and 1, where 1 indicates optimum conditions for photosynthesis, and 0 indicates complete shutdown for at least one month out of each year. **a** Soil water storage **b** evaporative demand (VPD), **c** temperature and **d** limitations imposed by frost

December too low to permit photosynthesis. Over most of the region in the summer months, the temperature averages slightly, to considerably below optimum (15°C) for habitats with lodgepole pine present (<0.9 selected by the decision-tree). The

Fig. 2 **a**, **b** Temporal trajectories of the environmental modifiers on a monthly time-step **a** temperature and soil water modifier, **b** Frost and VPD



soil water modifier is the most significant restrictor with up to 50% limitation on photosynthesis in September when soil drought peaks. Available soil water varies the most spatially among all climatically related variables, and August through to October represent the most critical months. Frost and VPD follow a similar pattern to temperature (Fig. 2c, d), but are less important than suboptimal temperatures. Frost restricts photosynthesis in the winter months by up to 30% in some places;

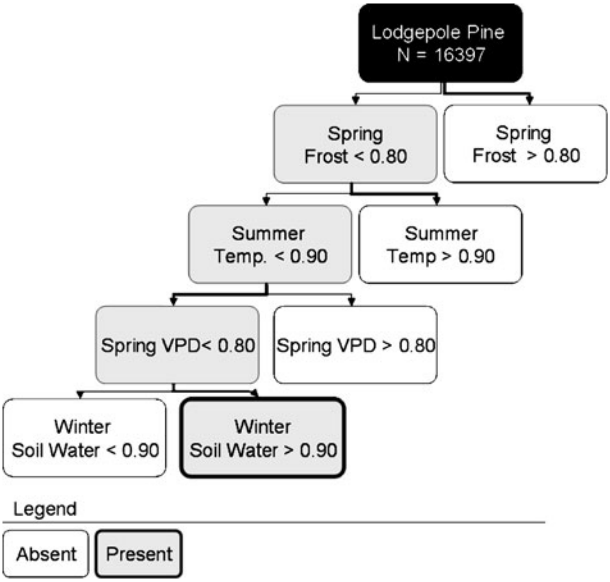


Fig. 3 Decision tree developed to predict presence and absence of lodgepole pine, based on the maximum effect of the four seasonal climate modifiers

VPD imposes a similar restriction of photosynthesis between June and July when the potential for photosynthesis is much higher.

To map the implications of the above-mentioned climatic restrictions on lodgepole pine distribution, we developed a decision tree that takes into account the relative importance of the four climate modifiers on photosynthesis throughout the year, (Fig. 3). The first decision rule is based on spring frost, with sites experiencing limited frost (15% of the plot database) likely to favour other species less tolerance than lodgepole pine (Cochran and Bersten 1973). The second decision separates an additional 15% o sites as having an absence of lodgepole pine based on summer temperature, with sites averaging less than optimum (15°C) the most common, i.e.,<0.9. A third separation is made to include only those sites where the spring VPD modifier is <0.80 (9% of sites removed using this decision), and among those selected, a further delineation is based on the winter soil water modifier of >0.90 indicating that the sites with lodgepole pine normally recharge the soil profile in winter through rain or snowmelt (13% of sites fail this final decision). Although a number of seasonal modifiers were used in the decision tree analysis, their importance differs with spring frost and summer temperature together accounting for 70% of the predictive power of the decision-tree analysis.

Accuracy assessments of the model produced similar results whether the data sets were for training or for validation (Table 2). Accuracies are referenced to

Table 2 Accuracy of the decision tree using training and validation data

N = 16397	Absence (%)	Presence (%)	Overall (%)
Training	63	74	68.5
Validation	64	73	68.5

the percentage of plots on which lodgepole pine was correctly assigned as being present or absent, and then combined into a weighted value, proportionately to the number of plots associated with each of the two categories. The overall accuracy of the validation model was 69%. The location of the presence/absence survey data plots are shown in Fig. 4a and a graphic representation of species distribution based on Little (1971) is presented in Fig. 4b. Figure 5a shows the model prediction of the current species' distribution. In general, the predictions were in agreement with Little's maps, and other bioclimatic simulations such as those of Sykes (2001), although the distribution of the coastal subspecies *Pinus contorta* var. *contorta* was not captured.

