Red pine abundance: current climatic control and responses to future warming

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FLANNIGAN, M.D., and WOODWARD, F.I. 1994. Red pine abundance: current climatic control and responses to future warming. Can. J. For. Res. **24**: 1166–1175.

This study investigated the relationship between climatic variables and the abundance of red pine (*Pinus resinosa* Ait.). Two aspects of this climate–abundance relationship were addressed. First, a model was developed to fit the present day range and abundance of red pine using available climatic variables in the expectation of better understanding the processes controlling distribution. Second, general circulation models were used to explore the implications of a 2 × CO_2 (greenhouse warming) environment on the range and abundance of red pine. Using a response surface, growing degree-days (base 10°C), and precipitation explained 54% of the variance in an independent data set of red pine volume per unit area. Possible explanations for the present day boundaries of red pine are competition for the southern limit, insufficient moisture for the southwestern limit, and insufficient warmth during the growing season at the northern limit. The greenhouse warming simulation suggested a dramatic northeastward shift of 600–800 km in the potential range of red pine and a decrease in total area, but it also suggested higher volumes per unit area.

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La présente étude examine la relation entre les variables climatiques et l'abondance du pin rouge (*Pinus resinosa* Ait.). Elle aborde deux aspects de cette relation entre le climat et l'abondance. D'abord on a élaboré un modèle qui a permis d'ajuster l'aire de distribution et l'abondance actuelles du pin rouge, à l'aide des variables climatiques disponibles dans l'espoir de mieux comprendre les processus régissant la distribution de cette essence. On a ensuite utilisé des modèles de circulation générale pour examiner les incidences d'un doublement des concentrations atmosphériques de CO_2 (réchauffement provoqué par l'effet de serre) sur l'aire de répartition et l'abondance du pin rouge. Le nombre de degrés-jours de croissance (au-dessus de 10°C) et la quantité de précipitations, appliqués à une surface de réponse, expliquaient 54% de la variance d'un ensemble indépendant de données sur le volume de pin rouge par unité de surfaces. La concurrence à l'égard de la partie méridionale de l'aire, la teneur insuffisante en eau à la limite sud-ouest et le manque de chaleur pendant la saison de croissance à l'extrémité septentrionale à trois raisons qui pourraient expliquer l'aire d'extension actuelle du pin rouge. Un réchauffement provoqué par l'effet de serre laisse supposer un déplacement spectaculaire vers le nord-est de 600 à 800 km de l'aire d'extension potentielle du pin rouge et une diminution de la superficie totale, mais laisse également entrevoir des volumes supérieurs de matière ligneuse par unité de surface.

[Traduit par la rédaction]

Introduction

Red pine (*Pinus resinosa* Ait.) is found in the Great Lakes – St. Lawrence Forest Region and in the southern sections of the Boreal Forest Region (Rowe 1972) of North America. This includes an area extending from southern Manitoba, eastward to Newfoundland, and as far south as West Virginia (Fig. 1) (Burns and Honkala 1990). Red pine survived the most recent glaciation in refugia in the Appalachians (Wright 1964) and probably reached its peak in abundance and northern extent during a hypsithermal between 7000 and 3000 years BP (Liu 1990). An accurate history of red pine movement and abundance from the pollen record is difficult because it is very hard to discriminate between red pine pollen and jack pine (*Pinus banksiana* Lamb.) pollen. In the present interglacial period red pine movements probably mirror that of white pine (*Pinus strobus* L.), a common associate.

Climate is a critical factor determining the distribution and abundance of tree species. For example, temperature influences both the abundance and the presence or absence of tree species through extreme minimum or maximum temperatures, frost, and insufficient warmth in the growing season (Woodward 1987, 1990). For red pine other factors such as the fire regime, the physical and chemical substrate conditions, as well as competition also play a role. Red pine is a fire-dependent species (Bergeron and Brisson 1990; Engstrom and Mann 1991) because fire is the agent for its regeneration. Fire opens up the canopy (red pine is intolerant of shade), "prepares" the seed bed (mineral soil exposure is required for seedling establishment), and removes competition. Fire regime is, of course, related to climate. Obviously, soil and nutrient status are important in determining the presence–absence of red pine and also its growth patterns. Red pine is most commonly found on sandy or gravelly soils on terrace and outwash plains, but rock outcrops and lacustrine clays will also support the species. Red pine commonly occurs and grows satisfactorily on soils of low to moderate fertility.

