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The equilibrium response of Canadian vegetation to climate and climatic change was modeled at three organizational levels of the vegetation mosaic. The climatic parameters used as model drivers (i.e., snowpack, degree-days, minimum temperature, soil moisture deficit, and actual evapotranspiration) are components of climate that physiologically constrain the distribution of dominant plant life-forms and species in Canada.

The rule-based Canadian Climate-Vegetation Model (CCVM) predicts the response of vegetation formations to climate. The rules define climatic thresholds across which one formation gives way to another. The CCVM simulation for current climatic conditions is more accurate and detailed than those of other equilibrium models.

A series of ecological response surfaces predict the probability of dominance for eight boreal tree species in Canada with a high degree of success. Variation in the probability of dominance is related to the species' individualistic response to climatic constraints within different airmass regions. A boreal forest-type classification based on the probabilities of dominance shows a high degree of geographic correspondence with observed forest-types.

Under two doubled-CO_2 climatic scenarios, CCVM predicts a reduction in arctic tundra and subarctic woodland, a northward shift in the distribution of boreal evergreen forest, and an expansion of temperate forest, boreal summergreen woodland, and two prairie formations. The response surfaces predict significant changes in species dominance under both climatic scenarios. Species exhibit an individualistic response to climatic change and respond differently under the different scenarios. All but one of the boreal forest-types derived from future probabilities of dominance are analogous to extant forest-types, but fewer types are distinguished. Geographic correspondence in the boreal forest regions simulated by the rule-based and response surface models under both the current and projected climates provides a link between the results of the two modelling approaches.

There are several constraints on the realism of the vegetation scenarios in this study, but they are arguably the most reliable and comprehensive predictions for Canada to date given the direct relationship between the climatic parameters and the distribution of vegetation and the simulation of vegetation at three different organizational levels.

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James Michael Lenihan

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Robert E. Frenkel

Professor of Geography in charge of major

Chairman of Department of Geosciences

Dean of Graduate School

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CHAPTER I:

INTRODUCTION

In a report prepared for the Intergovernmental Panel on Climate Change (IPCC), a body set up jointly by the World Meteorological Organization and the United Nations General Assembly, several hundred international scientists assessed how human activities may be changing the Earth's climate through the greenhouse effect. In the executive summary of the report (Houghton et al. 1990), the members of the panel express their certainty that "emissions resulting from human activities are substantially increasing the atmospheric concentrations of greenhouse gases" and that "these increases will enhance the greenhouse effect, resulting on average in additional warming of the Earth's surface". The scientists went on to predict that under a business-as-usual scenario there will be a 0.3° C per decade increase in the global mean temperature over the next century, a warming trend greater than any over the past 10,000 years. The IPCC scientists also state that the rate of warming is likely to be even higher because positive feedbacks to an enhanced greenhouse effect from natural sources and sinks of greenhouse gases were not considered in their computer simulations.

A relatively simple model of the climate system was used in the IPCC assessment. The best tools available for predicting climatic change are the more complex models of the global climate system known as general circulation models (GCMs). A GCM is an intricate set of computer programs that jointly solve equations of motion for atmospheric winds and equations for conservation and transport of thermal energy and water vapor (Schneider 1989). GCMs display considerable skill in the simulation of the present-day climate in their portrayal of the large-scale distribution of pressure, temperature, wind and precipitation, but it is widely recognized that even these highly-complex models are a less than complete representation of the real climate system (Dickinson 1989). Important components of the long-term climate, especially ocean processes, sea-ice, clouds, and surface features, are represented only in a fairly simplistic manner at present. And because the spatial resolution of GCMs is very coarse, mechanisms occurring on scales smaller than the smallest grid element (typically about 500 km x 500 km) must be represented by parameters that are derived empirically (i.e., not computed from first principles). Much of the disagreement among GCMs in their portrayal of climate and climatic change stems from different parameterizations of important subgrid processes such as convection, cloud formation, and precipitation (Schlesinger and Mitchell 1987). The coarse resolution of GCMs also precludes simulation of detailed mesoscale scenarios (Giorgi and Mearns 1991) which significantly hampers the analysis of impacts at local to regional scales (Gates 1985).

Limitations in computing resources have been the main constraint on the spatial resolution of GCMs. Current GCMs are about as finely-resolved as possible using the fastest and most powerful computers in the world. According to Giorgi and Mearns (1991), it would take two days of computing time on a CRAY supercomputer to simulate 1 day of climate with the National Center for Atmospheric Research's GCM at a scale fine enough to resolve mesoscale detail. Limited computer power also places constraints on the types of climatic change experiments conducted with GCMs. In contrast to the gradual build-up of greenhouse gases in the real world, all but a very few GCM simulations have assumed "instantaneous doubling" in the atmospheric concentration of greenhouse gases in which case the model suddenly has twice as much radiative heating due to CO_2 (Houghton et al. 1990). This causes immediate disequilibrium, and the model has to be run for several decades of simulated time in order to reach a new equilibrium. But time-dependent or "transient" experiments which allow a gradual increase in CO_2 are very much more expensive in computer time than equilibrium studies (Henderson-Sellers 1990). To date only three time-dependent GCM experiments have been published (Houghton et al. 1990), and currently the data from only one of these is widely available for impact studies.

More than twenty GCM simulations of the equilibrium response to an effective doubling of CO_2 have been conducted by various modeling groups. The results of these experiments are summarized in the IPCC report (Houghton et al. 1990). The main features of the predicted changes in climate were ranked by their "certainty", determined from the amount of agreement between models, the researchers' understanding of the model results, and their confidence in the representation of relevant processes. Among the relatively certain predictions are a global average warming of the Earth's surface in the range of 1.5-4.5° C once the climate system comes to equilibrium with an effective doubling of CO_2, which is expected to occur sometime near the end of the next century. The simulated surface warming at high latitudes in late autumn and winter (4-8° c) is enhanced due to decreased sea-ice and snow cover which reduces surface albedo. Both precipitation and evaporation are predicted to increase globally by 3 to 15%, and significant decreases in summer soil moisture are expected over northern mid-latitude continents.

Only over the period since the peak of the last glacial stage can we find a general analog for global climatic change of the magnitude predicted by these GCM experiments. The many radiocarbon-dated records of paleoclimate available for this period suggest the mean global surface air temperature has increased by approximately 4° C since 18 ka (thousand years ago) (Overpeck et al. 1991), which is well within the range of warming predicted for the next century. The paleoecological record (e.g., Huntley and Birks 1983, Webb 1988) suggests that the predicted warming is more than sufficient to cause large changes in the composition and distribution of vegetation. For example, a paleovegetation map for eastern North America at 18 ka based on fossil pollen data (Delcourt and Delcourt 1981) shows spruce and jack pine-dominated boreal forest blanketing the Great Plains, the Appalachian Region, and the upper Atlantic Coastal Plain. Warm-temperate mixed forests of oak, hickory, and southern pines are shown confined to the Gulf and lower Atlantic Coastal Plains. A second map for the mid-Holocene interval at about 5 ka illustrates the displacement of boreal forest by prairie on the Great Plains, the migration of boreal forest-types into present-day Canada behind the retreating Laurentide ice sheet, the formation and expansion of cool-temperate mixed conifer and northern hardwood forest types in southeastern Canada north of the Appalachian Region where warm-temperate hardwood forests are dominant, and the dominance of southern pine-dominated warm-temperate evergreen forests on the Gulf and Atlantic Plains.

Reconstructions such as these suggest that, for the most part, major vegetation units defined by physiognomic criteria (i.e., vegetation formations) retained temporal continuity throughout the 18,000 year period (Delcourt and Delcourt 1981, Ritchie 1987, Webb 1988). Summaries of the pollen record from the viewpoint of the individualistic response of species to climatic change suggests that assemblages within formations have been more ephemeral (Webb 1988). The pollen record also indicates migration rather than evolutionary change has been the predominant response of species to climatic change since 18 ka (Bradshaw and McNeilly 1991), and that the response time of vegetation has been sufficiently small compared to the time scale of the climatic forcing so that vegetation has generally been in quasi-equilibrium with climate over the past 18,000 years (Webb 1986, 1988).

The paleoecological record is the only source of empirical information on the magnitude, distribution, and rate of vegetation change that can result from climatic change as large as that predicted by doubled-CO_2 GCM experiments. But in several respects, the record of vegetation change since 18 ka is an imperfect analog for predicting the response to an enhanced greenhouse effect (Crowley 1990, Mitchell 1990). Climatic change over this period has been primarily in response to changes in insolation, the melting of ice sheets, and the warming of sea-surface temperatures (Kutzbach and Guetter

1986). In contrast, the future dominance of climatic forcing by greenhouse gases could lead to rates and patterns of climate and vegetation change without precedence in the geological record. For instance, the warming due to an enhanced greenhouse effect is predicted to be more rapid than any time during the past 18,000 years (Overpeck et al. 1991). And future climatic change is likely to be characterized by temperature increases in both the winter and summer (Houghton et al. 1990), while increases in the past were primarily in the summer (COHMAP Members 1988). These differences in climatic forcing and the response of the climatic system mean we must depend on models, and not paleoecological analogs, for making realistic predictions of future vegetation change. Nonetheless, one of the few ways to test the performance of these models under altered conditions (i.e., outside the range of the modern climatic data used in their calibration) is against the database provided by the geological record (Prentice et al. 1991).

There have been two basic approaches to modeling the vegetation response to an altered climate (Solomon 1986a, Prentice and Solomon 1991). The first approach utilizes dynamic vegetation models that are capable of predicting the transient response of vegetation to climate change. Most dynamic models simulate processes controlling individual tree establishment, growth, and mortality on small forest plots or "gaps" (e.g., 0.1 ha) (Shugart 1984). Plant growth is usually determined by climatic response functions based on empirical growth data, and other processes are represented by both deterministic and stochastic equations. Most forest gap models are variants of the FORET model (Shugart and West 1977), which in turn was originally developed from the JABOWA model (Botkin et al. 1972) which simulates gap dynamics in the northern hardwood forests of the eastern United States.

Many different forest gap models have been developed for different forest-types and some have been applied to simulate time-dependent changes in species composition and abundance under altered climates. For example, Davis and Botkin (1985) used the JABOWA model to examine the sensitivity of cool temperate forests to rapid temperature change. They found 100-200 year lags in the vegetation response to climatic cooling caused by different sensitivities of adult trees and younger stages, and by the different life histories of the dominant species. Solomon (1986b) used the FORENA model to simulate changes in vegetation at 21 locations in eastern North America. The simulations were all initiated from a bare plot and run for 400 model years under modern climatic conditions. After year 400, the climatic conditions were changed linearly to reach a GCM-defined doubled-CO_2 climate by year 500. The major effects of changes in climate included a dieback of extant trees at most sites, only a partial recovery of biomass and some conversion to prairie at the temperate deciduous forest sites, and a gradual replacement of conifers by deciduous hardwoods at the boreal/deciduous forest and boreal forest sites. Transient responses in species composition continued for as much as 300 years after climatic changes ceased. Pastor and Post (1988) used a another population-based forest growth model to investigate the possible responses of different boreal forest types in eastern North America to a warmer and generally drier climate. They found increases in forest productivity and biomass on soils that retained adequate water for tree growth and decreases on soils with inadequate water. Bonan et al. (1990) used a forest gap model to examine the sensitivity of Alaskan boreal forest-types to climatic warming over a period of 200 years. Cold black spruce forests were converted to warmer mixed hardwood-spruce forests, that in turn changed to dry aspen forest or steppe-like vegetation through a complex series of interactions involving increases in evapotranspiration, fire severity, and soil thaw depth and decreases in soil moisture. Overpeck et al. (1990) carried out sensitivity tests with a forest gap model on four forest-types in eastern North America and concluded that increases in forest disturbance could significantly alter the response of forests to future warming.

