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Models of climatic normals for genecology and climate change studies in British Columbia

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Abstract

Maps of interpolated climate normals have recently become essential tools for many types of forestry research, such as studying genetic adaptation of trees to local environments, modeling species ranges shifts, or forest productivity under climate change scenarios. In this paper, we evaluate two widely used climate models for British Columbia with respect to their general precision and regional bias. We discuss limitations due to the resolution of the current "state of the art" PRISM climate model and provide new methodology for "intelligent" up-sampling of the PRISM model for studies that require spatially explicit climate data. In order to stress the importance of choosing an adequate climate model and understanding its limitations, we provide two examples where baseline climate models caused misleading predictions of how the climate envelope of ecosystems shifts as a consequence of increased temperature, and how tree growth may respond to climate change.

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1. Introduction

Maps of interpolated climate normals have become essential tools for many types of forestry research in recent years. Climate normals are calculated from weather station data and are defined as the arithmetic mean of weather measurements over three consecutive decades (WMO, 1989). They represent long-term baseline information for various modeling purposes

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and have recently been used for ecosystem mapping (Gould et al., 2002; Host et al., 1996; Masson et al., 2003; Simpson et al., 2002), modeling of potential habitat of tree species and species ranges shifts under climate change scenarios (Dirnbock et al., 2003; Eeley et al., 1999; Iverson and Prasad, 1998), assessing forest productivity under current and potential future climates (Lindner et al., 2002; McKenney and Pedlar, 2003; Rehfeldt et al., 2001) identifying sample locations for in situ and ex situ conservation efforts (Greene et al., 1999; Guarino et al., 2001; Jones et al., 1997; Segura et al., 2003) assessing the risk of establishment of invasive species (Welk et al., 2002)

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investigating adaptation of forest trees to local climatic conditions (Rehfeldt, 1995; Rehfeldt et al., 2002, 1999), and matching tree planting stock to their optimal environment (McKenney et al., 1999; Parker and vanNiejenhuis, 1996).

Until relatively recently many researchers used climate normal information from nearby weather stations for their area of interest or relied on hand drawn climate maps (Custer et al., 1996; Sykes and Prentice, 1995; Talkkari and Hypen, 1996). However, a variety of statistical and other methods are now available to obtain spatially explicit climate data in digital format. Multiple regression has been used to predict climate for a given latitude, longitude and elevation (Goodale et al., 1998; Rehfeldt, 1995; Rehfeldt et al., 2001). More complicated climate surfaces were obtained with simple interpolation techniques (Brown and Comrie, 2002; Nalder and Wein, 1998; Price et al., 2000). Kriging, an optimal interpolation technique for certain types of data, seems to works well although climate data usually violates certain assumptions of this method (Agnew and Palutikof, 2000; Brown and Comrie, 2002; Nalder and Wein, 1998). Also, spline interpolation, which is similar to kriging, appears to be a suitable alternative in many cases (Fleming et al., 2000; McKenney et al., 2001; Price et al., 2000).

An advanced alternative is commercially available gridded climate data for the United States and Canada (Daly et al., 2000). These datasets are generated by an expert method called PRISM (parameter-elevation regressions on independent slopes model). Like all interpolation techniques, PRISM calculates the value of a target grid cell by assigning a combined weight to each weather station observation, which is a function of distance from the target, elevation difference to the target, and other factors. However, PRISM also uses "facets" to identify local climate regimes delineated by topographic and other terrain features (Daly et al., 2002). For example, rain shadows can be identified through leeward exposures of mountain ranges. Stations on the same facet as the target grid cell are given highest weight in the interpolation. The authors call this method "knowledge based" because it allows climatologists to define "facets" to accommodate known climatic anomalies in difficult mapping situations.

In order to make PRISM data available to other researchers, grids of climate variables that are

compatible with geographical information systems are generated. These are commercially available at 1.25 arcmin resolution, and some data is provided free of charge on the Internet at a 2.5 arcmin resolution. In British Columbia, there has been some reluctance to use this gridded data because of its low resolution in mountainous terrain. A 2.5 arcmin tile corresponds to an area of approximately 4.6 km \times 3.0 km in southern BC, which can easily span an elevation range of 1000 m or more. For studies that investigate adaptation of trees to climates over elevational gradients of a few 100 m, this data appears to be unusable, and it has been argued that climate data at about 50 m × 50 m grid size would be necessary. Province-wide datasets at this resolution would, however, be excessively large (380 million tiles) and it has been suggested that simple regression equations derived by Rehfeldt et al. (1999) will be more suitable than PRISM data for mountainous regions in British Columbia.