With some confidence in our model predictive powers using current climate, we applied the decision-tree analysis to climate projections to assess lodgepole pine distribution in the 30-year periods centered, respectively, on the decades 2020, 2050 and 2080. Figure 5b–d indicates that the species is likely to undergo large shifts from its current range over the next century. With projected increasing warming over the rest of the century, without a commensurate large increase in precipitation, the environment will be both too warm and too dry for lodgepole pine to compete well with other Northwest tree species. By 2020 the decision-tree model predicts an 8% decrease in the area suitable for the pine (approximately 8,000 km^2) with most of its range remaining intact. By 2050, however, a significant reduction in the species distribution is projected, particularly in central Oregon and central Washington (Fig. 5c). In British Columbia, large areas on the western side of the Rockies are projected to be unsuitable for lodgepole pine. By 2080, the species is projected to

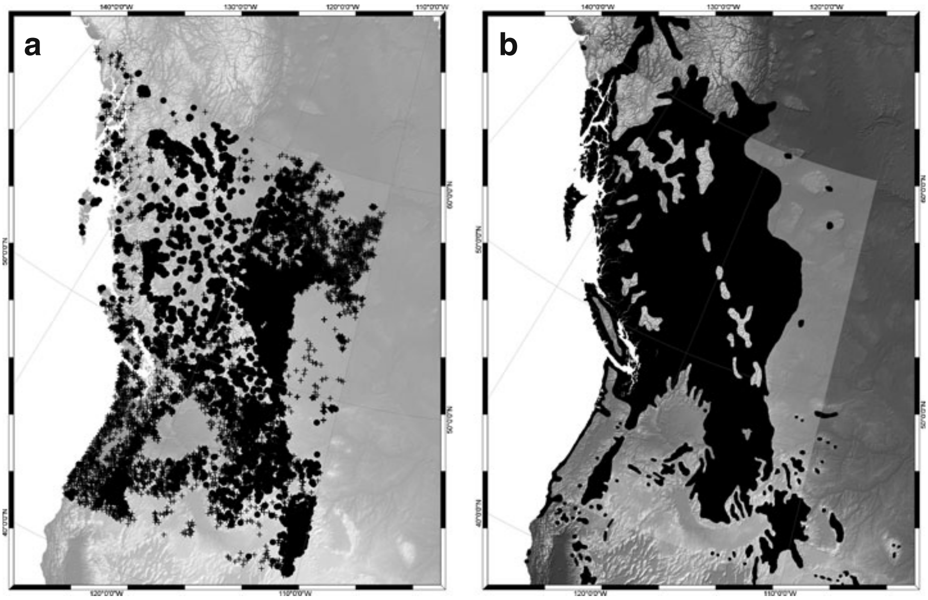


Fig. 4 The location of the presence/absence survey data plots and graphic representation of species distribution based on Little (1971)