The ability to predict the transient response of vegetation to climatic change is an attractive aspect of the dynamic approach, but several obstacles stand in the way of using currently available dynamic vegetation models in more extensive global change research (Solomon 1986a). For example, it is impractical to use gap-level models to predict shifts in vegetation beyond those at the local-scale because of the large number of points that would have to be simulated. Dynamic models also require much more information on the life history of species and their requirements than is easily available or even known for some areas of the globe. And even if such data were available and the models could be run at a sufficient number of points, simulations with existing gap models would, for the most part, cover only forested landscapes.

There is another approach to vegetation modeling which simulates the re-distribution of vegetation at some indeterminate point in time when vegetation exists in quasi-equilibrium with a changed climate. This equilibrium approach is temporally static, but unlike the dynamic approach, it generally requires far less information yet provides a comprehensive estimate of the potential magnitude of the vegetation response at regional to global scales (Solomon 1986a). Moreover, the restriction of equilibrium models to estimating steady-state conditions matches that of the great majority of the enhanced greenhouse experiments conducted with GCMs (Houghton et al. 1990).

The two principal methods for predicting the equilibrium response of vegetation to climate and climatic change are climate-vegetation classification and climatic response surfaces (Prentice and Solomon 1991). Both methods are based on the premise that vegetation distribution at regional to global scales is primarily controlled by climate (Woodward 1987), and that finer-scale variations due to such factors as topography, soils, disturbance regimes, and biotic interactions are averaged out at the coarser scales of application (White 1979, Huntley et al. 1989). The climate-vegetation classification method is based on correlations between geographic patterns of selected climatic and vegetation parameters on the present landscape. These correlations together with predicted values of the climatic variables can be used to forecast the redistribution of vegetation under an altered climate. A climatic response surface is an empirical function in which some measure of a taxon's abundance or importance is related to a weighted combination of climatic variables. When coupled with simulated future values of the climatic parameters, response surfaces can estimate the abundance or importance of different taxa under a changed climate.

The Holdridge (1947, 1967) vegetation model is a well-known example of the classification method that has been used to predict the equilibrium response to climatic change at a global-scale. The Holdridge model uses mean annual precipitation, biotemperature (i.e., the sum of the mean monthly temperatures greater than 0° C divided by twelve), and a potential evapotranspiration (PET) ratio (i.e., PET/mean annual precipitation) to delineate major life-zones. PET is defined as a linear function of biotemperature and thus adds no extra information to the model. Holdridge (1947, 1967) created an axis system using these climatic parameters that in the model defines equal-area, hexagonal-shaped zones in climatic space occupied by about thirty life-zones. The life-zones are thus delineated entirely in terms of the climatic variables rather than vegetational limits. That is, the scheme describes the plants that grow in a given climate, not where the climate is suitable for given plants to grow.

Emanuel et al. (1985a, 1985b) coupled the Holdridge model with a doubled-CO_2 climatic scenario in which precipitation was maintained at current levels. The results indicated that climatic warming could cause over 30 percent of the earth's vegetation to shift from one Holdridge life-zone to another. The largest changes were predicted to occur at high latitudes where the simulated temperature increase was the largest and the biotemperature intervals defining the vegetation zones are the smallest. Leemans (1990) ran the Holdridge model with a different doubled-CO_2 climatic scenario and found that almost 50% of the world's vegetation changed from one zone to another.

In contrast to the Emanuel et al. (1985a, 1985b) simulation, there was less of a decrease in the area of boreal forest and a greater increase in the extent of tropical life zones. Prentice and Fung (1990) used a modified Holdridge model (Prentice 1990) with yet another doubled-CO_2 climatic scenario and obtained results similar to those of Leemans (1990).

The Box (1981) climate-vegetation model is still another example of the classification method used to predict the equilibrium response to climate. Box (1981) correlated eight different climatic parameters with the range limits of seventy-seven life-forms and defined a "climatic envelope" for each life-form. The climatic parameters include the minimum and maximum monthly temperatures, the annual range of monthly temperatures, minimum and maximum monthly precipitation, annual precipitation, average precipitation of the warmest month, and a moisture index (i.e., annual precipitation/ Thornthwaite annual PET). If, at a given location, any one of these climatic parameters falls outside the defined limits for a given life-form, then the environment is considered unsuitable for it's survival. The Box model can predict combinations of growth forms at a given location and is thus capable of predicting canopy structure.

There is just one published study known to this author which applies the Box model to the problem of the vegetation response to climatic change. The climatic limits set by Box

(1981) for boreal short-needled trees were recalibrated by Sargent (1988) against the distribution of boreal evergreen forest on a forest regions map of Canada (Rowe 1972). Sargent (1988) then used the re-defined limits with a doubled-CO_2 climatic scenario to determine the potential redistribution of Canadian boreal forest. The results indicated that under a warmed climate, the area climatically suitable for boreal forest would shift northward and decrease by about 1×10^8 ha.

Rizzo and Wiken (1992) also used the climate-vegetation classification method to assess the sensitivity of Canadian ecosystems to climatic change. Nine measures of mean annual and seasonal values of temperature and precipitation were used as independent variables in a series of discriminant functions, one for each province in a modified version of the Ecoclimatic Regions of Canada classification scheme (Ecoregions Working Group 1989). The functions were calibrated using climatic data for current conditions distributed on a grid that included all of Canada east of the Cordillera. Doubled-CO_2 climatic data on the same grid were then processed through the discriminant functions. The results suggested major changes in Canada's ecosystems, including reductions in the areal extent of the arctic, subarctic, and boreal ecoclimatic provinces, and increases in the size of the temperate and grassland provinces.

Climate-vegetation classification models usually predict the distribution of physiognomic units at high levels in the organization of vegetation (e.g., assemblages of major life-forms or vegetation formations). The use of classification models in global change studies has been criticized (e.g., Davis 1989, Graham and Grimm 1990) for ignoring the individualistic response of species to climate change seen in the fossil record, but this criticism may be largely unwarranted when directed at vegetation models that predict the distribution of major physiognomic types. Pollen records from sites throughout eastern North America clearly demonstrate individualistic variation in species composition and abundance with environmental change (Webb 1987, 1988), but there is little evidence of "non-analogue" assemblages of major life-forms at the formation-level (Delcourt and Delcourt 1981, Webb 1988). For example, while it may be true that "boreal species were associated very differently from the modern boreal forests of Canada" (Davis 1981) at the last glacial maximum in North America, it is also true that, physiognomically, these associations comprised open to closed forests of boreal/montane needleleaved trees, and were therefore analogous to modern subarctic evergreen woodland or boreal evergreen forest at the formation-level of classification (Ritchie 1987). Davis (1989) states that "even the physiognomy of major vegetation units does not remain constant through time", but the single example she cites in support of her contention, oak savanna in North

America during the mid-Holocene, is analogous to the modern oak savanna of Wisconsin and Minnesota (Küchler 1964).

The individualistic response of species should be an integral part of any attempt to model the redistribution of vegetation at organizational levels below the physiognomic. Climatic response surfaces, the second method used to model the equilibrium response of vegetation to climate, are often used for simulation at the floristic-level of detail (Bartlein et al. 1986). Climatic response surfaces derived for surface pollen data have been used to simulate the distribution and abundance of individual taxa under current climatic conditions in eastern North America (Bartlein et al. 1986), northern North America (Anderson et al. 1991) and Europe (Huntley et al. 1989). These studies support the hypothesis that plant taxa response individualistically to the different climatic variables that have been employed as predictor variables (i.e., mean January temperature, mean July temperature, and mean annual precipitation). Response surfaces for pollen data have also been used to confirm the dynamic equilibrium hypothesis for continental-scale patterns of vegetation over the past 18,000 years (Prentice 1983, Prentice et al. 1991), to reconstruct paleoclimates (Prentice et al. 1991), and to test paleoclimatic hypotheses generated by GCM experiments (Webb et al. 1987).

There is only one published study known to this author which uses climatic response surfaces to predict the equilibrium response of individual taxa to projected climatic change due to an enhanced greenhouse effect. Overpeck et al. (1991) developed response surfaces for seven pollen types in eastern North America using three climatic variables (i.e., mean January temperature, mean July temperature, and mean annual precipitation). When the response surfaces were coupled with future values of climate simulated by three different GCM doubled-CO_2 experiments, changes in the equilibrium distributions of the seven taxa were greater than the overall changes for the same taxa over the past 10,000 years. Shifts in ranges and abundance maxima were predicted to be as much as 500 to 1000 km.

To date, nearly all applications of equilibrium models in global change studies have been alike in their use of annual or monthly measures of temperature and precipitation as model drivers. Since these aspects of climate and the distribution of plants are not necessarily related in a cause-and-effect manner (Woodward 1987), there is some uncertainty in the implicit assumption that the correlations central to these modeling efforts will persist under altered conditions (Prentice and Solomon 1991, Woodward and Rochefort 1991). For example, a prairie-forest boundary might be causally-related to a particular level of soil moisture deficit (Woodward 1987) which, in turn, is closely correlated to a threshold of mean annual precipitation under current conditions (e.g., 500 mm in the Holdridge (1947, 1967) model). Using the precipitation threshold to predict the position of the boundary under a warmed climate would result in an erroneous prediction if increased potential evapotranspiration accompanied by little or no change in precipitation yielded higher levels of soil moisture deficit. Non-causal relationships like that between annual precipitation and the forest-prairie ecotone may change with complex changes in climatic regimes, but physiological constraints on the survival, growth, and reproduction of plants will likely persist, at least within the ecological time-frame (i.e., in the absence of evolution).

STUDY OBJECTIVES

In this dissertation, vegetation models that include environmental constraints with a physiological and biological rationale were developed to more reliably predict the equilibrium response of Canadian vegetation to climatic change. The focus on Canada was, in part, prompted by the research agenda of the Global Processes and Effects Program at the U.S. Environmental Protection Agency's Environmental Research Laboratory in Corvallis, Oregon. As a cooperator in this program, the author helped develop a rule-based, equilibrium model for United States vegetation based on a process-level understanding of the response of vegetation to climate (Neilson et al. 1989, 1992a, 1992b). The models developed in this study represent a significant enhancement of the original approach, and are a first step in the geographic extension of the physiologically-based method of vegetation modelling to the rest of the globe.

The potential impact of projected climatic change on Canada's economy and social well-being would, in itself, be sufficient rationale for assessing the sensitivity of Canadian vegetation to an enhanced greenhouse effect (Kemp 1991). Natural vegetation is a major component of ecosystems which provide renewable resources supporting critical national industries and activities linked to forestry, agriculture, wildlife, and recreation. Changes in Canadian ecosystems with climatic warming could affect the traditional socio-economic fabric of the nation. For example, wood products provided by the boreal forest ecosystem are essential to the economies of the lumbering, pulp, and paper towns scattered across the northern reaches of the provinces from Quebec to Alberta, and forest products are an integral part of Canada's international trade as well. Major changes in the location, extent, or character of the boreal forest could result in severe dislocation of the softwood timber trade, and some of the forest harvesting centers might not survive. A better understanding of the relative sensitivity of Canada's ecosystems to climatic warming is a prerequisite to an evaluation of policy options for mitigating and responding to such changes.