In this paper we compare one of the simplest climate models with PRISM methodology and explore both model's limitations by calculating regional bias, error of the estimate, and the amount of variance they explain in original weather station data. Further, we provide two solutions for using PRISM data in mountainous terrain: (1) by using a PRISM derived equation based on latitude, longitude and elevation (2) by using an elevation adjustment for PRISM data based on the difference between the PRISM tile elevation and the observed elevation. In order to stress the importance of using good spatial climate data, we provide two examples of common climate change impact studies, where inadequate climate models caused misleading results. The first example is a bioclimate envelope study, where insufficient resolution of climate data in mountainous terrain leads to over-estimates of climate change impacts. The second case study provides a rather counter-intuitive example of how inadequate climate models caused misleading results regarding adaptation of a tree species to local climatic conditions.

2. Methods

2.1. Climatic data and variables

We used PRISM datasets at 1.25 and 2.5 arcmin resolution including average monthly temperatures,

average minimum and average maximum monthly temperatures, and monthly precipitation data. For this study we selected eight biologically relevant variables that Rehfeldt et al. (1999) previously used, and that could also be calculated from PRISM data: mean annual temperature (MAT), mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), mean annual precipitation (MAP) and mean summer precipitation (MSP). Three additional variables describing aridity and continentality are derived: summer heat:moisture index (SH:M) was calculated as mean temperature of the warmest month divided by summer precipitation in units of meters. Annual heat:moisture index (AH:M) was calculated as mean annual temperature plus 10 °C (to obtain positive values) divided by mean annual precipitation in meters. Continentality or temperature difference (TD) was calculated by subtracting the mean temperature of the coldest month from the mean temperature of the warmest month. Note that MAT, MCMT and MWMT are based on the average monthly maximum and minimum values of the PRISM dataset. Mean summer precipitation was calculated as the sum of monthly precipitation from May to September.

2.2. Elevation adjustment for PRISM data

PRISM provides predictions of climate variables for the average elevation of a 1.25 or 2.5 arcmin tile derived from 30 arcsec elevation data (LPDAAC, 2003). If there is a considerable difference between the average tile elevation and the location of interest (e.g., a sampling location or a test site), PRISM data will not give a good estimate of temperature variables for this particular location. We used the same regression approach as Rehfeldt et al. (1999) to estimate climate variables as a function of latitude, longitude and elevation except using PRISM climate data as independent observations instead of weather station data (of course these approximately 80,000 interpolated observations are not independent). Then, we took the first derivative of this equation to obtain the rate of change in a temperature variable in response to a change in elevation for any given latitude, longitude and elevation. This formula was then re-arranged to obtain an adjustment for a temperature variable as a function of the difference between the observed elevation and the PRISM tile elevation.

2.3. Testing models and adjustments with weather station data

Climate normals for the period 1961-1990 from 440 weather stations in British Columbia (Environment Canada 1994) were used to investigate how well models with and without elevation adjustment predict actually observed climate. While no statistical methodology exists to obtain an error estimate of predicted climate variables for regions of British Columbia that are not covered by weather stations, we attempted an "educated guess" how large the error of predictions might be by investigating the difference between actual and predicted climate at weather stations summarized for different climate regions. For this purpose, we used the biogeoclimatic ecological classification (BEC) system, which delineates the extent of different forest ecosystems in British Columbia (Meidinger and Pojar, 1991). The classification system is thought to delineate relatively homogeneous climatic conditions at the sub-zone level.

2.4. Example 1: Climate envelope modeling

Bioclimate envelope studies are a popular method to assess climate change impacts. Usually, biological sample data is used to generate a predictive model for a species distribution based on climate variables (Thuiller, 2003). Alternatively, mapped species ranges or ecosystems can be characterized with respect to their climatic envelope using geographical information systems (GIS). Here, we compare the climate envelopes of British Columbia's ecosystems using a spatial coverage of the biogeoclimatic ecological classification system rasterized at 1.25 arcmin as well as 400 m resolution according to the zone found at the tile center. The low resolution (1.25 arcmin) coverage is characterized with original PRISM data at matching resolution, and for the high resolution (400 m) model we use elevation adjusted PRISM data employing the methodology described above. Then, standard discriminant analysis (SAS Institute and Inc., 2000) was used as a predictive model, where observations (tiles with eight climate variables) are assigned to groups (BEC zones) based on the Mahalanobis distance between an observation and the mean vector of the closest group (which may not necessarily be the original BEC zone).

2.5. Example 2: Productivity of lodgepole pine

As a second example of how different climate models might affect research results, we investigated productivity of lodgepole pine seed sources from one of the commercially most important seed planning zones, Prince George-low elevation. These seed sources are the most comprehensively tested group of provenances in the lodgepole pine genotype-environment interaction study of Illingworth (1978). We used 20-year height data of trees grown at 32 test environments and regress them over model derived climatic normals for these test sites using a seconddegree polynomial function. The resulting response function of growth variables to environmental variables is commonly used to find the optimal planting environment for a genotype or seed source or to predict the impact of climate change on productivity of forest plantations. This example was based on the same data and methodology as (Rehfeldt et al., 2001, 1999) to which the reader should refer for more experimental detail and complete data analysis.