Growing evidence suggests that the Earth's climate is starting to warm up at an unprecedented rate because of increasing amounts of radiatively active gases such as water vapour, carbon dioxide (CO_2), methane, ozone, nitrous oxide, and chlorofluorocarbons (Wigley and Raper 1992). Possible
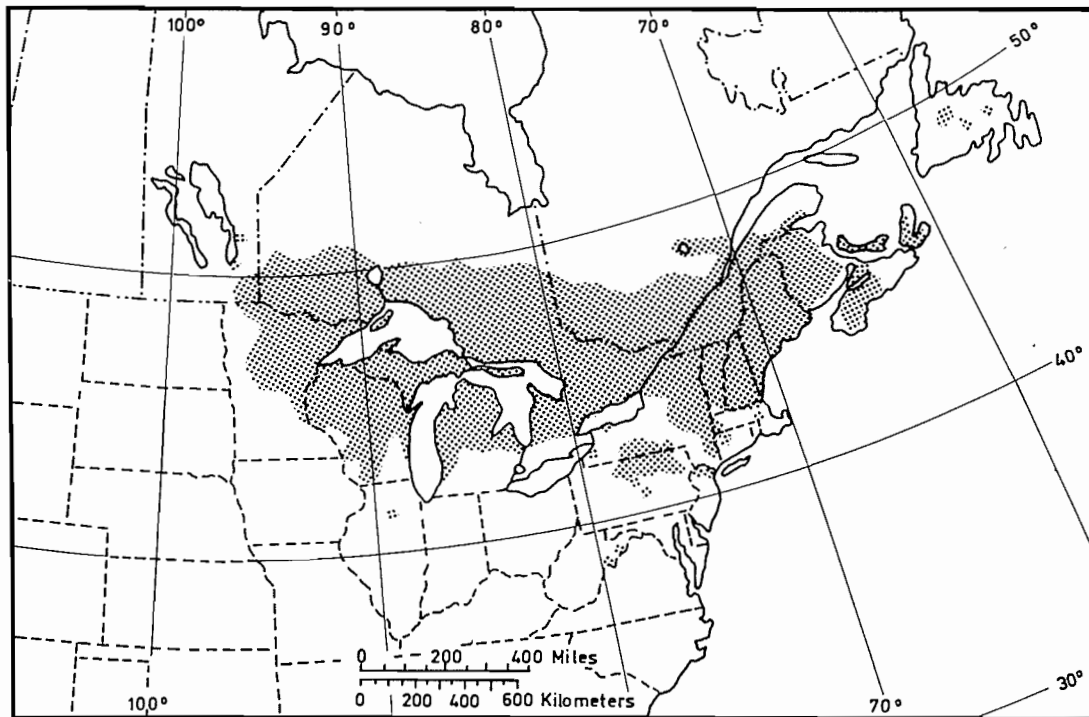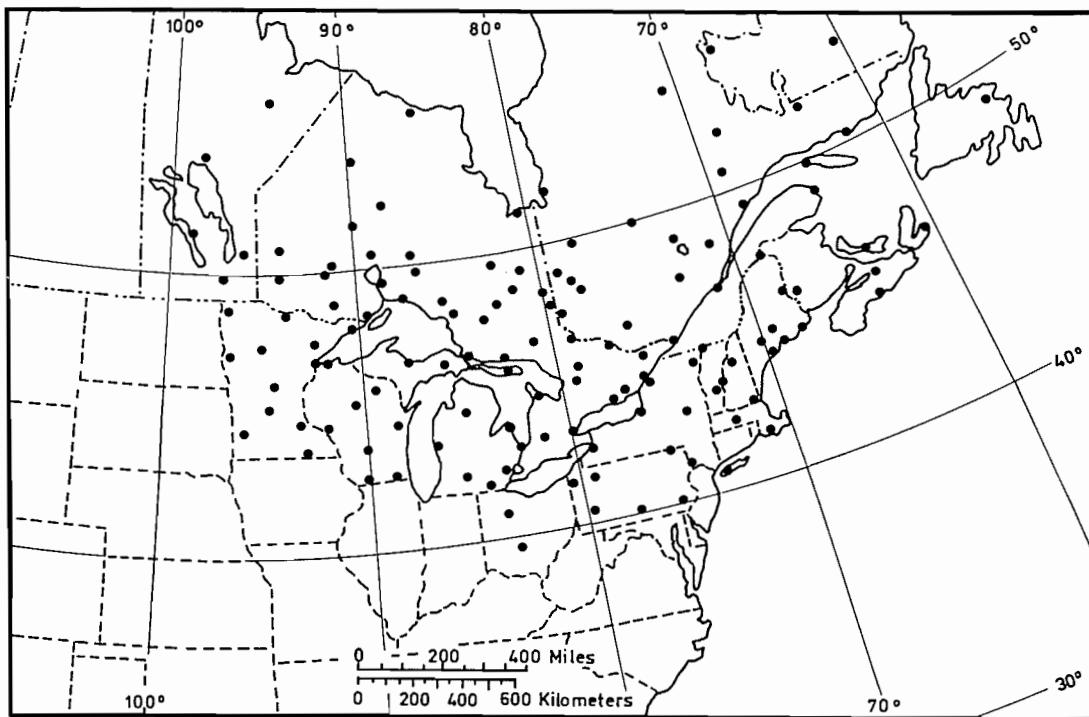
FIG. 1. The native range of red pine.

FIG. 2. Location of climate stations.

future climates based on general circulation models (GCMs) suggest that, by 2100, there will be a 3°C rise in mean temperature, averaged over the world (Houghton et al. 1990, 1992). This warmer world scenario is often called a 2 × CO_2 climate to reflect a doubling of CO_2 plus the CO_2 equivalents of other greenhouse gases.

A number of background facts and assumptions are used in this work on distribution modelling. We adhere to an approach pioneered by Gleason (1926), which perceives