The active participation of the boreal ecosystem in the global carbon cycle and the potential for biospheric feedbacks during climatic change are another motivation for a better understanding of the potential sensitivity of Canadian vegetation to an enhanced greenhouse effect. The boreal forests of Canada comprise about a third of the circumpolar boreal forest which is a major repository of the world's terrestrial organic carbon (Bolin 1986). And there is a strong evidence of a causal relationship between the seasonal dynamics of carbon dioxide and the seasonal growth of the boreal forests (Fung et al. 1987, D'Arrigo et al. 1987). Any net reduction in the areal extent of Canadian boreal forest could result in the release of enough carbon dioxide to constitute a significant positive feedback to climatic warming (Houghton and Woodwell 1989).

The objective of this dissertation was to develop a set of models to more reliably predict the equilibrium response of Canadian vegetation to climate and GCM-projected climatic change at three organizational levels of the vegetation mosaic. In Chapter II, a rule-based climate-vegetation classification model is developed to predict the equilibrium response of formation-level vegetation to climatic parameters bearing a direct relationship to the growth, reproduction, and survival of plants. The same set of climatic parameters are used in Chapter III to derive climatic response surfaces which predict the probability of dominance for eight Canadian tree species. A classification of boreal forest-types based on the probabilities of species dominance under current climatic conditions is also described in this chapter. In Chapter III, the models developed in the preceding chapters are used to predict the equilibrium response of vegetation formations, boreal forest-types, and individual species under two doubled-CO_2 climatic scenarios. In the final chapter, Chapter IV, the results of the study are summarized.

CHAPTER II:

A RULE-BASED VEGETATION FORMATION MODEL FOR CANADA

INTRODUCTION

In this chapter, a rule-based climate-vegetation classification model is developed to predict the equilibrium response of Canadian vegetation formations to the modern climate. Unlike the Holdridge (1947,1967) and Box (1981) classification models, the Canadian Climate-Vegetation Model (CCVM) is based on well-documented, physiologically-based relationships between climate and the composition and structure of vegetation. This chapter describes the development of the climatic and vegetation databases for calibration of the model, the rule-base structure of the model, and the physiological and biological basis for the climatic thresholds defining the rules. The accuracy of the model's simulation of vegetation distribution under current conditions is evaluated, as is the relative performance of the model in comparison to the Holdridge and Box models. Finally, geographic relationships between the climatic thresholds in the model and the large-scale structure and dynamics of the atmosphere are discussed.

METHODS

The Climatic Data Base

The foundation for much of the climatic data driving CCVM is the mean monthly temperature and total monthly precipitation values for Canada extracted from the International Institute for Applied Systems Analysis (IIASA) climatic data base. Leemans and Cramer (1990) assembled this database from several different data sources, selecting stations that included data for the period of 1930-1960. The monthly precipitation and temperature data for the selected stations were then interpolated to a geographic grid with a 0.5° latitude x 0.5° longitude (i.e., half-degree) resolution. The temperature values were corrected for altitude using a environmental lapse rate of 0.6° C/100 m, but the precipitation values remained uncorrected. The resolution of the IIASA data determined that of the current application of CCVM; there are just over 10,000 half-degree grid cells in each layer of the model database. However, since CCVM is a simple 1-D model, it could be applied at almost any resolution for which the climatic inputs can be specified.

In contrast to the Holdridge and Box equilibrium models, monthly or annual values for temperature and precipitation do not appear as drivers in CCVM, at least not directly. The thermal parameters in the model, degree-days and absolute minimum temperature, are more directly related to the survival, growth, and reproduction of plants as discussed below. In order to calculate degree-days (an index of the heat and length of the growing season), 365 mean daily temperatures at each grid cell were estimated by linear interpolation between the monthly temperature values. The number of degree-days were then computed from these estimates using a 0° C threshold (Woodward 1987). The absolute minimum temperature at each grid cell was estimated from the coldest mean monthly temperature using a quadratic regression model (Figure II.1) based on data from 271 airport stations (WeatherDisc Associates 1990).

It is axiomatic in plant ecology that moisture alone is not of great physiological importance to plants, but rather moisture as it interacts with energy (Stephenson 1990). The Holdridge and Box equilibrium models attempt to account for this interaction by including indices based on ratios between annual precipitation and annual potential evapotranspiration. Indices such as these cannot distinguish between climates where annual energy and water supplies are similar but the seasonal timing of the two are different. In order to explicitly incorporate the seasonal interactions of energy and moisture into CCVM, a simple water balance algorithm was developed that calculates snowpack, actual evapotranspiration, and soil moisture deficit at a monthly time step.

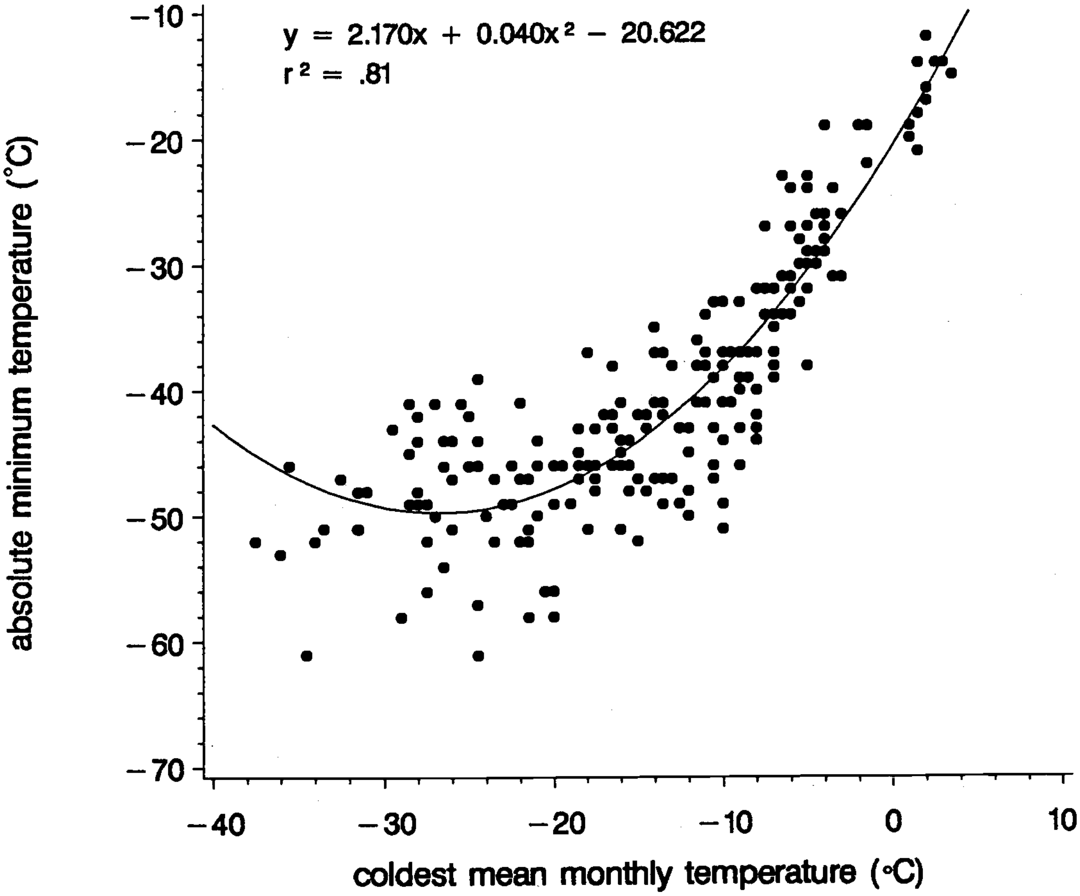


Figure II.1 Relationship between coldest mean monthly temperature and absolute minimum temperature. Data from 271 airfield meterological stations across Canada.

Lacking the data that would support a physically-based calculation of potential evapotranspiration (PET) across Canada, Eagleman's (1967) empirically-derived equation was used to calculate monthly PET. Required inputs into Eagleman's model are temperature (expressed as saturated vapor pressure) and relative humidity. Monthly values of relative humidity at the Canadian airport sites (WeatherDisc Associates 1990) were interpolated toward the half-degree grid using an inverse distance-squared algorithm. PET values derived from the Eagleman model have been shown to agree well with those from the physically-based Budyko and Penman methods (Eagleman 1967, 1973), both of which require several additional climatic parameters. In the same comparison, the performance of the Eagleman method was significantly better than that of the empirical Thornthwaite (1948) model which is based solely on temperature.

Actual evapotranspiration (AET) is estimated in the water balance algorithm as a percentage of monthly PET, and this percentage is calculated as a linear function of the percentage of soil saturation (Thornthwaite and Mather 1955). This provides a rough estimate of the decline in transpiration rates with decreasing soil moisture content (Denmead and Shaw 1962). A continental-scale data set specifying the water-holding capacity of Canadian soils was unavailable, so the field capacity of the soil at each grid cell was assumed to be 100 mm in this study. The storage of water in snowpack during the cold season is calculated in the water balance algorithm by accumulating monthly precipitation values in a storage term when the corresponding monthly temperatures are at or below freezing. In the first month with a mean temperature greater than zero, all the snowpack storage is made available for recharging soil moisture and/or adding to the runoff. Runoff is simply the overflow of excess liquid water when soils are saturated.

AET estimated with this algorithm is not constrained by leaf area or stomatal conductance and is, therefore, only an estimate of the true AET. It does, however, provide a quasi-mechanistic estimate of the seasonality of the water balance. The performance of the water balance algorithm was compared to a map of observed runoff and the runoff ratio for Canada (Hare and Thomas 1974). At the grid locations of 35 standard meteorological stations (Muller 1982), 71% and 78% of the runoff and runoff ratio estimates respectively fell within the appropriate contour intervals on the map. A similar comparison of the estimated annual snowpack/annual precipitation ratio and a map of observed values (Hare and Hay 1971) showed 84% agreement.

The Vegetation Data Base

The vegetation regions map in the National Atlas of Canada (1973) was used to develop a formation-level vegetation data set for Canada. The vegetation data served as a baseline for the calibration of CCVM. Aggregation of the original mapping units into formation types closely followed the formation-level grouping in the map legend. The formations and their distribution are shown in Figure II.2. The high arctic desert is characterized by the dominance of lichens and perennial herbs and a low cover by woody vegetation. The low arctic shrub tundra is distinguished by dominance of dwarf shrubs and graminoids, and the absence of upright trees. The subarctic evergreen woodland is the broad ecotone between tundra and closed forest (i.e. the region between the tree-line and the continuous forest line sensu Payette (1983)). The subalpine woodlands in the western mountains are also included in this type. The boreal evergreen forest comprises the greater part of the forested area of Canada and, at least on upland sites, is characterized by a closed canopy dominated by black spruce (<u>Picea</u> <u>mariana</u> (Mill.) B.S.P.), white spruce (<u>Picea</u> <u>glauca</u> (Moench) Voss), jack pine (<u>Pinus</u> <u>banksiana</u> Lamb.), and balsam fir (<u>Abies</u> <u>balsamea</u> (L.) Mill.). The absence of tree species more characteristic of temperate forests to the south also helps delineate the boreal forest. The temperate evergreen forest is characterized by the