3. Results and discussion

3.1. Expected error or bias of climate models

When a count of weather stations is mapped for each of 96 sub-zones of the biogeoclimatic ecological classification system, it becomes apparent that a large portion of the land base is not adequately covered (Fig. 1). Almost, two-third of the total area is represented by less than three stations per BEC subzone. Most of the 440 available stations are located on the coast and in the interior valleys. An unbalanced distribution of sample points can be problematic. For example, an equation based on 30 sample points for region A and three sample points for region B may lead to a considerable bias when predicting values for region B. For a portion of the land base (high elevation and northern regions) spatial climate models even predict variables completely outside their sampling range, where errors of the estimate cannot be calculated.

As an indicator of the overall error and regional bias of models, we investigate the absolute difference between predicted and observed climate at weather

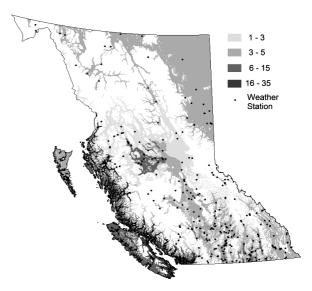


Fig. 1. Count of weather stations in sub-zones of the biogeoclimatic ecological classification system of British Columbia, representing climatically relatively homogeneous regions.

stations (Table 1). These deviations are then regressed over regional weather station coverage (Fig. 2). The intersection with the *y*-axis indicates an approximate error for regions that are not covered by weather stations, and the slope of the regression indicates how much the model's precision depends on good weather station coverage. We find that for temperature related variables and Rehfeldt's equations perform surprisingly well. The average and maximum errors are smaller (Table 1) and the slope of the regression line is always closer to zero (Fig. 2) indicating more precise predictions for areas with sparse weather station

Table 1 Average deviation and maximum deviation (in parethesis) of predicted climate variables from observed weather station data (as in Fig. 2)

Climate	Rehfeldt	PRISM	Elevation	
variable	equations	data	adjusted	
MAT (°C)	0.5 (2.7)	0.8 (4.0)	0.6 (3.5)	
MWMT (°C)	0.8 (5.9)	1.1 (13.9)	0.8 (6.9)	
MCMT (°C)	1.1 (7.5)	1.3 (10.2)	1.2 (7.6)	
TD (°C)	1.4 (8.4)	1.6 (10.9)	1.2 (7.8)	
MAP (mm)	403 (1927)	99 (945)	n/a	
MSP (mm)	87 (653)	38 (321)	n/a	
AH:M	8 (68)	3 (28)	2 (26)	
SH:M	23 (179)	11 (84)	9 (77)	

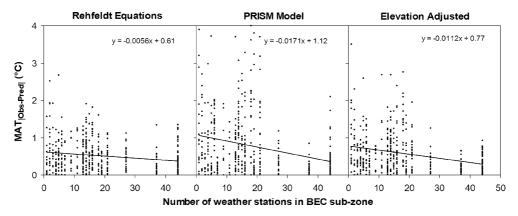


Fig. 2. Deviation of predicted MAT from observed values at weather stations (see also Table 1). Deviations are regressed as a function of regional weather station coverage. The intersection with the y-axis is used to derive an "educated guess" for the magnitude of errors for regions not covered by weather stations (as shown in Fig. 3).

coverage. The PRISM model, however, outperforms Rehfeldt's equations for precipitation related variables by a large margin.

In order to investigate if a portion of these deviations is actually spatial bias we displayed them on a map (Fig. 3). A random error should show a random pattern of over- and under-estimates, while bias could be detected by geographic patterns in the values for the 96 sub-zones. It appears that Rehfeldt equations provide unbiased temperature estimates for most of the province (Fig. 3a) whereas the PRISM model under-estimates temperature at lower elevations in montane regions (Fig. 3b). This, and presumably an over-estimate of temperatures at high elevations, is due to the tile size of PRISM data, which fails to accurately represent mountainous terrain. PRISM also somewhat over-estimates precipitation at higher elevation (Fig. 3d) but performs better than the Rehfeldt model, which severely under-estimates precipitation at high elevations and on the coast, while over-estimating it in the interior plateau of British Columbia (Fig. 3c).