vegetation as an assemblage of individual species with each species distributed according to its own physiological requirements as constrained by competitive interactions (Woodward 1987). Recent studies (Davis 1989; Whitney 1986) suggest that species move as individuals as opposed to the movement of vegetation as a community. We regard the present distribution and abundance of red pine to be in equilibrium with the present climate (i.e., the climate of the last few centuries; Davis (1990) suggests there may be a lag of a
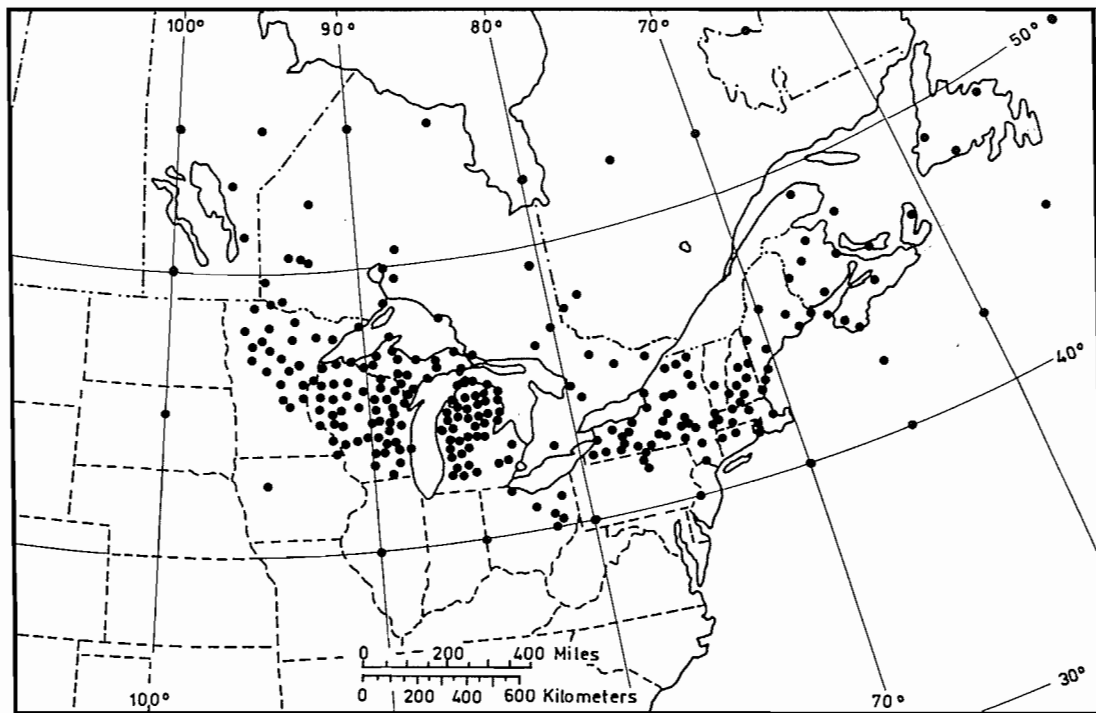
FIG. 3. Centroid location of inventory data. A number of points of zero red pine volume were added (including those over water) to facilitate the smoothing of the red pine volume as shown in Fig. 5.
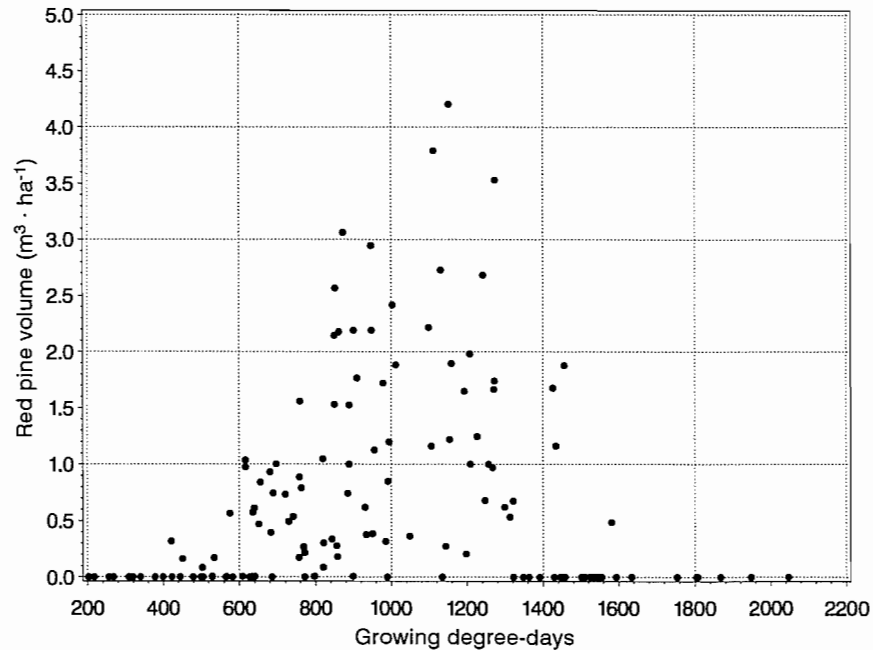

FIG. 4. Volume of red pine $(m^3 \cdot ha^{-1})$ versus growing degree-days (base 10°C).

century or more between climate and forest expansion). Payette et al. (1985) found that the assumption of equilibrium was correct for lichen–spruce woodland in northern Quebec, which indicates that the species of this vegetation type are in dynamic equilibrium with the climate and the fire regime.

The objective of this study was to model the present range and abundance of red pine in terms of climate, for two reasons. First, it was felt that the model may facilitate a better understanding of processes in the life cycle of red pine (Woodward 1987) that control its current geographical distribution. Second, the model could be used to project how red

pine may respond to scenarios of greenhouse warming, as represented by GCMs. The red pine model was derived from present climate–CO_2–distribution relationships, which meant that this was a static vegetation–climate model.

Methods

Three types of data sets were used for this study, namely, climate, GCM, and forest inventory. Climatic data were obtained from the Canadian Atmospheric Environment Service (Environment Canada 1982) and from the United States National Climatic Centre (state summaries). A total of 135 climate stations

were used in this study (Fig. 2), which covers the range of red pine, and beyond, in North America. The climate variables were obtained from 30-year averages (1951–1980) and included the mean January and July temperatures, the mean annual temperature, average January minimum temperature, growing degree days (base 5°C and 10°C), annual precipitation, and the frost-free period. Also used were the extreme minimum temperature recorded at the site, an index of continentality (Currey 1974), and the estimated potential evapotranspiration (Holdridge 1962). Continentality index (C) is described by the following equation

$$C = \frac{1.6A}{\sin \phi} - 14$$

where A is equal to the mean temperature of the warmest month subtracted from the mean temperature of the coldest month in degrees centigrade and ϕ is the latitude. All data from the United States were converted from degrees Farenheit to centigrade for temperature and from inches to millimeters for precipitation.

Additional climatic variables could have been used in this study. There is almost no end to the number of variables that could be used, such as monthly values of precipitation, minimum temperature, maximum temperature, mean temperature, vegetation indexes, extremes of temperature and precipitation, etc. Many variables are strongly correlated, which may lead to fortuitous good fits. In this study we decided to examine the macro scale, using just a few common climatic variables with botanical effects that can be traced to physiological and ecological mechanisms (Woodward 1987). So, for example, the extreme minimum temperature was included because studies have shown or suggested a relationship between the minimum temperature and the range of tree species (Sakai and Weiser 1973; Woodward 1987; Arris and Eagleson 1989).

Growing degree-days with a base of 10°C were included because Kozlowski and Borger (1971) found that red pine growth was reduced by low temperatures and inhibited at 10°C. In addition, Flannigan and Woodward (1993) found that temperatures must exceed 10°C for germination of red pine seed.