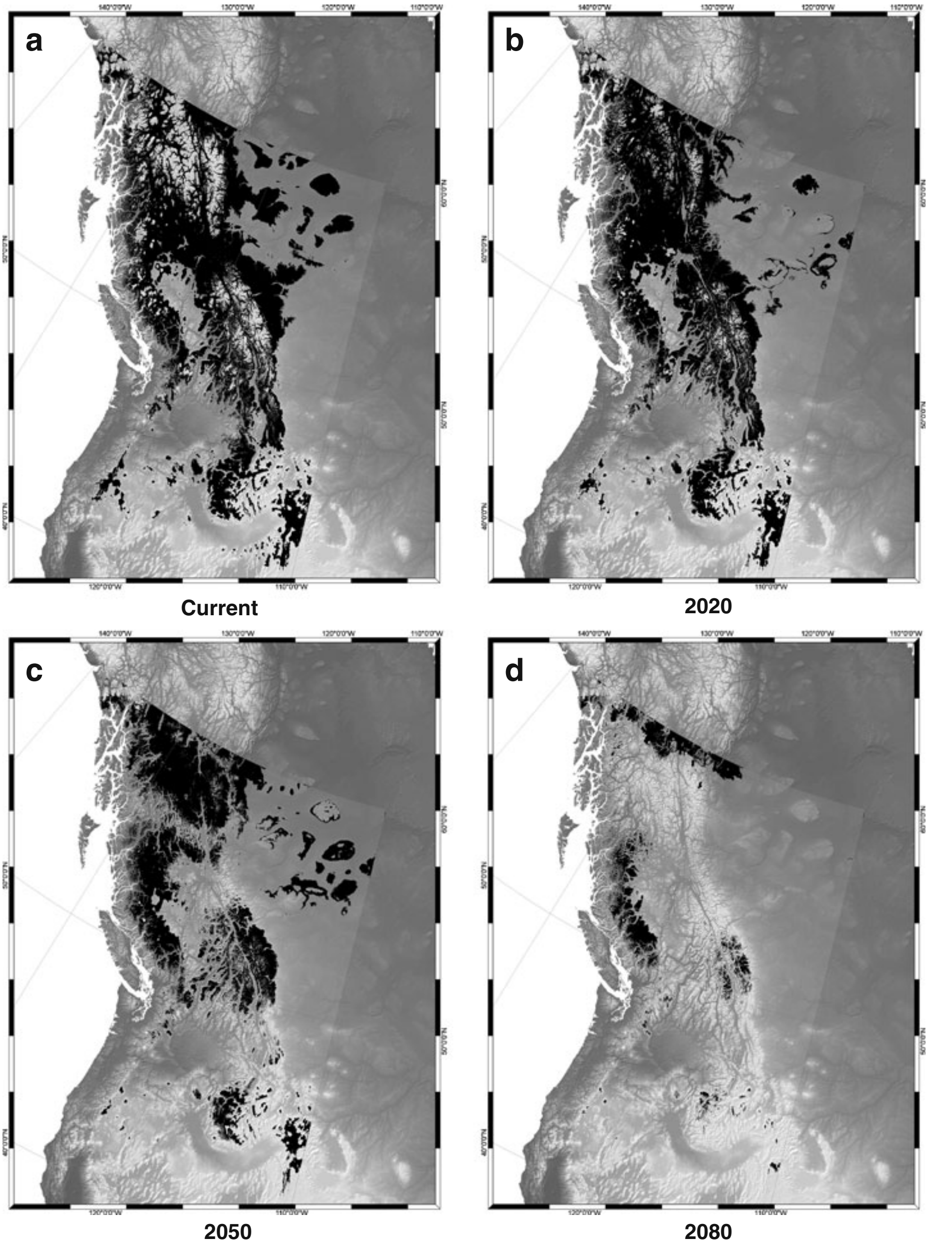


Fig. 5 **a–d** Prediction of lodgepole pine distribution under current climate and the three future 30-year periods: 2020, 2050 and 2080

be almost absent from Oregon, Washington and Idaho. Even in British Columbia and Alberta, the species' range is likely to be reduced significantly (Fig. 5d). The total area deemed suitable for the pine in the 2080 period is projected to be only 15,000 km^2, 17% of its current distribution. Of this area, 75% is currently modeled to occupy lodgepole pine, with the remaining 25% of the projected area, new habitat for the species.

4 Discussion

To undertake this analysis, we needed to project both current and future climatic conditions across the Pacific NW region in an appropriate form, and at a spatial resolution (1 km^2) to match model requirements with the accuracy of biological information available from ground-based survey plots. We utilised decision-tree analysis because of its efficiency and transparency in recognizing those physiological variables and the thresholds that define the climatic conditions within which lodgepole pine appears able to compete currently with other tree species. We believe the resulting accuracies of the approach, both with respect to the validation data, as well with the polygon comparisons of existing distributions, are encouraging and provide a reasonable basis for assessment of potential shifts in the species' range under an array of future climates.

In this paper, we applied the CGCM2 (Flato et al. 2000) scenario predictions based on the A2 scenarios, which is considered close to the upper bound of the SRES scenarios. The projections are in general agreement with other studies. Monserud et al. (2008) utilized three GCM climate outputs (CGCM2, UK Hadley Centre and the Max Plank Institute) and found all three predicted similar trends of changing climate over the next 100 years across Alberta. Mote et al. (2005b) compared the ability of 10 global climate models to track recently recorded trends in temperature and precipitation in the Pacific Northwest and reported that the Canadian model was consistent in predicting a relatively rapid rate in warming and increases in precipitation when compared to actual observations.