3.2. Elevation adjustment and explained variance

In order to eliminate regional bias in PRISM predictions that arises from tile size as shown above, we developed formulas from original PRISM data to adjust temperature predictions for specific locations with known elevation. The independent variables latitude (Lat), longitude (Long) and elevation (Elev) and their various combinations were retained in the

model if they contributed at least 1% to the variance explained. It should be noted that there is no danger in retaining too many variables because the objective is to obtain a close match to a continuous surface of samples that are not independent. The equations and their first derivatives are given below, where $\delta_{\rm Elev}$ is the actual elevation minus the PRISM tile elevation in meters, and latitude and longitude are entered as positive values in decimal degrees. 1

$$\begin{split} \text{MAT} &= 49.216 + 5.59 \times 10^{-4} \times \text{Lat} \times \text{Elev} \\ &- 0.958 \times \text{Lat} - 0.0183 \times \text{Elev} + 4.19 \\ &\times 10^{-6} \times \text{Long}^3 - 2.29 \times 10^{-6} \times \text{Lat} \\ &\times \text{Long} \times \text{Elev} \end{split} \tag{1}$$

$$\text{MWMT} = 78.3 - 0.691 \times \text{Long} - 0.0121 \\ &\times \text{Elev} + 2.946 \times 10^{-11} \times (\text{Lat} \\ &\times \text{Long})^3 + 6.661 \times 10^{-5} \times \text{Long} \\ &\times \text{Elev} + 357 \times \text{Long} \times \text{Lat}^{-2} \tag{2} \end{split}$$

$$\text{MCMT} = -264.32 + 0.0515 \times \text{Elev} + 6.584 \\ &\times \text{Lat} + 2.254 \times \text{Long} - 0.072 \\ &\times \text{Lat} \times \text{Long} - 0.0233 \times \text{Lat}^{-1} \\ &\times \text{Long} \times \text{Elev} + 5.444 \times 10^{-5} \\ &\times \text{Long}^3 \tag{3} \end{split}$$

¹ A program performing these calculations can be obtained at: http://www.genetics.forestry.ubc.ca/cfgc/climate-models.html.

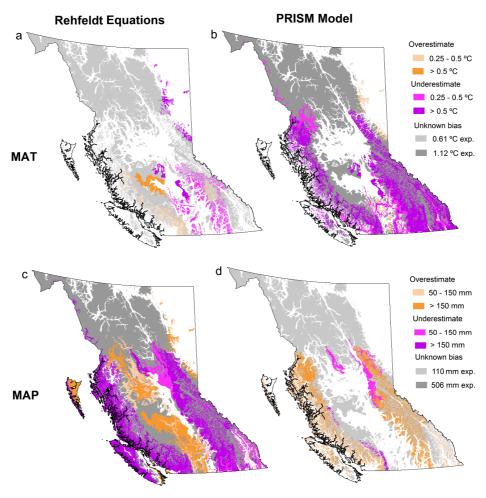


Fig. 3. Over- and under-estimates of mean annual temperature (MAT) and mean annual precipitation (MAP) for BEC sub-zones. White areas are unbiased. Grey areas lack weather stations and an estimated bias derived from Fig. 2 is indicated instead.

$$\delta_{\text{MAT}} = \delta_{\text{Elev}} \times (-0.0183 + 5.59 \times 10^{-4} \times \text{Lat}$$
$$-2.29 \times 10^{-6} \times \text{Lat} \times \text{Long}) \tag{4}$$

$$\delta_{\text{MWMT}} = \delta_{\text{Elev}} \times (-0.0121 + 6.661 \times 10^{-5} \times \text{Long})$$
 (5)

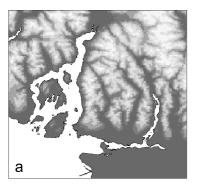
$$\delta_{\text{MCMT}} = \delta_{\text{Elev}} \times (0.0515 - 0.02325 \times \text{Lat}^{-1}$$

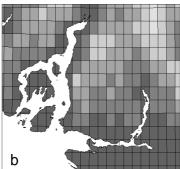
$$\times \text{Long}) \tag{6}$$

The first three formulas may be used as an alternative to Rehfeld's equations, although they are not optimized to explain the maximum variance in weather station data (Table 2). Eqs. (4)–(6) should be used to

Table 2 Variance explained by climate models and adjustments in weather station data

Climate	Rehfeldt	PRISM	PRISM	Elevation
variable	equations	equations	data	adjusted
MAT (°C)	0.96	0.92	0.88	0.95
MWMT (°C)	0.81	0.64	0.71	0.86
MCMT (°C)	0.95	0.89	0.93	0.95
TD (°C)	0.91	0.86	0.95	0.95
MAP (mm)	0.59	n/a	0.94	n/a
MSP (mm)	0.42	n/a	0.87	n/a
AH:M	0.34	0.93	0.93	0.93
SH:M	0.36	0.87	0.90	0.91





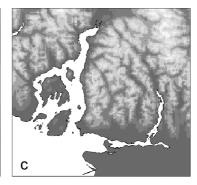


Fig. 4. Models of mean annual temperature for a $50 \text{ km} \times 50 \text{ km}$ tile of the Vancouver area based on polynomial equations (a), 2.5 arcmin PRISM data (b), and PRISM data adjusted for elevation (c).