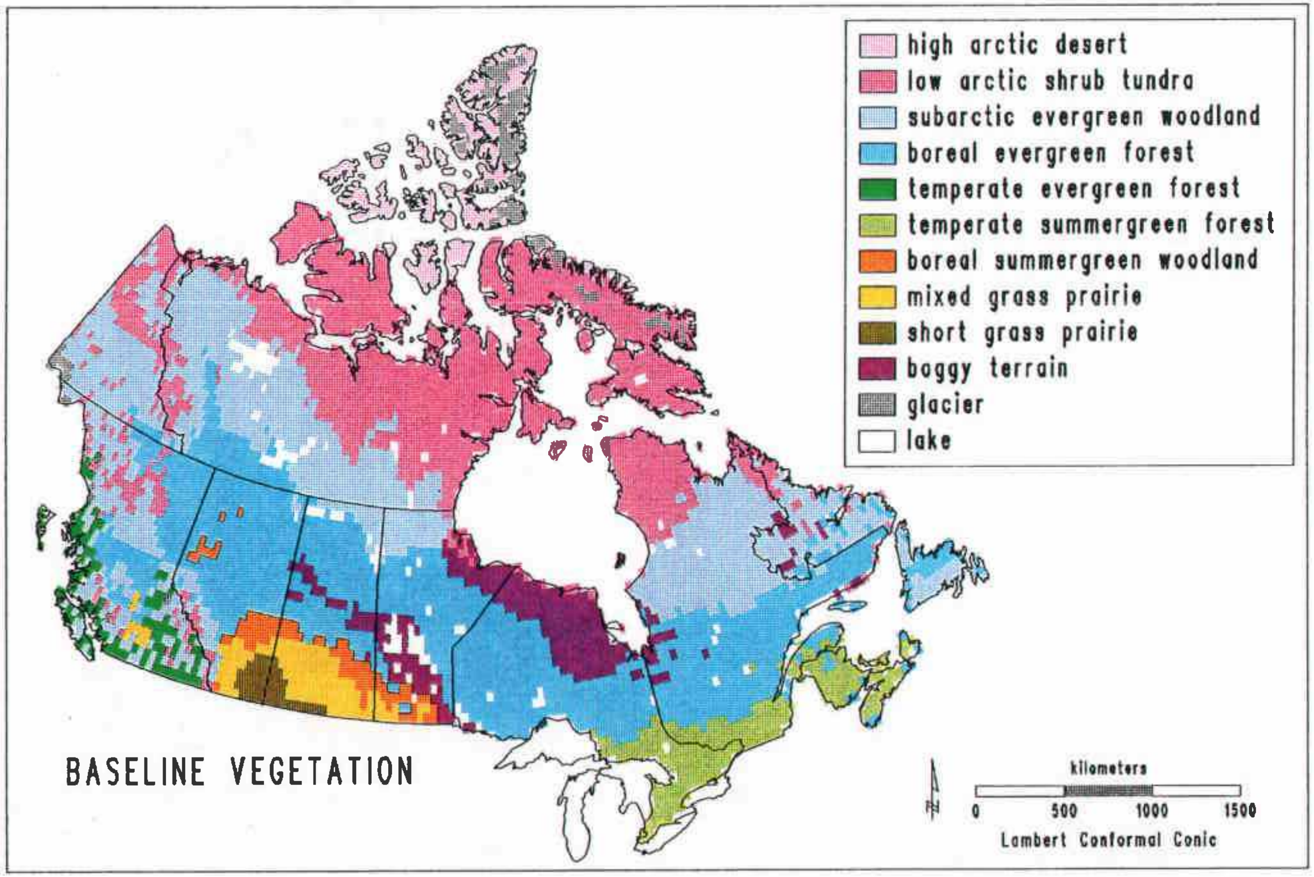
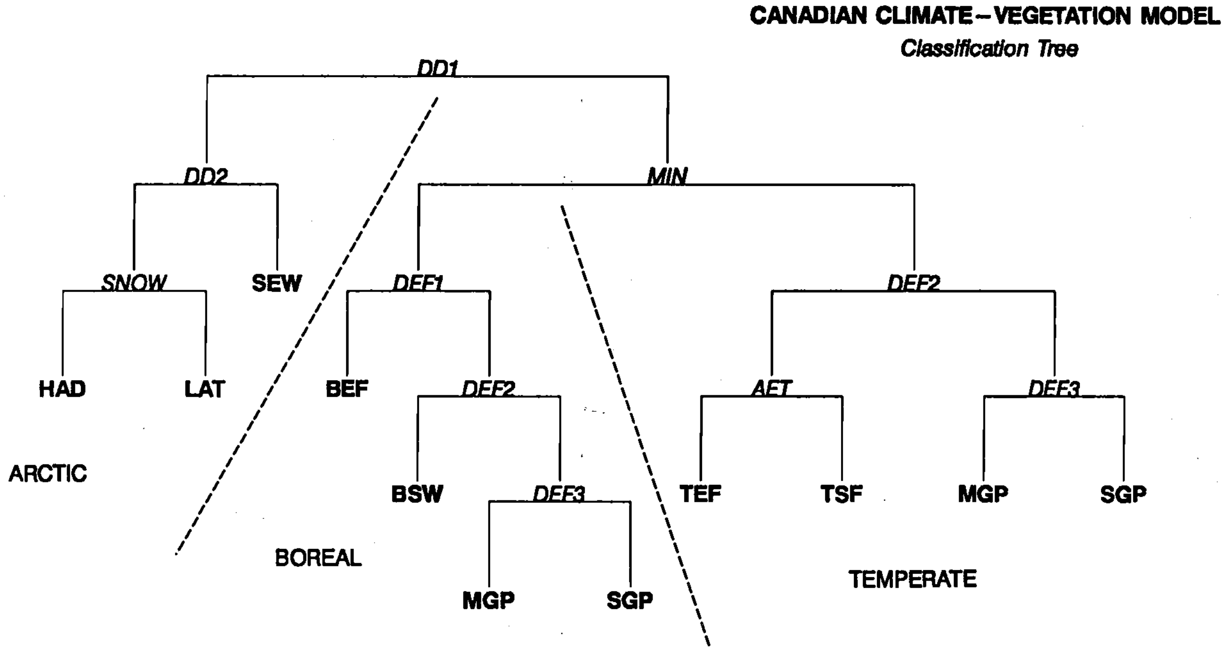


Figure II.2. Formation-level vegetation of Canada based on the vegetation regions map in the National Atlas of Canada (1973a) dominance of coniferous species that comprise the coastal and intermountain forests of southwestern British Columbia. These include Sitka spruce (Picea sitchensis (Bong.) Carr.), western hemlock (Tsuga heterophylla (Raf.) Sarg.), western red cedar (Thuja plicata Donn), and Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco). The temperate summergreen forest is a broad transition zone between boreal forest and the eastern deciduous forests of the United States. As defined here, this type is characterized by the co-dominance of broadleaf deciduous hardwoods, most notably sugar maple (Acer saccharum Marsh.). The boreal summergreen woodland occupies the transitional zone between boreal forest and prairie in south-central Canada, and is characterized by parklike stands of trembling aspen (Populus tremuloides Michx.) with grassy understories. The mixed grass prairie is characterized by the dominance of wheatgrass (Agropyron spp.), while the dominance of blue grama (Bouteloua gracilis (H.B.K.) Lag. ex Steud.) distinguishes the short grass prairie.

The Model Structure

CCVM is structured as a rule-base embedded in a binary classification tree (Figure II.3). The branching pattern of the tree is used to determine the vegetation formation-membership of each grid cell much like one uses a dichotomous key to classify a plant to species. At each branch node in the



DD1	1330	^{0}C	boreal tree reproduction
DD2	735	^{0}C	boreal tree resistance to winter dessication
SNOW	96	mm	woody plant protection from winter dessication
MIN	−42	^{0}C	temperate tree resistance to frost damage
DEF1	115	mm	forest leaf area
DEF2	180	mm	woodland leaf area
DEF3	249	mm	mixed grass leaf area
AET	172	mm	summergreen tree carbon gain

HAD	High Arctic Desert
LAT	Low Arctic Shrub Tundra
SEW	Subarctic Evergreen Woodland
BEF	Boreal Evergreen Woodland
BSW	Boreal Summergreen Woodland
TEF	Temperate Evergreen Forest
TSF	Temperate Summergreen Forest
MGP	Mixed Grass Prairie
SGP	Short Grass Prairie

Figure II.3. Classification tree and climatic thresholds for the Canadian Climate-Vegetation Model. Follow left (right) branch from a branch node when value of climatic parameter is less (more) than the climatic threshold.

tree there is a splitting rule (e.g., DD1) which appears in the model source code as a conditional statement of the form: if variable j is less than level x (e.g., if degree-days are less than 1330° C). The true/false solutions to the conditional statements determine the path of traversal through the classification tree towards one of the vegetation formations at the terminal nodes of the tree. The splitting rules define critical climatic thresholds which physiologically constrain the distributions of major plant life-forms and across which one vegetation formation gives way to another.

The climatic and vegetation data sets described above were used to calibrate the rules. The vegetation formation at each grid cell was pre-classified in accordance with the baseline map (Figure II.2). Starting from initial estimates of the threshold values, the classification tree and the climatic data were used to predict the vegetation formation at each cell. Maps of the baseline and predicted vegetation were compared in a geographic information system to assess the current performance of the model, and the threshold values were adjusted accordingly. This procedure was repeated through several iterations until the rule-base was fully calibrated. The hierarchical structure of the classification tree favored a systematic approach to rule calibration (i.e., rules were calibrated in order of their position from the root to successively higher branch nodes in the tree). Most rules exhibited one or more "balance points" (Neilson et al. 1992). That is, adjusting the threshold value of a rule continued to increase the correct classification of a particular formation, but there was a point at which further adjustment occurred at the expense of the correct classification of other formations. The final calibrated values of the rules (shown at the lower left in Figure II.3) are near these balance points.

The Physiological and Biological Rationale for the Rules

Beginning at the root of the classification tree (Figure II.3), a degree-day rule (DD1) splits the arctic formation group from the boreal/temperate formation group; this split corresponds to the ecotone between subarctic evergreen woodland and boreal evergreen forest (i.e., the continuous forest line sensu Payette (1983)). There have been several studies of tree regeneration along transects across this ecotone (Larsen 1989), and all have documented a gradual decline in sexual reproduction as one moves from closed boreal forest to open subarctic woodland. For instance, Black and Bliss (1980) conducted field and chamber studies of seed viability, germination, and seedling survival as related to temperature and the length of the growing season. They concluded that 1330 degree-days was the lower limit for reliable establishment of black spruce, the dominant species at the northern forest border in Canada. A shorter growing season below this threshold results in irregular establishment which, together with frequent fire and inhibition of seedling growth by lichen mats (Elliott-Fisk 1988), conserves the open nature of the subarctic woodland. The calibrated value of the DD1 rule (Figure II.3) converged on the same degree-day threshold value reported by Black and Bliss (1980).

Moving down into the arctic section of the classification tree (Figure II.3), the degree-day rule at the next branch node (DD2) splits subarctic evergreen woodland from the arctic desert and tundra formations; this split corresponds to the limit of upright tree growth (i.e., the tree line sensu Payette (1983)). Many hypotheses have been put forth to explain the occurrence of tree-lines in arctic and alpine regions (Tranquillini 1979). One explanation is that new shoots of trees may mature insufficiently due to a shortness of the growing season and a resulting decline in dry matter production. Consequently, the transpiration resistance of cuticles and outer tissues is not adequate to give protection against winter desiccation to shoots projecting above the snow surface (Wardle 1974, Tranquillini 1979). Experimental evidence for the close relationship between length of growing season and cuticular resistance to transpiration has been provided by Tranquillini (1979) and others. Woodward (1987) compiled the results of many of these studies and estimated heat sums required for full leaf expansion. For boreal tree species, these sums range from 600 to 950 degree-days, a result in accordance with the calibrated threshold in CCVM of 735 degree-days (Figure II.3).