Grid-point data of average monthly temperature and precipitation were obtained from four GCMs for the $1 \times CO_2$ and $2 \times CO_2$ scenarios from the Canadian Atmospheric Environment Service. The models used were from: (i) GISS (Goddard Institute for Space Studies), (ii) UKMO (United Kingdom Meteorological Office), (iii) GFDL (Geophysical Fluid Dynamics Laboratory), and (iv) CCC (Canadian Climate Centre). A number of assumptions are made in these models and the outputs are to be regarded as scenarios rather than forecasts. Nevertheless, despite their shortcomings, in our judgement the GCMs simulate present day climate over large regions with sufficient accuracy to warrant their use in this study.

The inventory data were obtained from the Canadian Forest Service and the USDA Forest Service (USFS). A total of 234 sites were used (Fig. 3) and volume and area of red pine by county were obtained from the USFS. In Canada, Rowe's forest sections were used but only volume data were available. Rowe (1972) divided Canadian forests into eight forest regions. These forest regions were subdivided on the basis of distribution patterns of vegetation and physiography into 90 forest sections. After converting units of measurement each inventory site included centroid latitude and longitude and the volume of red pine per unit of area (cubic metres per hectare). In this paper, abundance and volume of red pine per hectare are synonymous.

Our first task was to find a common base for the forest inventory and climatic data. Three options were available: (i) interpolate inventory data to the climate station locations; (ii) interpolate climate data to the inventory sites; (iii) interpolate inventory and climate data to a standard grid. Option (i) was selected in this study because some of the climate data are very dependent on the local site, e.g., minimum temperature, frost-free period, etc., and the inventory data are representative of a larger area.

The inventory data (red pine volume) were interpolated to the climate stations using a two-dimensional cubic spline (Thiebaux and Pedder 1987), usually referred to as a thin-plate cubic spline (Duchon 1976). The cubic spline is one of the most accurate interpolation techniques available. For this preliminary study we selected the two-dimensional cubic spline to maintain obvious and straightforward relationships. The solution takes the form:

$$[1] \quad Z(x_j, y_j) = \alpha_0 + \alpha_1 x_j + \alpha_2 y_j + \sum_{i=1}^{n} \beta_i \phi(r_{ij})$$

where

$$[2] \quad r_{ij} = [(x_i - x_j)^2 + (y_i - y_j)^2]^{1/2}$$

and

$$[3] \quad \phi(r_{ij}) = r_{ij}^2 \ln(r_{ij})$$

The coefficients $\alpha(\alpha_0, \alpha_1, \alpha_2)$ and $\beta(\beta_1, \beta_2, ..., \beta_n)$ can be found by solving the linear system:

$$[4] \quad \mathbf{SB} = \mathbf{C}$$

where

$$\mathbf{S} = \begin{bmatrix} \Phi & \mathbf{A} \\ \mathbf{A}^T & 0 \end{bmatrix}$$

$$\mathbf{B} = \begin{bmatrix} \beta \\ \alpha \end{bmatrix}$$

$$\mathbf{C} = \begin{bmatrix} \mathbf{Y} \\ 0 \end{bmatrix}$$

Φ is a symmetric $n \times n$ matrix whose values are the $\phi(r_{ij})$ for all combinations of observing stations (e.g., $i = 1-n$ and $j = 1-n$)

$\mathbf{A}$ is an $n \times 3$ matrix for components of the first part of eq. 1 for all observing locations

$$\begin{bmatrix} 1 & x_1 & y_1 \\ 1 & x_2 & y_2 \\ . & . & . \\ . & . & . \\ . & . & . \\ 1 & x_n & y_n \end{bmatrix}$$

$\mathbf{Y}$ is an $n \times 1$ matrix of the observed values

The matrix $\mathbf{S}$ is an $(n + 3) \times (n + 3)$ matrix with every value on the main diagonal equal to 0.

Because $\mathbf{S}$ is a square matrix, a solution for β and α can be found that exactly fits the observed values. The solution of β and α is

$$[5] \quad \mathbf{B} = \mathbf{S}^{-1} \mathbf{C}$$

The constraint that the surface fits the observed data exactly can be relaxed. The thin-plate cubic spline can smooth the observed field by an approach similar to Reinsch (1967) for a one-dimensional spline. By smoothing we hoped to improve the overall fit of the surface to independent data even though the surface may violate the observed data. Smoothing is accomplished by adding a constant q to the diagonal of the matrix Φ (e.g., $\Phi' = \Phi + q\mathbf{I}$, whereas $\mathbf{I}$ is an $n \times n$ identity matrix).

First, a forward stepwise linear regression was performed using red pine volume as the dependent variable and the climatic variables as independent variables. Then a number of climatic response surfaces were calculated to see which yielded the best fit. Climatic response surfaces were used on North American pollen data by Bartlein et al. (1986). On a response surface the abundance of red pine can be represented by Z, which is a height on a surface at coordinates (X, Y) where X and Y are any number of climatic variables. Response surfaces are usually nonlinear and can be described by polynomials or, as in this study, by a
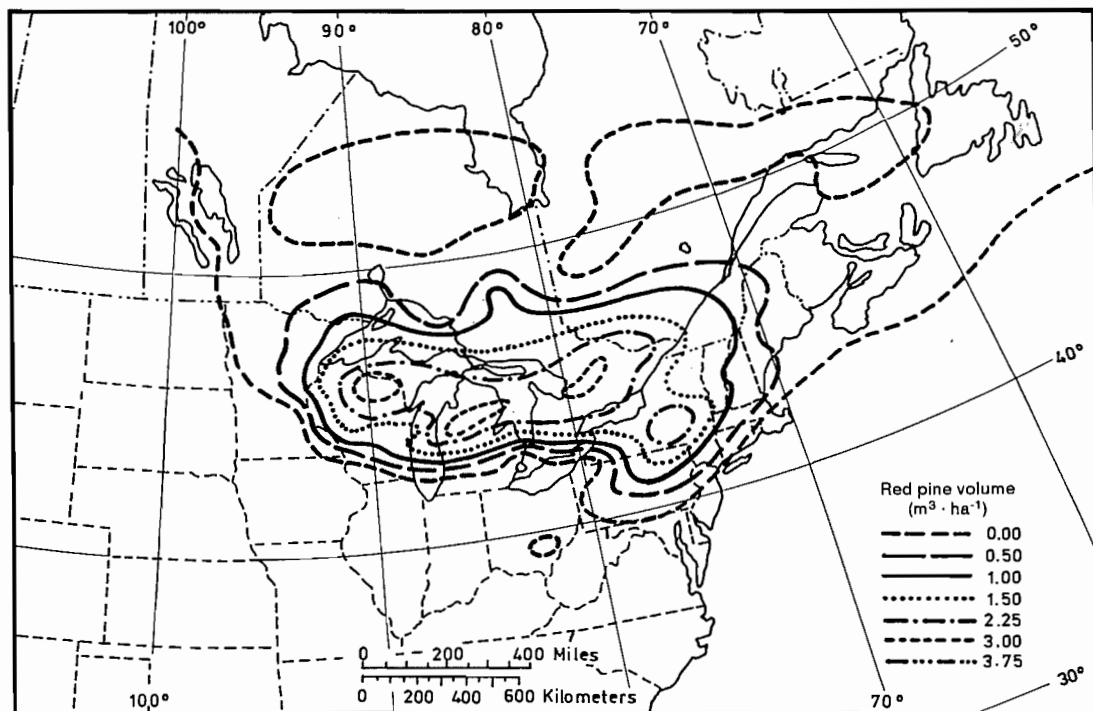
FIG. 5. Red pine volume ($m^3 \cdot ha^{-1}$) smoothed with a thin-plate cubic spline.