adjust PRISM climate data for a sample point when its elevation is known. The same formulas may be used to perform "intelligent" up-sampling of PRISM data using a high resolution digital elevation model (DEM). An illustration of regional up-sampling is given in Fig. 4. The left panel applies the mean annual temperature equation to a digital elevation model with a grid size of 400 m. The middle section depicts the original 2.5 arcmin PRISM data, and the right panel shows the PRISM data after elevation adjustment. The elevation adjusted surface (c) is not as smooth as the equation derived surface (a) and sometimes the boundary of tiles can still be seen. This cannot be avoided because there is no simple mathematical relationship how temperature changes from one tile to the next as a function of their difference in elevation. On the other hand, the equation-derived surface generally underestimates the temperature by 0.4 °C for this particular region compared to PRISM (temperature predicted by Rehfeld's equations is on average 0.9 °C lower for this region than PRISM data). Unless the study area is very small and the absolute value is not important, we recommend using the elevation adjustments Eqs. (4)–(6) rather than the Eqs. (1)–(3).

3.3. Variance explained in weather station data

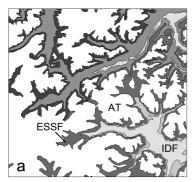
All models explained temperature related variables observed at weather stations rather well, but PRISM was clearly superior to Rehfeld's equations in explaining precipitation related variables (Table 2). Surprisingly, the four times higher resolution 1.25 arcmin PRISM dataset resulted in r^2 -values identical to those of the 2.5 arcmin PRISM model (data not

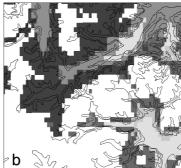
shown). After careful investigation of the 1.25 arcmin PRISM dataset it appears that this is an interpolated version of the 2.5 arcmin dataset, thus providing no additional information. The temperature adjustment using for the PRISM model had a noticeable effect on the explained variance in mean annual temperature and mean warmest month temperatures (last column in Tables 1 and 2, last panel in Fig. 2). Furthermore, bias for montane regions observed in Fig. 3 is removed (maps not shown). One should note that the importance of the elevation adjustment is not well reflected in the amount of variance explained because weather stations are not typically located on steep slopes but in areas where PRISM tile elevation matches actual elevation well (for example, airports and cities). Furthermore, one should keep in mind that this is not an independent test since the same weather station data has been used to develop each model.

Note that various attempts using regional models covering partial areas or various groups of ecosystems in British Columbia did not significantly change or improve elevation adjustment formulas as indicated by r^2 -values in Table 2. This suggests that the polynomial models can be developed for relatively large regions. Further, we did not find elevation adjustment models that resulted in significant improvements of PRISM precipitation variables for selected regions, ecosystems, or full models for British Columbia.

3.4. Example 1: Climate envelope modeling

The climate envelope of ecosystems or species ranges can be described by simple summary statistics of the climate observations they include. For example,





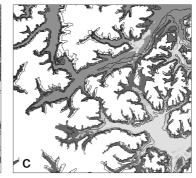


Fig. 5. Ecological zones for a 50 km × 50 km tile of the coast mountains of British Columbia (IDF, interior Douglas-Fir; ESSF, Engelmann Spruce—Subalpine Fir; AT, Alpine Tundra). Mapped zones (a), modeled zones based on 1.25 arcmin PRISM climate data (b), and based on PRISM data adjusted for elevation at 400 m resolution (c).

the interior Douglas-Fir ecosystem, usually located in valleys (Fig. 5a, IDF), has a range of mean annual temperature from 2.7 to 6.9 °C based on original PRISM data, but has a climate envelope of 2.6–8.1 °C using high resolution elevation adjusted data. The corresponding climate envelope for Alpine Tundra ecosystems, covering mountaintops (Fig. 5a, AT) is –3.3 to 1.3 °C before, and –5.3 to 1.2 °C after adjustment. For the mid-slope ecosystem Engelmann Spruce—Subalpine Fir (Fig. 5a, ESSF) the envelope changes from an original –2.2 to 3.1 °C to –2.9 to 3.8 °C after adjustment.

Because PRISM climate variables are based on a considerably smoothed elevation surface, the derived climatic envelopes for ecosystems appear narrower, especially for mountaintop and valley ecosystems. As a consequence, the impact of climate change would generally be over-estimated with insufficient resolution. Using original PRISM data, a predicted increase of 2 °C MAT would imply that 48, 41, and 44% of the future IDF, ESSF, and AT climate envelope would no longer overlap with the current envelope (e.g., IDF: $2 \,^{\circ}\text{C} \times (6.9 - 2.7 \,^{\circ}\text{C})^{-1} \times 100 = 48\%$). With the high-resolution model and elevation adjustment, the estimated shift would only be 36, 30, and 32% for IDF, ESSF, and AT, respectively.