The snowpack rule (SNOW) at the next node down in the arctic section of the tree (Figure II.3) distinguishes high arctic desert from low arctic shrub tundra; a split that corresponds to the northern limit of most woody plant growth (Edlund 1986). The dwarf shrubs and krummholz of the shrub tundra are also at risk from winter desiccation given the frozen soils, the high saturation deficit of frigid air, and the windswept nature of much of the Arctic during the cold season. Snowpack protects low shrubs from winds and provides them with a more humid environment, thus reducing the rate of winter transpiration (Warren-Wilson 1959, Bliss 1971, Saville 1972, Billings 1974). The thermal protection provided by snow cover may also be important to the survival of broad-leaved evergreen shrubs as they are more susceptible to frost damage than summergreen types (Woodward 1987). The importance of the protection provided by snow is evident in the mosaic patterning of vegetation in the high arctic desert. Lowland depressions where snow accumulates are the only habitats that support any woody growth (Edlund 1983). The calibrated value of the SNOW rule, 96 mm of snow in water equivalents (Figure II.3), is roughly equivalent to a snow depth of 96 cm using an average density conversion factor of 0.1 (Hare and Thomas 1974). This depth is very close to 100 cm, the reported limit of shrub heights in the high arctic desert (Bliss 1988).

The absolute minimum temperature rule (MIN) splits the boreal formation group from the temperate formation group (Figure II.3). The split corresponds to the ecotone between the boreal evergreen forest and temperate forest formations. Ecophysiological research provides strong evidence for the physiological control of this ecotone by minimum temperature. In experimental studies of the freezing resistance of North American trees, Sakai and Weiser (1973) and George et al. (1974) found the approximate threshold of survival for many evergreen conifers and summergreen hardwoods is -40 to -45° C. Pure, supercooled water nucleates spontaneously *in vitro* at about -40° C (Woodward 1987), suggesting these species are solely dependent on deep supercooling (Burke et al. 1976, Sakai and Larcher 1987) as a mechanism of avoiding intercellular freezing. However, boreal and subalpine conifers and summergreen hardwoods in the Populus and Betula genera were found to survive even the lowest experimental temperatures (typically -70 to -80° C). These species apparently avoid intercellular freezing by a process called "extraorgan freezing" (Sakai and Larcher 1987) in which water diffuses from a supercooled organ to a specific space outside the organ, so that no freezable water is left within the organ. The calibrated level of the MIN rule (Figure II.3) (i.e., -42° C;

predicted by a coldest monthly mean temperature of -13° C in the regression model, Figure II.1) is near the mid-point of the range of experimentally observed threshold temperatures for northern temperate tree species.

Moving into the boreal section of the classification tree (Figure II.3), there is a series of annual soil moisture deficit rules (DEF1, DEF2, and DEF3). The DEF1 splits boreal evergreen forest from the rest of the group, DEF2 splits boreal summergreen woodland from the prairie types, and DEF3 splits mixed grass from short grass prairie. Several authors (Gholtz et al. 1976, Grier and Running 1977, and Waring et. al 1978) have shown there is a positive relationship between leaf area and measures of the water available to plants during the growing season. More importantly from a physiological standpoint, Woodward (1987) has shown that, in the absence of thermal constraints on growth, the hydrological budget may be used to predict the maximum leaf area which can develop at a site. Woodward (1987) assumes that vegetation exists in dynamic equilibrium with the water balance at a given site, so that there is just enough leaf area to insure nearly all the available soil water is transpired by the end of the growing season. If there is too much leaf area, it will be reduced through drought stress. If there is too little leaf area, then plants will capitalize on the resulting moisture surplus by producing more leaf area, given sufficient energy.

Woodward's (1987) model uses energy and water balance equations to calculate soil moisture deficit, then uses the deficit to predict leaf-area index, and finally uses the leaf-area index to predict vegetation structure. In CCVM, vegetation structure is predicted directly from the annual soil moisture deficit. Through calibration, three thresholds of deficit have been defined corresponding to the forest-woodland, woodland-prairie, and mixed grass-short grass prairie ecotones (Figure II.3). Note that two of the soil moisture deficit rules used in the boreal section (DEF2 and DEF3) are also used in the temperate section of the classification tree to split forest from prairie and mixed grass from short grass prairie.

Several authors (e.g., Halliday 1937, Bird 1961, Looman 1979) report expansion of tree cover in woodlands and invasion of prairies by trees since fire suppression began about seventy years ago. They conclude that fire is important in the maintenance of these formations in south-central Canada. However, the only broad-scale study of the southern border of the boreal evergreen forest (Zoltai 1975) suggests tree cover has remained unchanged since settlement, despite human modification of the natural fire regime. Regardless of the relative importance of fire in these systems, the probability of fire at broad spatio-temporal scales is largely determined by climatic variables, especially the seasonality of precipitation and the duration and intensity of dry periods

(Flannigan and Harrington 1988, Clark 1989). This suggests that fire as an ecological factor is ultimately dependent on climate. The annual soil moisture deficit levels used in CCVM to define conditions unfavorable for the establishment of a closed canopy in a woodland (i.e., DEF1), or trees in a prairie (i.e., DEF2), are a simplification of the more complex relationship between soil moisture, fire, and vegetation dynamics. Mean values used to describe climate conceal the episodic patterns of weather that create conditions favorable for establishment processes of specific physiognomic types, or conditions conducive to mortality (Neilson 1987). During moist periods, tree encroachment may be checked by fire; but even in the absence of fire, intermittent drought may be sufficient to maintain open woodlands and treeless prairies (Coupland 1958).

A summertime actual evapotranspiration rule (AET) splits the temperate evergreen forest of British Columbia from the temperate summergreen forest of southeastern Canada (Figure II.3). Waring and Franklin (1979) have identified two climatically-related factors that contribute to the dominance of conifers in the Pacific Northwest. The first is the potential for active net photosynthesis outside of the growing season of summergreen hardwoods. The moderate air temperatures in the Pacific Northwest (even in the winter months), combined with most conifers' broad temperature optima for photosynthesis

(Larcher 1969), means that significant amounts of carbon can be fixed during periods of the year when summergreen trees lack foliage. Also, water stress can limit net photosynthesis during the growing season of summergreen hardwoods. In the summer-dry regime of the Pacific Northwest, summer precipitation and soil moisture reserves may not be great enough to meet the demands of PET. Such conditions greatly limit stomatal conductance (Running 1976), which in turn reduces carbon dioxide uptake.

The water balance calculations in this study show very low annual soil moisture deficits in the temperate evergreen forest region of British Columbia. Apparently moisture stress constraints on photosynthesis are not a significant factor contributing to the dominance of conifers. However, summer AET is significantly lower in this region compared to that in the mixed forest region of southeastern Canada. The lower AET is a result of lower evaporative demand driven primarily by lower summer temperatures in southwestern Canada. Thus, the most significant factor contributing to conifer dominance in the Canadian portion of the temperate evergreen forest is probably the capacity of conifers for active net photosynthesis outside the growing season of deciduous hardwoods. The calibrated level of the summer AET rule (Figure II.3) is a threshold level below which summergreen hardwoods cannot fix enough carbon to maintain their competitiveness with evergreen conifers. Above this threshold, the superior photosynthetic rate of summergreen hardwoods (Shultz 1982) compensates for their leafless season, and they are as productive as conifers.

RESULTS

The CCVM simulation of the distribution of Canadian vegetation formations under current climatic conditions (Figure II.4) shows marked agreement with the actual distribution as portrayed on the base-line vegetation map (Figure II.2). CCVM does not include provisions for boggy terrain and glaciers, so the area occupied by these units under current conditions is mapped as "unclassified" (Figure II.4) and was excluded from the quantitative evaluation of the simulation results. Overlay analysis in a geographic information system showed seventy-four percent of the surface area of Canada is correctly classified by CCVM. The formation-specific accuracy of the model ranges from 50% to 89% (Table II.1). Chance alone would be expected to produce some agreement between the base-line map and the simulation, so the kappa statistic (Monserud 1990) was also used in an area-based assessment of the degree of correspondence between the two. The overall kappa statistic is .69, which according to a subjective scale of assessment (Monserud 1990) indicates good to very good agreement between actual and predicted vegetation. Assessments of kappa

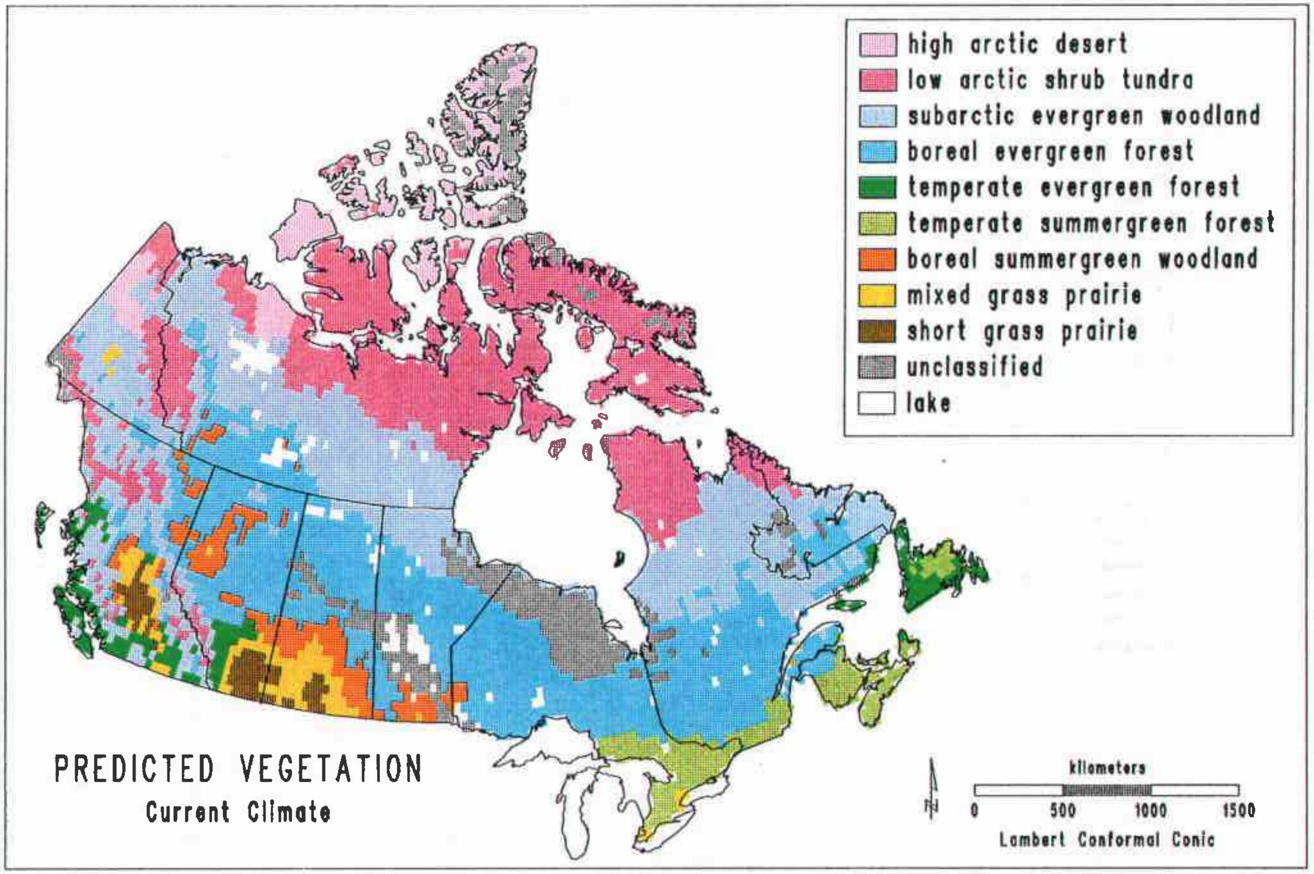


Figure II.4. Formation-level vegetation predicted by the Canadian Climate-Vegetation Model

Table II.1. Comparison of the areal extent of the vegetation formations predicted by the Canadian Climate-Vegetation Model (CCVM) and the observed areal extent of the formations. Table entries along each row show percentages of the observed area of each formation classified into the different formations by the model. Bold entries are percent correct classifications for each formation. Distribution of observed formations based on vegetation regions map in the National Atlas of Canada (1973a).