thin-plate cubic spline. Though not used here, the volume of red pine Z could be fitted to a surface described by three or more climatic variables. In essence, the response surface is a type of static vegetation model. To determine how well the response surfaces performed, the original data set was divided into two sets and the response surface generated from the first set of data (dependent) was used to estimate the volume of red pine in the second set (independent).

The GCM data from the $1 \times CO_2$ run were used to estimate the volume of red pine based on the best response surface from the observed data. This was done to ensure that the model data would yield a red pine distribution close to reality. After this the $2 \times CO_2$ data were employed to generate red pine volume in a greenhouse world for comparison with the present range and abundance.

Results

Using a forward stepwise regression 37% of the variance was explained in the red pine volume data. The regression equation has seven variables (extreme minimum temperature (15%), continentality (5%), average January minimum temperature (4%), annual precipitation (4%), growing degree-days (base 5°C) (4%), mean January temperature (2%), and mean July temperature (2%)) though no single variable explains a large amount of the variance. The fact that no single climatic variable dominated is probably due to nonlinear relationships or, alternatively, to the fact that there is only a weak relationship, if any, between the climatic variables and red pine volume. An example of a nonlinear relationship can be seen in Fig. 4, which shows a plot of growing degree-days (base 10°C) against the volume per unit area of red pine. Red pine volumes are low or zero at both high and low values of growing degree-days. Even in the growing degree zone of maximum volumes in Fig. 4 (1100–1300 growing degree-days) there are volumes at or close to zero, possibly due to the area being too dry or having inappropriate soils.

The interpolated red pine volume data for all 135 sites

are shown in Fig. 5 using a SAS Institute Inc. (1990) contouring package. Because of the paucity of sites in the north the contouring package had trouble matching the observed northern limit of red pine (0.0 red pine volume) though all the values are small (less than $0.5 \ m^3 \cdot ha^{-1}$). The best response surface was obtained by using growing degree-days (base 10°C) and precipitation as the two coordinates. Figure 6 shows the relationship of red pine volume, calculated by the thin-plate cubic spline, with climatic variables, growing degree days (base 10°C), and precipitation. This response surface explained 54% of the variance in the red pine volume data.