High- and low-resolution climate data also differs in their suitability to generate multivariate predictive models of BEC zones. Using discriminant analysis to assign observations to BEC zones based on eight climate variables leads to more misclassification errors with 1.25 arcmin PRISM data (Fig. 5b) than with 400 m elevation adjusted data (Fig. 5c). The

obvious reason for the poor model fit using original PRISM data is insufficient spatial resolution in mountainous terrain, especially since the commercially available 1.25 arcmin PRISM dataset appears to be an interpolated version of the 2.5 arcmin dataset for British Columbia. Tree species ranges in British Columbia closely follow BEC zone delineations; so similar problems would arise when trying to model species ranges directly from sample data. Results from applying climate change scenarios with this predictive model will be published separately.

3.5. Example 2: Productivity of lodgepole pine

A comparison of elevation adjusted PRISM data and polynomial climate models with respect to modeling productivity of lodgepole pine showed minimal differences with respect to temperature related climate variables (Table 3). Both climate models yield very similar surfaces of temperature variables for British Columbia. However, we expected that significantly improved estimates of precipitation variables of the PRISM model would lead to a better model fit of response functions that describe height growth of lodgepole pine as a result of climate variables at the test site. Surprisingly, the opposite was the case (Table 3). Rehfeldt et al. (1999, 2001) noted that polynomial equations predict precipitation poorly, and we have previously shown that these estimates have indeed a large error of the estimate and strong regional bias (Fig. 2; Table 1). Nonetheless, response functions based on this model show an excellent fit and such models are used to predict performance of

Table 3 The amount of variation explained (r^2) by a single climate variable using a second-order polynomial response function to predict 20-year height (as in Fig. 5)

Climate variable	Rehfeldt equations		Elevation adjusted	
	r^2	P-value	r^2	P-value
MAT (°C)	0.76	< 0.0001	0.74	< 0.0001
MWMT (°C)	0.26	0.0003	0.16	0.0101
MCMT (°C)	0.66	< 0.0001	0.63	< 0.0001
TD (°C)	0.70	< 0.0001	0.53	< 0.0001
MAP (mm)	0.57	< 0.0001	0.21	0.0020
MSP (mm)	0.68	< 0.0001	0.12	0.0498
AH:M	0.23	0.0008	0.05	0.2626
SH:M	0.45	< 0.0001	0.18	0.0040

populations as a function of climate change. However, we suspect that these response functions are artifacts and we use the most pronounced example from Table 3 MSP to investigate this in more detail (Fig. 6).

First, marginal planting environments where lodgepole pine grows poorly (the two ends of the response function) are also environments that have the least coverage by weather stations and the largest errors. Given an expected error or bias of 87 mm, which may sometimes be as high as 653 mm (Table 1), it is obvious that the high and low estimates of MSP on the marginal sites could be entirely due to regional over- and under-estimates of this variable. This creates a highly significant relationship between growth and an environmental variable that looks like a typical response function when there is in fact no relationship

at all (this can easily be modeled starting with a random scatter plot and then applying a larger error to the climate variable for the low performance test sites and a smaller error for the test sites with good performance). When using PRISM climate estimates to analyze the same data, the relationship is barely significant because errors and bias in PRISM data for MSP is only about half as severe (Table 1). This artifact may be a problem for any study where the organism under investigation has its optimal habitat where weather station coverage is best. Also, custom climate models for a geographically restricted study site may create this artifact because it is a common weakness of interpolation and regression methods to become unreliable near the edges of an area for which they have been developed.

The second mechanism where a poor climate model may create a superior model fit relates to the way some organisms, such as lodgepole pine and other widespread tree species, adapt to local environments. Genetic variation of growth and adaptive traits in tree species is usually the result of adaptation to local environments and gene flow from surrounding populations. As a consequence, broad geographic patterns of genetic variation, or clines, are often found in tree species that have a continuous distribution over a large geographic area. Using a global polynomial approach to predict climate normals usually fails to account for local climate variation (such as rain shadows) and only predicts broad geographic patterns of climate variables that may match clines of genetic

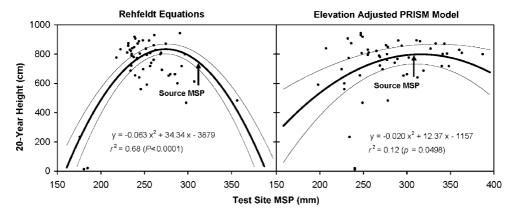


Fig. 6. Response function of height growth for Prince George low elevation seed sources to mean summer precipitation (MSP). Predicted mean and 95% confidence intervals are given. The arrow indicates the average local MSP where Prince George low elevation seed sources have been collected.

variation rather well. The resulting significant correlation between predicted climate and genetic variation is obviously due to spatial autocorrelations in both datasets, which quite easily may result in false positives (Epperson, 2003).