Monserud et al. (2008) modelled changes in lodgepole pine distributions using a number of climate scenarios including the same Canadian climate scenario, within Alberta, and predicted very similar patterns to ours in lodgepole pine distribution through time, noting a slight increase in the potential distribution in 2020 but a significant decrease by the end of the twenty-first century. McKenney et al. (2007) in a detailed study defined the current climatic niches for 130 North American tree species and then assess the conditions of these niches on maps of predicted future climate. For lodgepole pine, under the same climatic scenario, maps showed the niche of the species reducing significantly in Washington, Oregon and Alberta and in the interior of British Columbia. The species increased its niche by 2080 into the northeast corner of British Columbia and portions of the Yukon.

We believe that the Canadian climate model scenario provides an appropriate demonstration of the methodology to link process-based model of forest growth to future climate scenarios.

A warming trend should increase drought stress, even without a decrease in precipitation. With warming, there should be less frost and potentially a longer growing season, which could prove advantageous to more drought-adapted Northwest species such as ponderosa pine, Douglas-fir, and western larch. We did not include the effects of increasing atmospheric CO_2 concentrations in this analysis, although we recognize that continual increases in atmospheric CO_2 are expected and could enhance photosynthesis and water-use efficiency (Marshall and Monserud 1996). In areas likely to encounter increased drought, we would, expect little response to rising atmospheric concentrations in CO_2 (Eamus and Jarvis 1989).

From our analysis, projected climatic changes are likely to be increasingly unfavourable for lodgepole pine. But, with any study that predicts the future distribution of species, caveats are required. One caveat is that simply because climatic conditions may favour other species is no guarantee that they will replace lodgepole pine. Other variables such as landscape connectivity and seed availability could prevent replacement by other species (Iverson and Prasad 2001). Another major consideration is whether the normal patterns of disturbance will persist under a changing climate. Many studies predict an increase in fire and insect infestation associated with increased temperature and water stress (Flannigan et al. 2005; Kurz et al. 2008). In addition, we recognize that lodgepole pine has considerable genetic variability across its range (Rehfeldt et al. 1999; Sykes 2001) all of which was subsumed to simplify the analysis presented in this paper but deserved consideration (Stape et al. 2004).

Acknowledgements Funding for this research was provided in part by the NSERC Strategic Project: STPGP 336174-06, Foothills Model Forests Funding provided by the Grizzly Bear Program of the Foothills Research Institute located in Hinton, Alberta, Canada (http://www.fmf.ab.ca) and by NASA grant NNXO9AR59G. We thank colleagues from the Canadian Forest Service (Pacific Forestry Centre), Natural Resources Canada, Victoria, British Columbia, Canada for providing valuable advice in model calibration and model application. We thank Dr Todd Schroeder for development of the global radiation surfaces, Dr Tongli Wang (UBC) and Dr Andreas Hamann (UA) for derivation of the climate surfaces, Dr Michael Wulder and Dr Gordon Stenhouse for methodological advice and encouragement and Raphael Roy-Jauvin for editorial assistance. Plot data in Alberta and British Columbia was compiled by Dr Andreas Hamann (UA) and from FIA data by Dr Todd Schroeder.

References

Almeida AC, Landsberg JJ, Sands PJ (2004) Parameterisation of 3-PG model for fast-growing *Eucalyptus grandis* plantations. Ecol Manag 193:179–195

Austin MP (1985) Continuum concept, ordination methods and niche theory. Ann Rev Ecolog Syst 16:39–61

Barrow EM, Yu G (2005) Climate scenarios for Alberta. A report prepared for the Prairie Adaptation Research Collaborative (PARC) in co-operation with Alberta Environment, University of Regina, Saskatchewan. http://www.parc.ca/research_pub_scenarios.htm

Bechtold WA, Patterson PL (2005) The enhanced forest inventory and analysis program—national sampling design and estimation procedures. General Technical Report SRS-80, US Department of Agriculture, Forest Service, Southern Research Station, Ashville, NC, US

Berry PM, Dawson TP, Harrison PA, Pearson RG (2002) Modelling potential impacts of climate change on the bioclimatic envelop e of species in Britain and Ireland. Glob Ecol Biogeogr 11: 453–462

Breiman L, Friedman JH, Olshen RA, Stone CG (1984) Classification and regression trees. Wadsworth International Group, Belmont

Cochran PH, Bersten CM (1973) Tolerance of lodgepole and ponderosa pine to low night temperatures. Science 19:272–280