	Formation Predicted by CCVM								
Observed Formation	PLD	AST	SEW	BEF	TEF	TSF	BSW	MGP	SGP
Polar Lichen Desert	**89**	11							
Arctic Shrub Tundra	8	**76**	15		1				
Subarctic Evergreen Woodland	1	11	**72**	11	3		1	1	
Boreal Evergreen Forest			9	**77**	4	2	6	1	1
Temperate Evergreen Forest		3	25	4	**52**		2	10	4
Temperate Summergreen Forest				22		**75**		3	
Boreal Summergreen Woodland				21	11		**62**	6	
Mixed Grass Prairie				6	5		24	**50**	15
Short Grass Prairie			2		4			24	**70**

statistics for individual formations (Table II.2) range from very good to poor.

To test the performance of CCVM against that of the Holdridge model, results were compared with those of Smith et al. (1991) under current climatic conditions. Smith et al. (1991) also used the IIASA climatic data in their simulation, so the comparison is straightforward in that respect. The sets of Canadian vegetation formations simulated by each of the models, however, are not the same. For purposes of comparison, the members of each set were grouped into five broad types (Table II.3). The Holdridge model, as applied by Smith et al. (1991), makes no distinction between high arctic desert and low arctic shrub tundra, temperate evergreen forest and temperate summergreen forest, or mixed grass prairie and short grass prairie. These pairs were assigned to tundra, temperate forest, and prairie types respectively. The cold parkland, unique to the Holdridge set of formations, is described as treeless boreal desert in the original Holdridge scheme (Smith et al. 1991). This formation was assigned to a prairie type (i.e., the only treeless type in the boreal zone of Canada). The boreal summergreen woodland, unique to the CCVM set, was placed in a boreal forest type. The Holdridge forest-tundra and the CCVM subarctic woodland evergreen were assigned to a forest-tundra type, and the Holdridge boreal forest and the

Table II.2. Kappa statistics for the comparison between the areal extent of the vegetation formations predicted by the Canadian Climate-Vegetation Model and the observed areal extent of the formations. Distribution of observed formations based on vegetation regions map in the National Atlas of Canada (1973a). Class limits for the subjective assessment scale (Monserud 1990) are: <.40, poor; .40-.55, fair; .55-.70, good; .70-.85, very good; >.85, excellent.

Vegetation Formation	Kappa	Assessment
High Arctic Desert	.78	very good
Low Arctic Shrub Tundra	.73	very good
Subarctic Evergreen Woodland	.63	good
Boreal Evergreen Forest	.74	very good
Temperate Evergreen Forest	.37	poor
Temperate Summergreen Forest	.78	very good
Boreal Summergreen Woodland	.38	poor
Mixed Grass Prairie	.49	fair
Short Grass Prairie	.55	good
Overall	.69	good

Table II.3. Kappa statistics for the comparisons between the observed areal extent of the vegetation formations and the areal extent of the formations predicted by the Canadian Climate-Vegetation Model (CCVM) and the Holdridge (1947) model (Smith et al. 1991). Distribution of observed formations based on vegetation regions map in the National Atlas of Canada (1973a). Class limits for the subjective assessment scale (Monserud 1990) are: <.40, poor; .40-.55, fair; .55-.70, good; .70-.85, very good; >.85, excellent.

Vegetation Formation	CCVM	Holdridge
Tundra	.84	.78
Forest-Tundra	.62	.39
Boreal Forest	.80	.63
Temperate Forest	.61	.57
Prairie	.68	.55
Overall	.75	.61

CCVM boreal evergreen forest were placed in the boreal forest type.

The overall and individual kappa statistics were recalculated to show the agreement between the baseline vegetation map and the map of CCVM's simulation when the formations were re-grouped as described above (Table II.3). Kappa statistics were also calculated to assess the degree of correspondence between the baseline map and the map produced by Smith et al.'s (1991) application of the Holdridge scheme (Table II.3). The overall kappa statistics indicate that CCVM outperforms the Holdridge model in this comparison. The individual kappa values show all five of the individual formations are predicted with more accuracy by CCVM. Therefore, in addition to being more physiologically-based than the Holdridge scheme, CCVM also simulates the formation-level vegetation of Canada in more detail and with greater accuracy.

No digital data were available to allow a statistical comparison of CCVM's prediction with those generated by the Box model. Visual comparisons were made between distributions of different life-forms in Canada as simulated by the Box model (Box 1981) and those of individual formations predicted by CCVM. These comparisons are appropriate since formations in CCVM are defined largely on the basis of the dominance of single life-forms equivalent to those used by Box (1981). The results of the comparisons generally favored CCVM. In the Box model, shrub-dominated tundra is very poorly predicted, the predicted distribution of temperate summergreen broad-leaved trees and boreal needle-leaved trees are both too far north, temperate needle-leaved trees are absent in the Pacific Northwest, and the predicted extent of the grass-dominated region in the Prairie Provinces is too restricted. Box (1981) notes many of these same prediction errors in an evaluation of his model.

DISCUSSION

An Examination of the Model Residuals

Some of the misclassification produced by CCVM is undoubtedly generated by imperfections in the rule-base. In some instances, deficiencies in the climatic data contribute to the misclassification of grid cells. But more commonly, the problem lies in the baseline vegetation data against which the model performance is being compared. For example, a map of misclassified cells (Figure II.5) shows that a significant portion of the error occurs in British Columbia. The extremely complex topography of this mountainous region is contributing to the error in two different ways. First, resampling the correspondingly complex vegetation mosaic on the baseline vegetation map at the half-degree resolution of the database introduced some imprecision into the vegetation data. A significant portion of the misclassification of arctic shrub

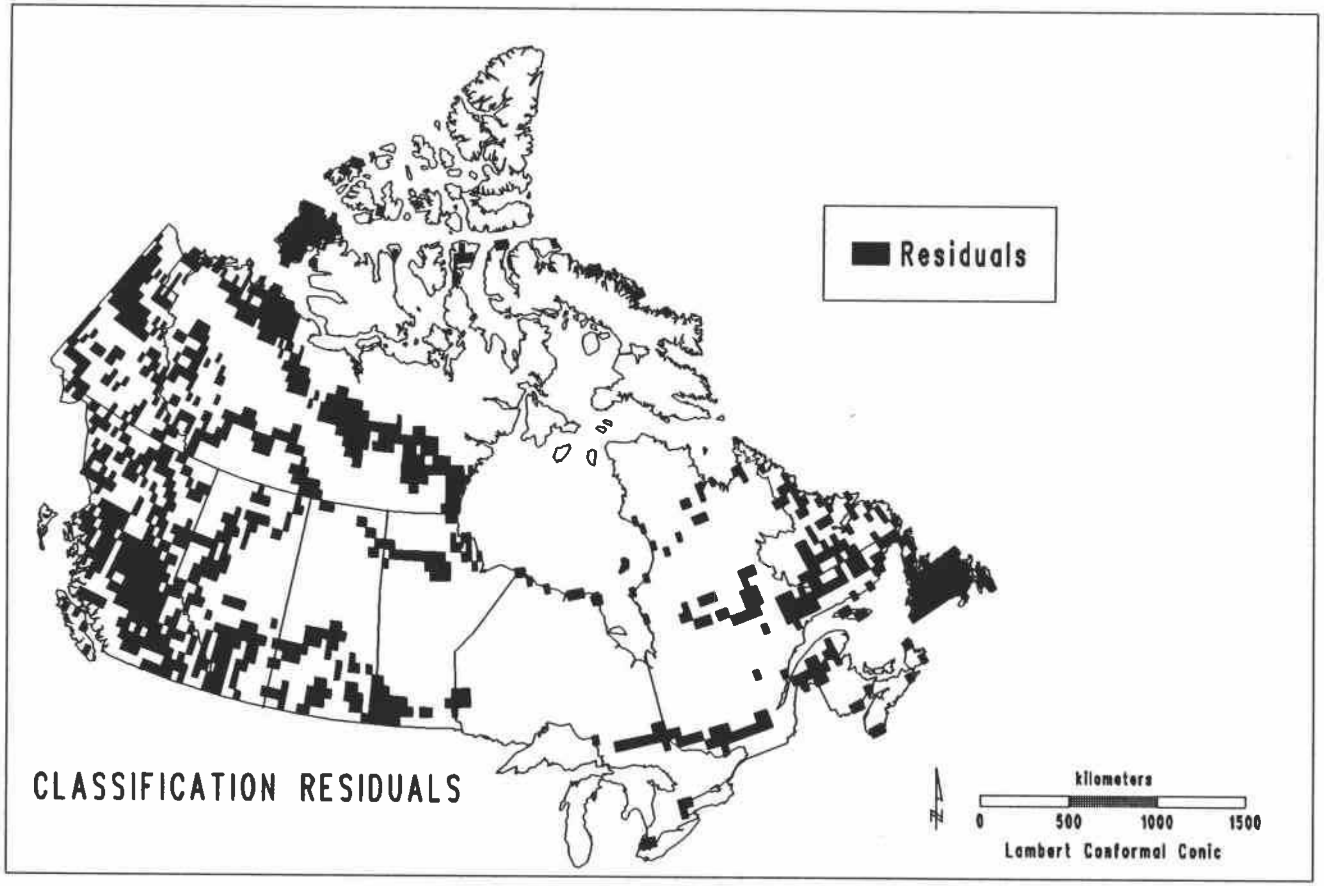


Figure II.5. Cells that were not correctly classified (i.e., residuals) according to the pre-classification tundra, subarctic evergreen woodland, and temperate evergreen woodland in British Columbia is due to this type of pre-classification error. Secondly, in the interior of the province, meteorological stations are situated in semi-arid valleys and plateaus surrounded by orographically wetter highlands (Kendrew and Kerr 1955). Precipitation in the IIASA data set, being uncorrected for elevation, does not capture strong orographic influences on precipitation variability. Thus precipitation in interior British Columbia is under-represented in the model database. This results in an under-prediction of soil moisture and the misclassification of boreal and temperate evergreen forest as summergreen woodland and prairie.

Furthermore, a vegetation map in the Atlas of British Columbia (Chapman et al. 1956) that is more detailed than baseline vegetation map suggests that much of the central-interior and northeast regions of the province (i.e., the Cariboo and Peace River Parklands respectively), pre-classified as boreal forest on the base-line map, might be better characterized as boreal summergreen woodland. The detailed map also shows the southern-interior plateau and river valleys as dry temperate woodland, and a photograph of this type included with the map shows extensive grass cover under scattered ponderosa pine (*Pinus ponderosa* Laws.). In these instances, the boreal summergreen woodland and prairie formations simulated by CCVM are in greater accordance with vegetation on the more detailed vegetation map than vegetation on the baseline map.