4. Conclusions

For temperature related variables, Rehfeldt's equations explained more variance in weather station data and had less regional bias than PRISM data. We developed an elevation adjustment, which resulted in an equal or larger amount of variance explained in weather station data than Rehfeldt's equations and also removed bias in montane regions. These equations are also useful for up-sampling of the PRISM model with a high resolution digital elevation model for studies that require spatially explicit climate data. For precipitation related variables, PRISM clearly proved to be the superior model. Rehfeldt's polynomial equations severely under-estimated precipitation on the coast and at high elevations, while over-estimating precipitation in the interior plateau.

For modeling studies that attempt to predict response of organisms to changes in environmental conditions (such as global warming) we suggest including a sensitivity analysis of how predictions change based on the provided error and bias estimates of climate models. All investigated models typically over- or under-estimate temperature related variables by 0.5–1 °C and regional deviations may be as high as 2–4 °C where weather station coverage is poor. Deviations of predicted mean annual precipitation is typically 100 mm for the PRISM model and 400 mm for the Rehfeldt model. We have shown that this magnitude of error may result in severe artifacts in studies that investigate adaptation and response of organisms to climate change. Caution should be used to interpret results of those studies if sufficiently accurate baseline climate data is not available.

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References

- Agnew, M.D., Palutikof, J.P., 2000. GIS-based construction of baseline climatologies for the Mediterranean using terrain variables. Clim. Res. 14, 115–127.
- Brown, D.P., Comrie, A.C., 2002. Spatial modeling of winter temperature and precipitation in Arizona and New Mexico. USA Clim. Res. 22, 115–128.
- Custer, S.G., Farnes, P., Wilson, J.P., Snyder, R.D., 1996. A comparison of hand- and spline-drawn precipitation maps for mountainous Montana. Water Resour. Bull. 32, 393–405.
- Daly, C., Gibson, W.P., Taylor, G.H., Johnson, G.L., Pasteris, P., 2002. A knowledge-based approach to the statistical mapping of climate. Clim. Res. 22, 99–113.
- Daly, C., Taylor, G.H., Gibson, W.P., Parzybok, T.W., Johnson, G.L., Pasteris, P.A., 2000. High-quality spatial climate data sets for the United States and beyond. Trans. ASAE 43, 1957– 1962.
- Dirnbock, T., Dullinger, S., Grabherr, G., 2003. A regional impact assessment of climate and land-use change on alpine vegetation. J. Biogeog. 30, 401–417.
- Eeley, H.A.C., Lawes, M.J., Piper, S.E., 1999. The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. J. Biogeogr. 26, 595–617.
- Epperson, B.K., 2003. Geographical Genetics, vol. 38. Princeton University Press, Princeton, NJ.
- Fleming, M.D., Chapin, F.S., Cramer, W., Hufford, G.L., Serreze, M.C., 2000. Geographic patterns and dynamics of Alaskan climate interpolated from a sparse station record. Global Change Biol. 6, 49–58.
- Goodale, C.L., Aber, J.D., Ollinger, S.V., 1998. Mapping monthly precipitation, temperature, and solar radiation for Ireland with polynomial regression and a digital elevation model. Clim. Res. 10, 35–49.
- Gould, W.A., Edlund, S., Zoltai, S., Raynolds, M., Walker, D.A., Maier, H., 2002. Canadian Arctic vegetation mapping. Int. J. Remote Sens. 23, 4597–4609.
- Greene, S.L., Hart, T.C., Afonin, A., 1999. Using geographic information to acquire wild crop germplasm for ex situ collections: II. Post-collection analysis. Crop Sci. 39, 843– 849.
- Guarino, L., Jarvis, A.R.J.H., Maxted, N., 2001. Geographic information systems (GIS) and the conservation and use of plant genetic resources. In: Engels, J.E.A. (Ed.), Proceedings of the International Conference on Science and Technology for Managing Plant Genetic Diversity in the 21st Century (SAT21), Kuala