Growing degree-days (base 10°C) and annual precipitation from the $1 \times CO_2$ GCM runs were used with the response–surface model from the observed data to generate red pine volume. The resulting distribution did not fit the present day distribution very well, probably because of the weakness in estimates of precipitation by the GCMs. The CCC GCM was the only model that predicted the range of red pine with any degree of accuracy (Fig. 7). This was modified by increasing the GCM precipitation by 20%, partially compensating for the poor precipitation estimate and this resulted in a red pine range closer to the actual range (Fig. 8). Using this revised method the $2 \times CO_2$ data were used to produce the range and abundance distributions as shown in Fig. 9. In this scenario the northern limit of red pine has pushed northwards 600 km while the southern limit has moved north and east by almost 800 km. The $2 \times CO_2$ results (Fig. 9) also indicate higher potential maximum volumes of red pine, which suggests a better growing environment. Figure 10 illustrates the response surface for extreme minimum temperature and continentality. There appears to be no clear connection between minimum temperature and the northern limit of red pine. However, there is evidence that the southern limit is related to extreme minimum temperature; red pine occurs in locations where the extreme minimum is below
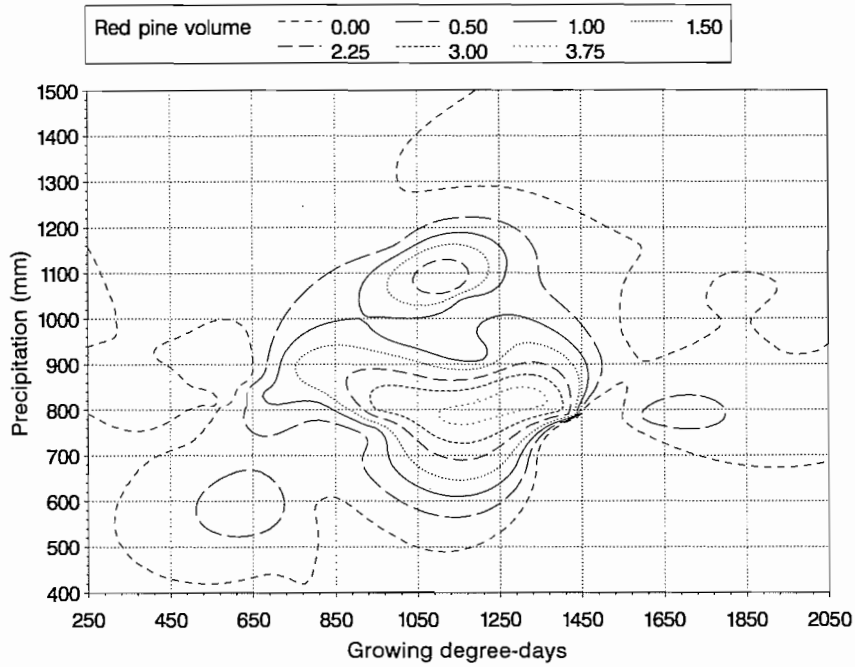
FIG. 6. Response surface of smoothed red pine volume ($m^3 \cdot ha^{-1}$) described by growing degree-days (base 10°C) and precipitation.
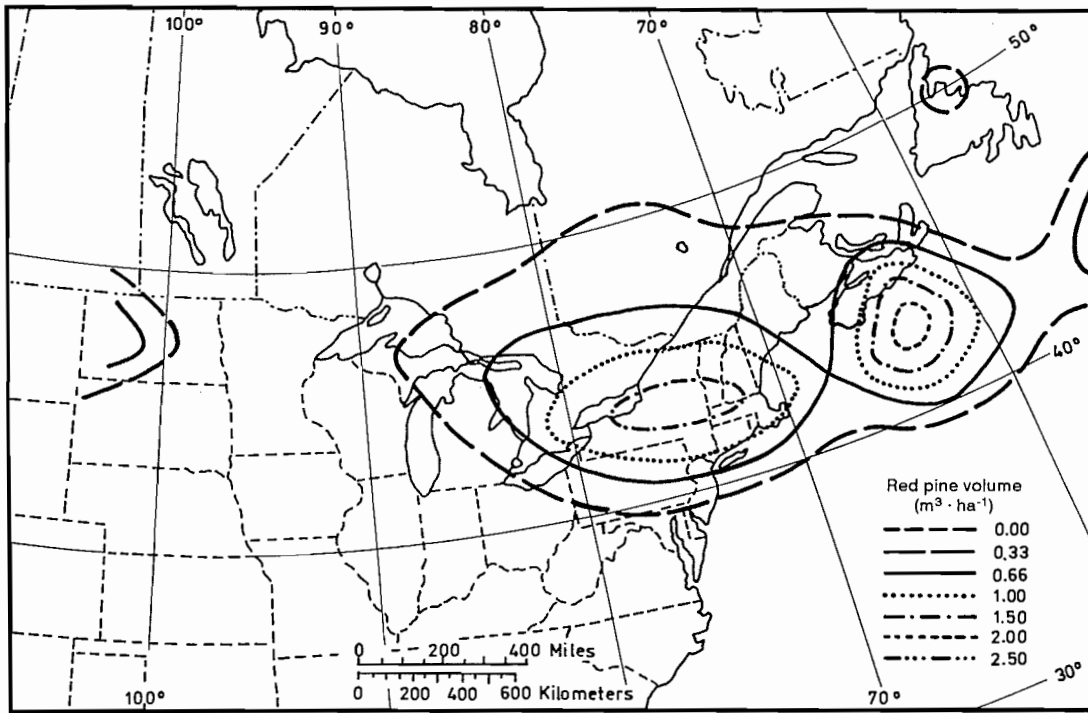

FIG. 7. Red pine volume ($m^3 \cdot ha^{-1}$) obtained from the response surface (growing degree-days and precipitation (Fig. 6) using the climatic data from the CCC $1 \times CO_2$ GCM run).

−30°C except in some coastal areas (low continentality values).

Discussion

Degree-days and precipitation have been shown to be important in modelling the distribution and abundance of red pine. The strongest aspect of the precipitation – red pine relationship is at low values of precipitation. When precipitation falls below 580 mm red pine is essentially absent