Another significant area of apparent misclassification is in the northern half of the Yukon Territory. Here CCVM predicts high arctic desert in the Ogilive Mountains where the baseline map shows low arctic shrub tundra. The few meteorological stations in the northern Yukon are located in valley bottoms which receive less precipitation than surrounding mountains (Kendall and Kerr 1955). Thus an underestimation of snowpack may be contributing to prediction error here. On the other hand, the Land Cover Associations map for Canada based on LANDSAT imagery (National Atlas of Canada 1989) shows much of this same region classified as barren tundra with less than 5% vegetation cover, so perhaps the prediction of high arctic desert is not entirely in error. Rowe's (1972) description of vegetation in the upper drainage of the Yukon River suggests a small region of prairie in the south-central part of the province is probably accurate.

The Prairie Provinces (i.e., Alberta, Saskatchewan, and Manitoba) are another region where more detailed vegetation maps suggest CCVM's simulation is more accurate than the baseline data. For instance, the prediction of extensive boreal summergreen woodland in the northwest sector of the Alberta is not in accordance with the baseline map, which shows most of this region as boreal evergreen forest. However, before vegetation regions were aggregated into formation types, the baseline map itself showed "aspen-spruce" as the predominant cover type in this sector of Alberta. A more detailed vegetation map in the Atlas of Alberta (University of Alberta 1969) shows this same region as "aspen poplar" or "aspen poplar with grass, parklike". The prediction of temperate evergreen forest along the western border of the prairie region also accords with the more detailed map which shows lodgepole pine forests in this region. In southern Saskatchewan, the greater extent of short grass prairie predicted by CCVM compares favorably to the distribution of blue grama grassland on the vegetation map in the Atlas of Saskatchewan (Richards and Fung 1969). The discrepancy between actual and predicted vegetation at the southern Saskatchewan-Manitoba border is mostly due to inaccuracies in the baseline vegetation data arising from resampling a complex woodland-prairie mosaic at the half-degree resolution of the data base.

Another region of misclassification is centered on the Amundsen Gulf in the Northwest Territories. Here, Banks Island and a region north of Great Bear Lake, classified as low arctic shrub tundra on the baseline map, are assigned to high arctic desert by CCVM. In fact, Banks Island has a full range of shrub tundra to polar desert (Ritchie et al. 1987). Furthermore, climatic data from Sachs Harbor (Muller 1982) on

Banks Island shows mean total precipitation outside the growing season (i.e., "snowpack" as defined in CCVM) is anomalously low compared to other shrub tundra sites. Precipitation data for this low elevation station may or may not be representative of precipitation in the surrounding highlands. Thus errors in the climatic and/or vegetation baseline data may contribute to prediction error in the Amundsen Gulf region.

Much of the remaining error in prediction occurs as bands along east-west trending ecotones. None of these transitional zones are as sharply-defined as the boundaries shown on the base-line map. This is especially true of the poorly-defined shrub tundra-subarctic woodland ecotone (Larsen 1989) where the widest band of misclassification occurs. Most of this type of misclassification is probably acceptable given the somewhat arbitrary placement of vegetation boundaries on any continental scale map.

The misclassification of vegetation on the Island of Newfoundland cannot be attributed to any source of error other than that generated by imperfections in the rule-base itself. CCVM predicts temperate evergreen and temperate summergreen forest where the baseline map shows subarctic woodland and boreal forest respectively. Winter temperatures are relatively mild in this maritime setting (Banfield 1983), so factors other than winter frost damage must preclude development of temperate formations on the island. Because of the maritime influence, there is a relatively short and cool growing-season on the island. CCVM's calculations show that only a very small portion of the north-east quadrant of the island experiences a growing season comparable to that of temperate forests to the south. Nevertheless, degree-day sums do exceed the lower threshold for subarctic woodland. Cold, wet soils and post-settlement fire are probably responsible for the development and maintenance of this formation over much of the island (Rowe 1972, Damman 1983). The more productive boreal forest formation is found in the north-east quadrant of the island where the highest heat sums occur. Here several representatives of the mixed forests to the south are locally present. In fact, stands of eastern white pine (*Pinus strobus* L.) were at one time of economic significance in this sector of the island (Rowe 1972). Logging, fire, and thick moss layers are factors which may reduce the competitiveness of temperate tree species on the Island of Newfoundland where the climatic regime is only marginally suitable for their growth (Damman 1964).

The Climatic Thresholds and the Large-scale Structure and Dynamics of the Atmosphere

Climatic thresholds constraining the distribution of vegetation formations in Canada have their genesis in the large-scale structure and seasonal dynamics of the atmosphere.

The cold dry Arctic air masses that persist year-round over the high arctic desert (Barry and Hare 1974) generate very little of the snowpack necessary to the winter survival of low arctic shrubs. The gradual increase in growing season warmth and the associated increase in winter survival and reproduction of trees across the tundra-forest transition is a function of the increasing frequency of relatively warm Pacific and tropical air across the mean summer position of the Arctic Front (Bryson 1966, Barry 1967). The absolute minimum temperature threshold that constrains the northward extent of temperate summergreen hardwoods in southeastern Canada coincides with the mean winter position of the arctic front (Bryson 1966). The competitiveness of summergreen hardwoods within the mixed temperate forests of this region is maintained by the relatively high evaporative demand of warm and moist tropical air extending into southeastern Canada during the summer months (Hare and Thomas 1974). In south-central Canada, the increasing frequency of dry Pacific air in the summer across the forest-woodland-prairie transition gives rise to ever greater soil moisture deficits which, in turn, produce the gradient in vegetation structure and composition (Borchert 1950).

CONCLUSION

CCVM is a rule-based, equilibrium model developed for the purpose of predicting the response of Canadian vegetation to climate change. As judged by comparisons against vegetation maps at regional to continental scales, the model accurately predicts the distribution of formation-level vegetation under current climate. The CCVM simulation of Canadian vegetation is more detailed and more accurate than those produced by the Holdridge or Box models. Climatic thresholds define vegetation ecotones in CCVM, and the geographic positioning of these thresholds is apparently determined by the large-scale structure and seasonal dynamics of the atmosphere. The physiological and biological basis of the rules in CCVM should results in estimates of the potential response of Canadian vegetation to an enhanced greenhouse effect that are more reliable than those produced by other classification models based on non-causal relationships between climate and vegetation.

CHAPTER III:

CLIMATIC RESPONSE SURFACES FOR SELECTED BOREAL TREE SPECIES RELATED TO CANADIAN FOREST-TYPE CLASSIFICATION

INTRODUCTION

The physiologically-based approach to equilibrium modeling applied in the development of the formation-level classification model in Chapter II is extended to species-level response surface modeling in this chapter. The dominance of eight important tree species in the boreal forest region of Canada is modeled as a response to the same set of climatic parameters used in Chapter II. The relative success of the response surfaces in estimating the probability of species dominance over the spatial extent of North America is evaluated, and the variation in the probability of dominance is related to the species' individualistic response to climatic constraints within different airmass regions. A forest-type classification for the boreal forest domain derived from the probabilities of species dominance is compared to a classification of observed forest-types and the geographic distribution of the derived types is also discussed in relation to seasonal airmass dynamics.

METHODS

Both climatic and vegetation data were acquired for use in the development of the climatic response surfaces. The basic climatic inputs were monthly values of mean temperature, total precipitation, and mean relative humidity over the spatial extent of North America (i.e, Canada and the conterminous United States). The temperature and precipitation data were extracted from a global database distributed over a 0.5° latitude x 0.5° longitude (i.e., half-degree) grid (Leemans and Cramer 1990). Relative humidity data at airport meteorological stations across North America were extracted from the Worldwide Airfield Summary data (WeatherDisc Associates 1990) and interpolated to the half-degree grid using an inverse distance-squared algorithm.

The five climatic parameters used as predictor variables in the response surfaces were calculated from the input data. The predictor variables were degree-days, absolute minimum temperature, annual snowpack, annual soil moisture deficit, and actual evapotranspiration summed over the summer months. The number of degree-days was calculated from daily temperatures (estimated by linear interpolation between monthly values) using a 0° C threshold. Absolute minimum temperatures were estimated from the coldest mean monthly temperatures by regression. A water balance algorithm was developed to calculate snowpack, soil moisture deficits, and actual evapotranspiration. The algorithm includes a decreasing soil moisture availability function and provisions for the effects of the accumulation and melting of snow on soil moisture. Potential evapotranspiration was estimated using Eagleman's (1967) empirical function which accounts for the influence of vapor pressure on PET. The methods employed in calculating the values of the predictor variables, and their relationship to the survival, growth, and reproduction of dominant plant life-forms in Canada, are more fully described in Chapter II.

A set of response variables recording the presence or absence of dominance for eight important boreal tree species (Table III.1) was generated from vegetation maps for Canada (National Atlas of Canada 1973a) and the United States (Küchler 1964). On each map, vegetation regions are characterized by a unique combination of dominant species listed in the map legend. This information was used in a raster GIS to generate a new map for each of the eight species showing the geographic extent over which a given

Table III.1. Important tree species of the boreal forest region.

Common Name	Scientific Name
black spruce	*Picea mariana* (Mill.) B.S.P.
white spruce	*Picea glauca* (Moench) Voss
jack pine	*Pinus banksiana* Lamb.
trembling aspen	*Populus tremuloides* Michx.
balsam fir	*Abies balsamea* (L.) Mill.
eastern white pine	*Pinus strobus* L.
sugar maple	*Acer saccharum* Marsh.
lodgepole pine	*Pinus contorta* Dougl. var. *latifolia* Engelm.

species was listed as dominant. The response data indicating the dominance or non-dominance of each species at each cell in the half-degree grid was generated from this series of maps.

The presence or absence of species dominance, rather than species occurrence, was chosen as the response variable of interest because response in terms of dominance was more appropriately scaled to the climatic data. At the half-degree resolution of the database, the data is mainly representative of the regional macroclimate, and does not capture much of the microclimatic variation at more local scales. The area of species dominance defines the "core" of a species distributional range in which the regional macroclimate is well within the physiological tolerance of the species. Where a species is present but not dominant, as is often the case at the periphery of a distributional range, the regional macroclimate is usually marginally tolerable for the species, and it's occurrence is often tied to local variations in topography or substrate which produce physiologically-tolerable microclimates (Neilson et al. 1992a). The choice of species dominance as the response variable thus served to focus the analysis on the species response to the regional macroclimate as represented by the climate data.

This study is focused on the climatic response of Canadian vegetation, but the geographic extent of the data sets was extended beyond Canada into the conterminous United States in this chapter to assure that the response surfaces could be used to predict the species response to climatic change in Chapter IV. Because the response surfaces were globally-fitted to the multidimensional hyperspace defined by the predictor variables, they cannot be extrapolated beyond that "climate space" (Prentice et al. 1991). For each climatic predictor, the range of future values simulated for Canada under the 2xCO_2 climate scenarios used in Chapter IV is within the range of the current values used in this chapter. Thus the response surfaces can be used to predict the species response to climatic change within Canada without extrapolation. Alaska was not included within the geographic extent of the data sets due to the unavailability of a suitable vegetation map.

Logistic regression (Cox 1970, Bartlein et al. 1986) was used to model the response of species dominance to the climatic predictors. The ordinary least-squares multiple regression model normally used in response surface methodology is inappropriate when the response variable is not continuous (Hosmer and Lemeshow 1989). In the logistic regression model, a binary response variable is related to one or more predictor variables through the logistic function. Using the maximum likelihood estimates of the regression parameters, the probabilities of a given state of the response variable can be calculated for different levels of the predictor variables. The resulting "probability surfaces" (Wrigley 1977) can be mapped in geographic space when the data are spatially-distributed.