- Lumpur, Malaysia, 12–16 June 2000 Managing plant genetic diversity.
- Host, G.E., Polzer, P.L., Mladenoff, D.J., White, M.A., Crow, T.R., 1996. A quantitative approach to developing regional ecosystem classifications. Ecol. Appl. 6, 608–618.
- Illingworth, K., 1978. Study of lodgepole pine genotype-environment interaction in BC. In: Proceedings International Union of Forestry Research Organizations (IUFRO) Joint Meeting of Working Parties: Douglas-Fir Provenances, Lodgepole Pine Provenances, Sitka Spruce Provenances and Abies Provenances, Vancouver, British Columbia, Canada, pp. 151–158.
- Iverson, L.R., Prasad, A.M., 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecol. Monogr. 68, 465–485.
- Jones, P.G., Beebe, S.E., Tohme, J., Galwey, N.W., 1997. The use of geographical information systems in biodiversity exploration and conservation. Biodiversity Conserv. 6, 947–958.
- Lindner, M., Badeck, F.W., Bartelheimer, P., Bonk, S., Cramer, W., Dieter, M., Dobbeler, H., Dursky, J., Duschl, C., Fabrika, M., Fromdling, D., Gundermann, E., Hennig, P., Holzer, W., Lasch, P., Leischner, B., Liesebach, M., Pommerening, A., Pott, A., Pretzsch, H., Schlott, W., Scholz, F., Spellmann, H., Suckow, F., Suda, M., Wolff, B., 2002. Integrating forest growth dynamics, forest economics and decision making to assess the sensitivity of the German forest sector to climate change. Forstwissenschaftliches Centralblatt 121, 191–208.
- LPDAAC, 2003. GTOPO30 data from the Land Processes Distributed Active Archive Center, http://lpdaac.usgs.gov/main.html.
- Masson, V., Champeaux, J.L., Chauvin, F., Meriguet, C., Lacaze, R., 2003. A global database of land surface parameters at 1-km resolution in meteorological and climate models. J. Clim. 16, 1261–1282.
- McKenney, D.W., Hutchinson, M.F., Kesteven, J.L., Venier, L.A., 2001. Canada's plant hardiness zones revisited using modern climate interpolation techniques. Can. J. Plant Sci. 81, 129–143.
- McKenney, D.W., Mackey, B.G., Joyce, D., 1999. Seedwhere: a computer tool to support seed transfer and ecological restoration decisions. Environ. Model. Software 14, 589–595.
- McKenney, D.W., Pedlar, J.H., 2003. Spatial models of site index based on climate and soil properties for two boreal tree species in Ontario, Canada. Forest Ecol. Manage. 175, 497–507.
- Meidinger, D., Pojar, J., 1991. Ecosystems of British Columbia. BC Ministry of Forests, Special Report series 6, Victoria, British Columbia.
- Nalder, I.A., Wein, R.W., 1998. Spatial interpolation of climatic Normals: test of a new method in the Canadian boreal forest. Agric. Forest Meteorol. 92, 211–225.

- Parker, W.H., vanNiejenhuis, A., 1996. Regression-based focal point seed zones for Picea mariana from northwestern Ontario. Can. J. Bot.—Revue Canadienne de Botanique 74, 1227–1235.
- Price, D.T., McKenney, D.W., Nalder, I.A., Hutchinson, M.F., Kesteven, J.L., 2000. A comparison of two statistical methods for spatial interpolation of Canadian monthly mean climate data. Agric. Forest Meteorol. 101, 81–94.
- Rehfeldt, G.E., 1995. Genetic-variation, climate models and the ecological genetics of larix occidentalis. Forest Ecol. Manage. 78, 21–37.
- Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A., Milyutin, L.I., 2002. Intraspecific responses to climate in *Pinus sylvestris*. Global Change Biol. 8, 912– 929.
- Rehfeldt, G.E., Wykoff, W.R., Ying, C.C., 2001. Physiologic plasticity, evolution, and impacts of a changing climate on *Pinus contorta*. Climatic Change 50, 355–376.
- Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., Hamilton, D.A., 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. Ecol. Monogr. 69, 375–407.
- SAS Institute Inc., 2000. SAS/STAT user's guide, release 8.0. SAS Institute Inc., Cary, NC.
- Segura, S., d'Eeckenbrugge, G.C., Lopez, L., Grum, M., Guarino, L., 2003. Mapping the potential distribution of five species of Passiflora in Andean countries. Genet. Resour. Crop Evol. 50, 555–566.
- Simpson, J.J., Hufford, G.L., Fleming, M.D., Berg, J.S., Ashton, J.B., 2002. Long-term climate patterns in Alaskan surface temperature and precipitation and their biological consequences. IEEE Trans. Geosci. Remote Sens. 40, 1164–1184.
- Sykes, M.T., Prentice, I.C., 1995. Boreal forest futures—modeling the controls on tree species range limits and transient responses to climate-change. Water Air Soil Pollut. 82, 415–428.
- Talkkari, A., Hypen, H., 1996. Development and assessment of a gap-type model to predict the effects of climate change on forests based on spatial forest data. Forest Ecol. Manage. 83, 217–228.
- Thuiller, W., 2003. BIOMOD—optimizing predictions of species distributions and projecting potential future shifts under global change. Global Change Biol. 9, 1353–1362.
- Welk, E., Schubert, K., Hoffmann, M.H., 2002. Present and potential distribution of invasive garlic mustard (*Alliaria petiolata*) in North America. Divers. Distributions 8, 219–233.
- WMO, 1989. Calculation of monthly and annual 30-year standard normals, WCDP No. 10, WMOTD No. 341. World Meteorological Organization, Geneva.