(Fig. 6). This is intuitively correct, because the forests with red pine at the west and southwest limits give way to grassland, mostly due to insufficient moisture to support a forest (Melillo et al. 1990). This relationship between 580 mm and the southwest limit of red pine may be fortuitous. This transition from forest to grassland might be the result of irregular severe droughts or frequent fires (Walter 1979), conditions that would go undetected when using averaged climatic variables as we did in this study.
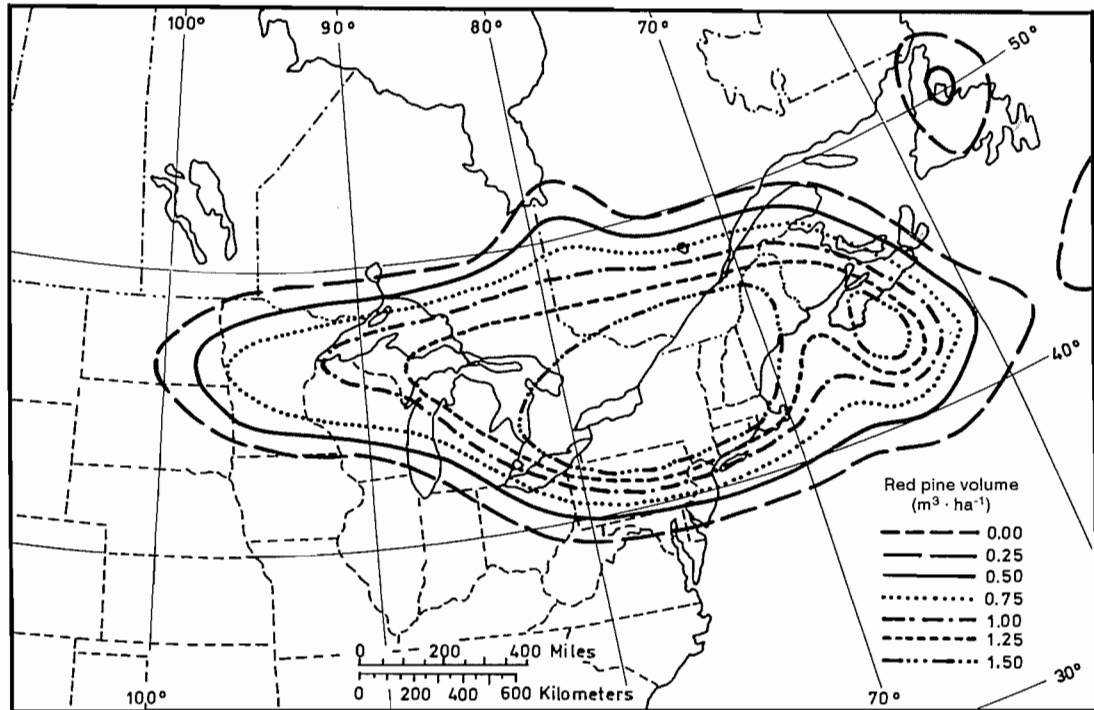
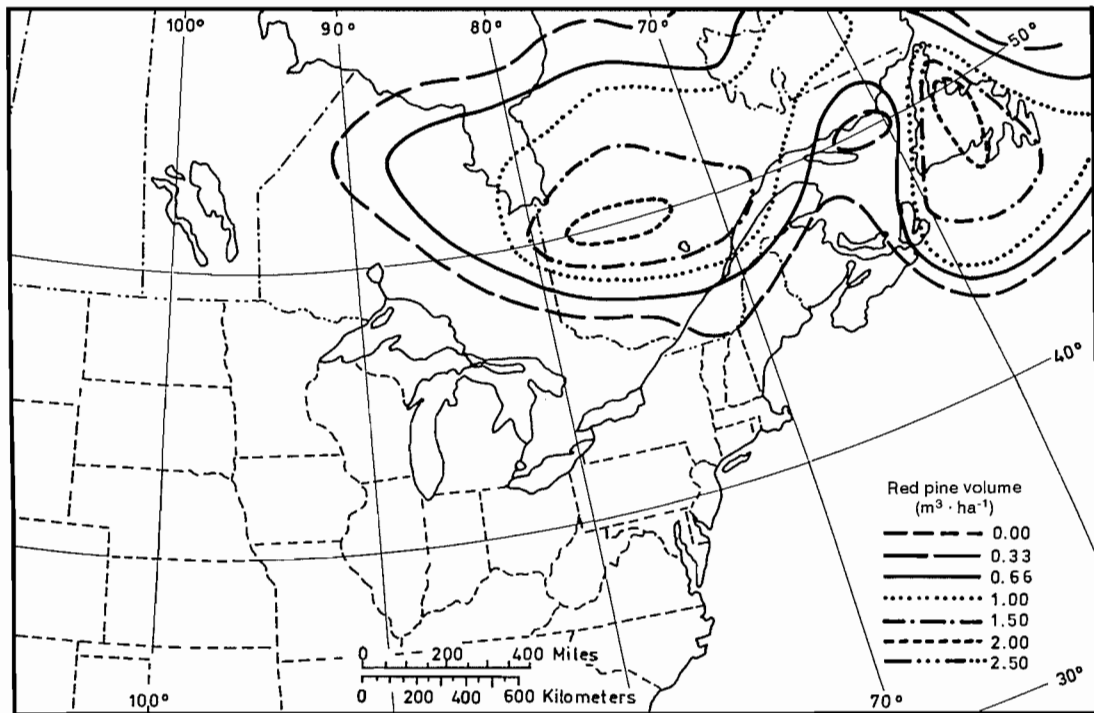FIG. 8. Same as Fig. 7 except the GCM precipitation was increased by 20%.

FIG. 9. Red pine volume ($m^3 \cdot ha^{-1}$) using the response surface with climatic data from the CCC $2 \times CO_2$ GCM run. (The precipitation was increased by 20%).

In terms of growing degree-days there is a two-sided non-linear relationship. Low values of growing degree-days correspond to the northern limit of red pine, which suggests that there is insufficient warmth during the growing season to complete a critical phase of growth or regeneration. High values of growing degree-days found south of the present day range could restrict red pine in a number of ways. First,

a competitor may be favoured over red pine in this warmer climate, ultimately causing competitive elimination of red pine over time. Second, the warmer climate may actually be damaging to a life-cycle process of red pine, such as leaf flush during a winter mild spell followed by freezing weather. Third, the fire regime in this warmer climate may be inappropriate for red pine regeneration; that is, fires in the decid-
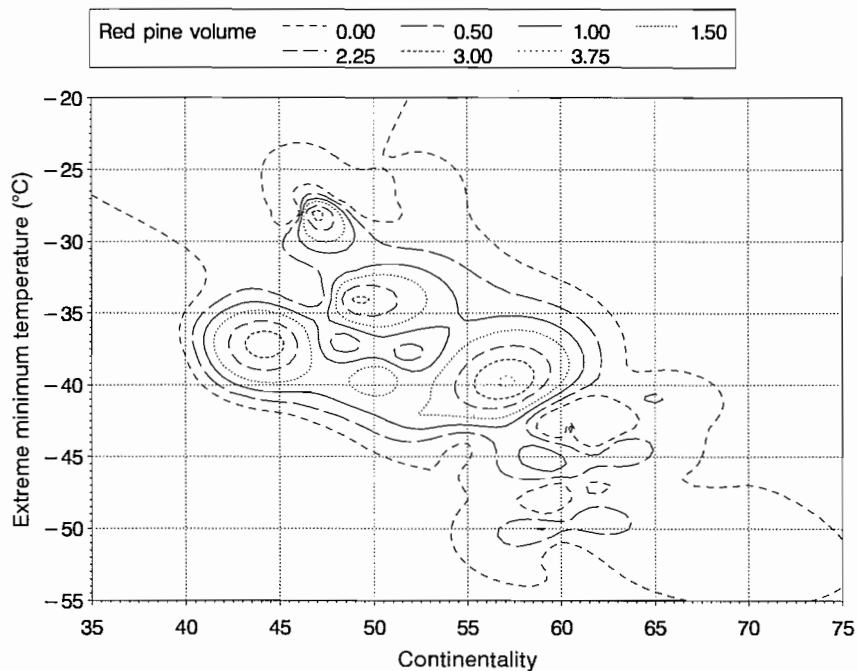
FIG. 10. Response surface of red pine volume ($m^3 \cdot ha^{-1}$) described by extreme minimum temperature (°C) and an index of continentality.

uous forest are usually of lower intensity and are relatively infrequent creating conditions suboptimal for red pine regeneration.