Coops NC, Waring RH, Landsberg JJ (1998) Assessing forest productivity in Australia and New Zealand using a physiologically-based model driven with averaged monthly weather data and satellite derived estimates of canopy photosynthetic capacity. Ecol Manag 104:113–127

Coops NC, Waring RH, Schroeder T (2009) Combining a generic process-based productivity model and a statistical classification method to predict presence and absence of tree species in the Pacific Northwest, U.S.A. Ecol Model 220:1787–1796

Critchfield WB, Little EL Jr (1966) Geographic distribution of the pines of the world' US Department of Agriculture Miscellaneous Publication 991, pp 1–97

De'ath G (2002) Multivariate regression trees: a new technique for modeling species–environment relationships. Ecology 83:1105–1117

Dye PJ, Jacobs D, Drew D (2004) Verification of 3-PG growth and water-use prediction in twelve Eucalyptus plantation stands in Zululand, South Africa. Ecol Manag 193:197–218

Eamus D, Jarvis PJ (1989) The direct effects of increases in global atmospheric CO_2 concentration on natural and commercial temperate trees and forests. Adv Ecol Res 19:2–56

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. Science 289:2068–2074

Elith J, Graham CH, Anderson RP (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151

Flannigan MD, Logan KA, Amiro BD, Skinner WR, Stocks BJ (2005) Future area burned in Canada. Clim Change 72:1–16

Flato G, Boer GJ, Lee WL, McFarlane NA, Ramsden D, Reader MC, Weaver AJ (2000) The Canadian centre for climate modelling and analysis global coupled model and its climate. Clim Dyn 16:451–467

Green RN, Marshall PL, Klinka K (1989) Estimating site index of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) from ecological variables in southwestern British Columbia. Science 35: 50–63

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186

Hall RJ, Price DT, Raulier F, Arsenault E, Bernier PY, Case BS, Guo X (2006) Integrating remote sensing and climate data with process-based models to map forest productivity within west-central Alberta's boreal forest: Ecoleap-West. For Chron 82:159–176

Hamann A, Wang T (2005) Models of climatic normals for genecology and climate change studies in British Columbia. Agric Meteorol 128:211–221

Hijmans R, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. Glob Chang Biol 12:2272–2281

Hu J, Moore DJP, Burns SP, Monson RK (2009) Longer growing seasons lead to less carbon sequestration by a subalpine forest. Glob Chang Biol 16:771–783. http://www3.interscience.wiley.com/journal/122377223/abstract?CRETRY=1&SRETRY=0

IPCC (2001) Intergovernmental panel on climate change. Cambridge University Press, Cambridge. http://www.ipcc.ch/pub/online.htm

Iverson LR, Prasad AM (1998) Predicting abundance of 80 tree species following climate change in the eastern United States. Ecol Monogr 68:465–485

Iverson LR, Prasad AM (2001) Potential changes in tree species richness and forest community types follow climate change. Ecosystems 4:186–199

Kimball JS, Running SW, Nemani R (1997) An improved method for estimating surface humidity from daily minimum temperature. Agric Meteorol 85:87–98

Knowles N, Dettinger MD, Cayan DR (2006) Trends in snowfall versus rainfall in the western United States. J Climate 19:4545–4559

Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L (2008) Mountain pine beetle and forest carbon feedback to climate change. Nature 452: 987–990

Landsberg JJ, Waring H, Coops NC (2003) Performance of the forest productivity model 3-PG applied to a wide range of forest types. Ecol Manag 172:199–214

Law BE, Goldstein AH, Anthoni PM, Unsworth MH, Panek JA, Bauer MR, Fracheboud JM, Hultman N (2001) Carbon dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. Tree Physiol 21:299–308

Little EL Jr (1971) Atlas of United States trees, volume 1, conifers and important hardwoods U.S. Department of Agriculture Miscellaneous Publication 1146, 9 pp

McKenney DW, Pedlar J, Hutchinson M, Lawrence K, Campbell K (2007) Potential impacts of climate change on the distribution of North American trees. Bioscience 57:939–948

McKenzie D, Peterson DW, Peterson DL, Thornton PE (2003) Climatic and biophysical controls on conifer species distributions in mountain forests of Washington State, USA. J Biogeogr 30: 1093–1108