Annual precipitation is not ideal for describing the climatic constraint in red pine autecology. Precipitation amount by itself does not indicate climatic seasonality, and data on evapotranspiration are also necessary to calculate the wet or dry nature of the climate. Yet, in this study, precipitation yielded a better fit than estimated evapotranspiration. Also, growing degree-days, if taken alone, incompletely measure the thermal growth regime. For plant growth the distribution of growing degrees throughout the year is important. Also, degree-days generated on days with temperatures >30°C may not be as beneficial; temperatures near 20°C appear to be optimum for red pine growth (Kozlowski and Borger 1970). Finally, plant responses to temperature may not necessarily be linear as assumed by the degree-day concept.

The unexplained variance may be due to a number of reasons. Fire is not accounted for in a direct way even though the fire regime is dependent on climate. The fire regime cannot be described accurately by the simple climatic variables used in this study. The temporal distribution of precipitation is critical for the fire regime rather than the total amount (Flannigan and Harrington 1988), such that two stations with identical monthly precipitation amounts could have completely different fire regimes, causing significant changes in the forest (Zackrisson 1977). Soil type and nutrients could also account for some of the unexplained variance. As well, forest pests and disease can affect the distribution of tree species (Spurr and Barnes 1980). Moreover, human activities such as logging and fire control are not accounted for in this model. Finally, climate and forest inventory data have inherent errors in measurement and discrepancies in the methodology.

Some results in this study differ from other findings. For example, Denton and Barnes (1987) state that the relationship between the distribution of pines (including red pine) and climate was not strong in their study area of Michigan.

The abundance of red pine (Fig. 5) declines gradually northward and eastward from the area of maximum abundance. The maximum abundance is not in the centre of distribution but is along a northwest–southeast line close to the southern limit of red pine. This suggests that the processes restricting present red pine expansion at the northern limit are probably different from those operating in the south. Perhaps, this is indicative of climatic control in the north as opposed to competitive control in the south. It would be interesting to match the pattern of red pine abundance with that of other tree species. For example, is the maximum abundance of other tree species close to the southern limit like it is for red pine? Bonan and Sirois (1992) suggest from physiological data that growth is optimal at the southern range limit for *Picea mariana* (Mill.) B.S.P.

There seems to be a relationship of red pine distribution to temperature. The species is restricted to regions where the minimum temperature was approximately −30°C or colder except in coastal areas (low continentality values in Fig. 10). This could be coincidental or indicative of southern competitor(s) that cannot survive in temperatures −30°C or lower. The lack of a relationship between the extreme minimum temperature and the northern limit of red pine is consistent with research conducted by Sakai and Weiser (1973) who found that twigs of red pine were uninjured by temperatures of −80°C. Earlier work (Haddow 1948) has suggested that red pine distribution is related to the frost-free period. No indication of this relation was present in the data but the frost-free period is a strong function of the local site and may not show up in a synoptic scale study like this. Schooley et al. (1986) found that female strobili on red pine are very sensitive to temperatures below 0°C, implying that late spring frosts might restrict red pine from frost prone areas.

Simple correlation of climatic variables with abundance of a species does not indicate causality but can suggest testable hypotheses. Indeed, a number of studies on germination, survival, phenology, fire regime, cold hardiness, and myc-

orrhizal association of red pine are currently underway (data on file) to investigate some of the suggested relationships between climatic variables and the distribution of red pine (Flannigan 1993).

The dramatic shift in the range of red pine in a $2 \times CO_2$ environment is consistent with changes in distribution predicted by other modelling efforts. Overpeck et al. (1991) found similar movement in the northern pines, including red pine, when modelling pollen abundance with data from three GCMs. Davis and Zabinski (1992) also demonstrated dramatic shifts in the range of four eastern North American tree species in a study using the climatic data from two climate change GCMs.

There are many implications of the striking shift in the range and abundance of red pine. The finding in this study that the southern limit, particularly in the southwest, has shifted farther north and east than the northern limit, indicates that the full geographical range of red pine could shrink in a warmer greenhouse world. At present, red pine is not migrating to the southwest because the forest gives way to grassland. There is a good possibility then that forests around the western Great Lakes will be replaced by grassland in a $2 \times CO_2$ world.

The volume of red pine will increase as the climate warms according to the CCC GCM. However, even if the CCC $2 \times CO_2$ scenario becomes reality in the next century, red pine distribution would not be as shown in Fig. 9. The existing red pine south of the forecast distribution would not die off that rapidly. There would be a resilience in the existing red pine and a lag of perhaps centuries because red pine is relatively long-lived (200–300 years) (Fowells 1965). In the north, red pine expansion might be hindered by inappropriate soils (Melillo et al. 1990). A crucial and confounding factor in these predictions is the large effect that might emerge through interactions between a changing climate and the fire regime. Flannigan and Van Wagner (1991) suggested a 50% increase in the area burned in Canada under a $2 \times CO_2$ world. Also, if the southern limit of red pine is determined by competition, then the competitors may not be able to migrate as fast as the climate permits. Further, the intensity of competition may change as the climate changes. The migration of red pine and other tree species could be delayed or enhanced by human activities. Harvesting and fire control, for examples, would slow the migration of red pine whereas other species may be favoured by these activities. For red pine, plantations may help the northward march; as some of the plantations are near or north of the natural range already and these sites could be used as a springboard for expansion.

Summary

In this study growing degree-days and precipitation were the two most important variables determining red pine abundance. Among the possible explanations for present day boundaries are competition at the southern limit, insufficient moisture at the southwestern limit, and insufficient warmth during the growing season at the northern limit. Greenhouse warming may precipitate a dramatic movement of red pine to the northeast once the species has had sufficient time to migrate. According to this static vegetation model the abundance of red pine in terms of maximum volume per unit area would increase even though the total area would be reduced. However, this is contingent upon the ability of the species to tolerate and react to rapid changes in climate. The forest fire regime is a confounding factor that was not addressed in this work.

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