Marshall JD, Monserud RA (1996) Homeostatic gas-exchange parameters inferred from 13C/12C in tree rings of conifers. Oecologia 105:13–21

Melendez KV, Jones DL, Feng AS (2006) Classification of communication signals of the little brown bat. J Acoust Soc Am 120:1095–1102

Monserud RA, Yang Y, Huang S, Tchebakova N (2008) Potential change in lodgepole pine site index and distribution under climate change in Alberta. Can J For Res 38:343–352

Mote PW, Hamlet AF, Clark MP, Lettenmaier DP (2005a) Declining mountain snowpack in western North America. Am Meteorol Soc 86:1–39

Mote P, Salathé E, Peacock C (2005b) Scenarios of future climate for the Pacific Northwest. Climate Impacts Group, University of Washington, October 2005. http://cses.washington.edu/db/pdf/kc05scenarios462.pdf. Accessed 3 October 2009

Nightingale JM, Coops NC, Waring RH, Hargrove WW (2007) Comparison of MODIS gross primary production estimates for forests across the U.S.A. with those generated by a simple process model, 3-PG. Remote Sens Environ 109:500–509

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Pearson RG, Dawson TP, Berry PM, Harrison PA (2002) Species: a spatial evaluation of climate impact on the envelope of species. Ecol Model 154:289–300

Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton DA Jr (1999) Genetic responses to climate in *Pinus contorta*: niche breadth, climate change and reforestation. Ecol Monogr 69:375–07

Rodriguez R, Espinosa M, Real P, Inzunza J (2002) Analysis of productivity of radiata pine plantations under different silvicultural regimes using the 3-PG process-based model. Aust For 65: 165–172

Root TL, Price JT, Hall KR (2003) Fingerprints' of global warming on animals and plants. Nature 421:57–60

Sands PJ, Battaglia M, Mummery D (2000) Application of process-based models to forest management: experience with ProMod, a simple plantation productivity model. Tree Physiol 20:383–392

Schwalm CR, Black TA, Amiro BD, Arain MA, Barr AG, Bourque CP, Dunn AL, Flanagan LB, Giasson MA, Lafleur PM, Margolis HA, McCaughey JH, Orchansky AL, Wofsy SC (2006) Photosynthetic light use efficiency of three biomes across and east-west continental-scale transect in Canada. Agric Meteorol 140:260–286

Schroeder TA, Hember R, Coops NC, Liang S (2009) Validation of incoming shortwave solar radiation surfaces for use in forest productivity models. J Appl Meteorol Climatol 48:2331–2458

Schroeder TA, Hamann A, Coops NC, Wang T (2010) Occurrence and dominance of six Pacific Northwest conifer species. J Veg Sci 23(3):586–596

Stape JL, Ryan MG, Binkley D (2004) Testing the utility of the 3-PG model for growth of *Eucalyptus grandis xurophylla* with natural and manipulated supplies of water and nutrients. Ecol Manag 193:219–234

Swenson JJ, Waring RH, Fan W, Coops NC (2005) Predicting site index with a physiologically based growth model across Oregon, USA. Can J For Res 35:1697–1707

Sykes MT (2001) Modelling the potential distribution and community dynamics of lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) in Scandinavia. Ecol Manag 141:69–84

Thuiller W, Albert C, Araujo MB, Berry PM, Cabeza M, Guisan A, Hickler A, Midgley GF, Paterson J, Schurr FM, Sykes, Zimmermann NE (2008) Predicting global change impacts on plant species' distributions: future challenges. Perspect Plant Ecol Evol Syst 9:137–152

Waring RH (2000) A process model analysis of environmental limitations on growth of Sitka spruce plantations in Great Britain. Forestry 73:65–79

Wang G, Huang S, Monserud RA, Klos RJ (2004) Lodgepole pine site index in relation to synoptic measures of climate, soil moisture and soil nutrients. For Chron 80:678–686

Whitehead RJ, Russo GL (2005) Beetle-proofed lodge pole pine stands in interior British Columbia have less damage from mountain pine beetle. Natural Resources Canada. Canadian Forest Service. Victoria BC Information Report BC-X-402

Williams JW, Jackson ST, Kutzbach JE (2007) Projected distributions of novel and disappearing climates by 2100 AD. Proc Natl Acad Sci U S A 104:5738–5742