In this study, a response surface for each of the eight species was generated by stepwise logistic regression (SAS Institute 1989a). All powers and interactions in the general, third-degree polynomial model for the five predictor variables were available for stepwise selection. The threshold of the residual chi-square for entry or removal of terms in a model was set at the .05 significance level, and the goodness of fit of each model was tested using the likelihood ratio statistic (Wrigley 1977). The predictive success of the response surfaces was evaluated by cross-tabulating observed and predicted responses, and by visually comparing the mapped probability surfaces to the species dominance maps. The relationship between the probability of species dominance and each of the individual climatic predictors was also investigated graphically.

A non-hierarchical method for clustering large data sets (SAS Institute 1989b) was used to assign the grid cells into groups according to the probabilities of dominance generated by the response surface models. The algorithm employed performs a disjoint cluster analysis using a Euclidean distance measure and an iterative, nearest-centroid sorting method (Anderberg 1973). A user-specified number of clusters is formed by minimizing the sum of squared distances from the cluster means. In this study, a series of analyses was made with the number of clusters set at two to twenty, and the maximum value of the Calinski and Harabasz (1974) index was used to indicate the "true" number of clusters in the data set. The performance of this index as a stopping rule in cluster analysis was judged superior to twenty-nine other measures in a comparative study by Milligan and Cooper (1985).

The objective of the cluster analysis was to derive a classification of forest-types in the boreal forest region based on the climatically-determined probabilities of species dominance. Limiting the domain of the cluster analysis to grid cells within the boreal forest region was the most effective means to accomplish this goal. The boreal forest region was defined as the set of grid cells where the probability of dominance for at least one of five predominantly boreal species was greater than 50%. The five species defined as predominantly boreal were black and white spruce, jack pine, trembling aspen, and balsam fir (Ritchie 1987). The area of North America outside the boreal forest region was defined by grid cells where species with more temperate affinities (i.e., lodgepole pine, eastern white pine, sugar maple) were the only taxa with probabilities greater than 50%, or where all eight species had probabilities below the threshold. Grid cells outside the boreal forest region were excluded from the cluster analysis.

The group membership of grid cells at the clustering level identified by the stopping rule was supplied to the GIS to produce a map of derived forest-types. A map of observed forest-types was produced by aggregating regions on the vegetation map of Canada (National Atlas of Canada 1973a). The aggregation scheme was designed to produce a forest-type classification comparable to that produced by the cluster analysis, but strictly on the basis of floristic criteria without regard to the spatial distribution of the resulting forest-types. Rowe's (1972) description of the forest regions of Canada was employed as supplementary information in the development of the aggregation scheme. Area-based calculations of the kappa statistic (Monserud 1990) provided measures of the spatial correspondence between the observed and derived forest-type maps.

RESULTS AND DISCUSSION

The Response Surface Models

For each of the eight response surfaces obtained by stepwise logistic regression (Appendix I), the likelihood ratio test indicated that the goodness of fit was highly significant at the .001 level. When the probabilities of species dominance estimated by the response surfaces are mapped in geographic space alongside the species dominance maps (Figure III.1), it is evident that the climatic variables predict species dominance with a relatively high degree of success. The predictive success of the response surfaces is also depicted in the classification table (Table III.2) showing the number of correct and incorrect predictions when a 50% probability level is taken as the threshold between dominance and non-dominance.

Figure III.1

The observed distribution of species dominance (top panel) and the distribution of the climatically-determined probabilities of species dominance (bottom panel). The observed distribution of species dominance (in black) is the combined extent of regions in which the species was listed as a dominant on the two vegetation maps (National Atlas of Canada 1973a, Kuchler 1964). The probabilities of species dominance (in three classes mapped as different shades of gray) were estimated by the climatic response surface from values of the climatic predictors at each grid cell.

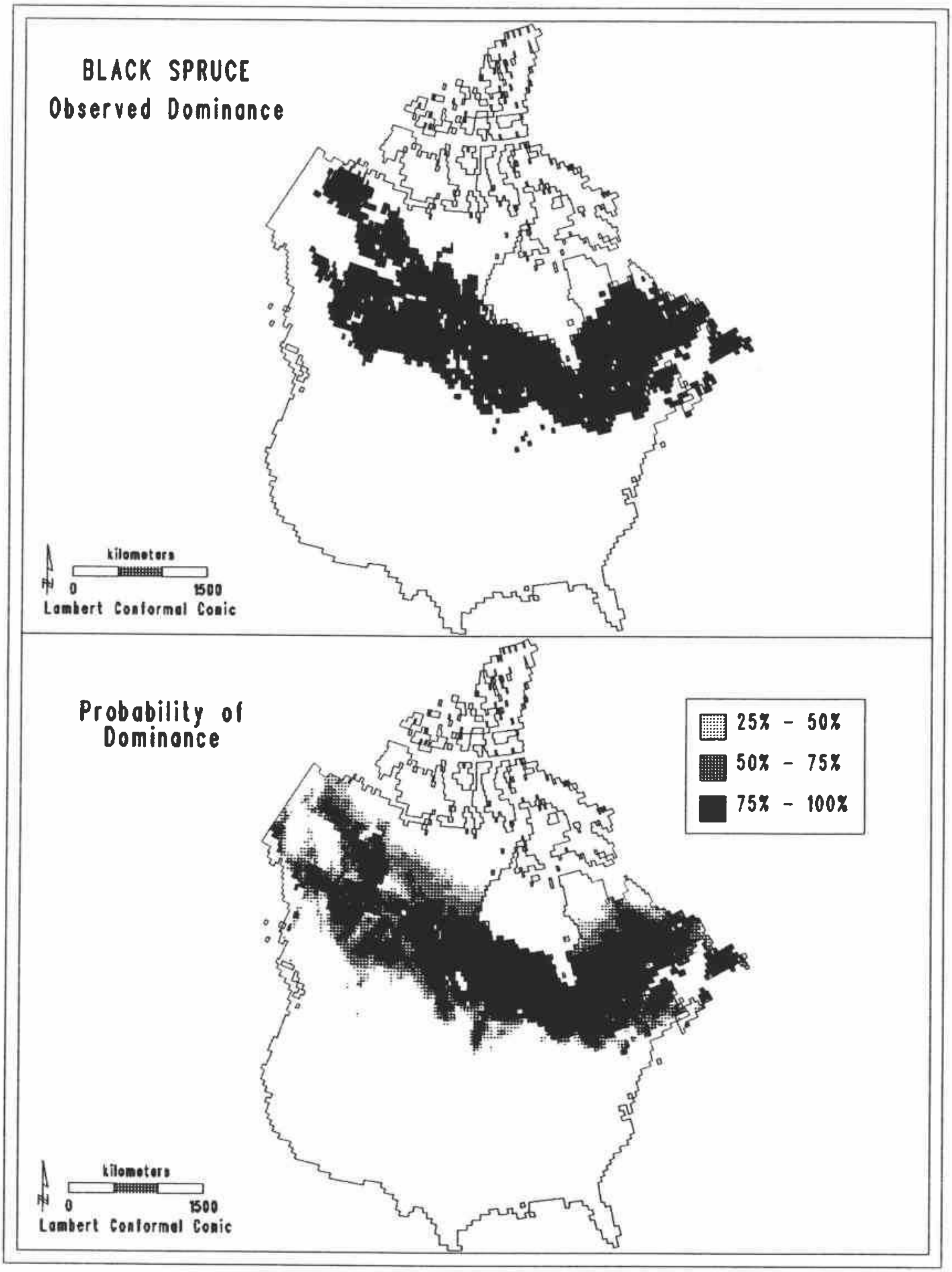


Figure III.1.a

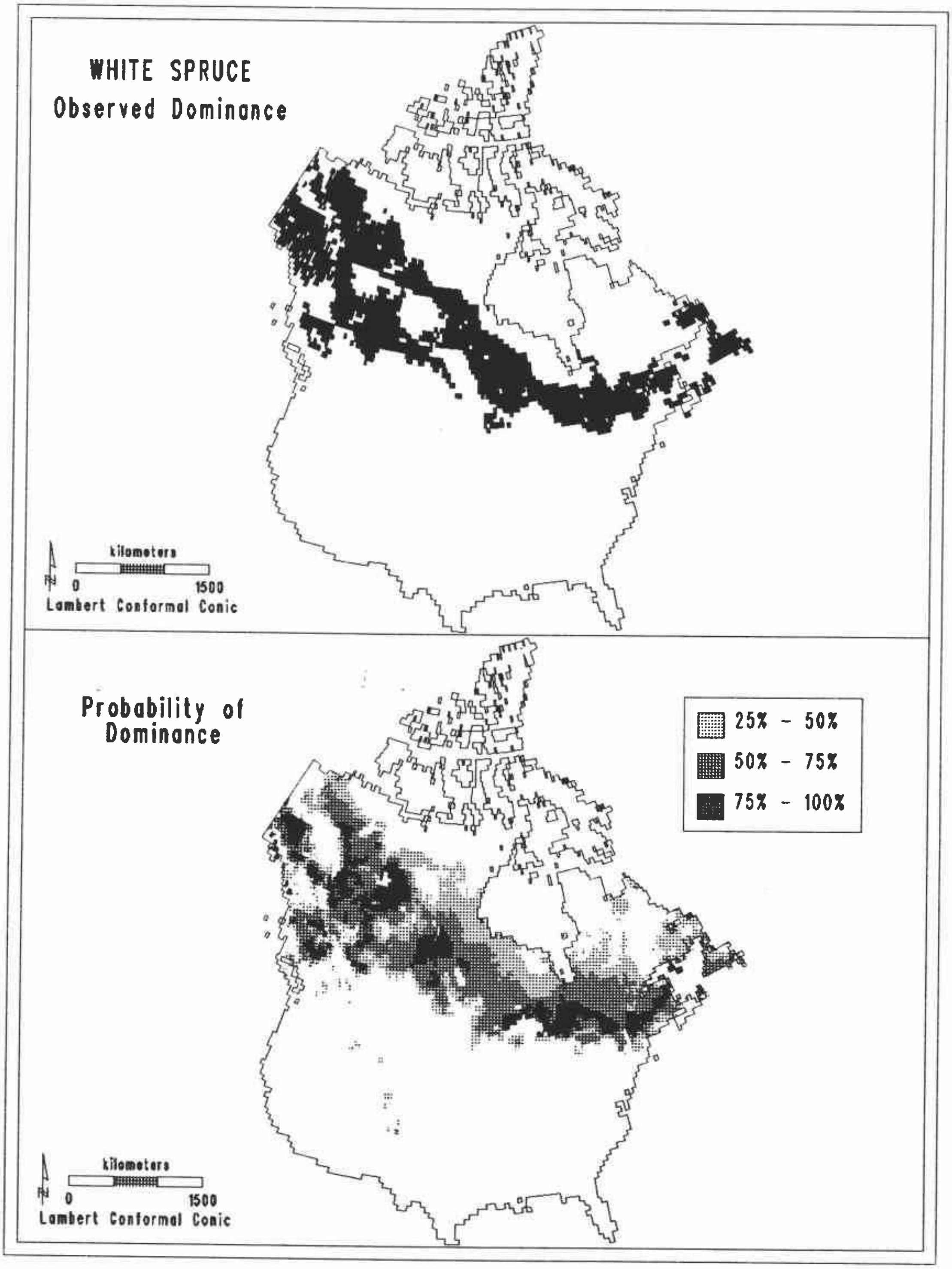


Figure III.1.b

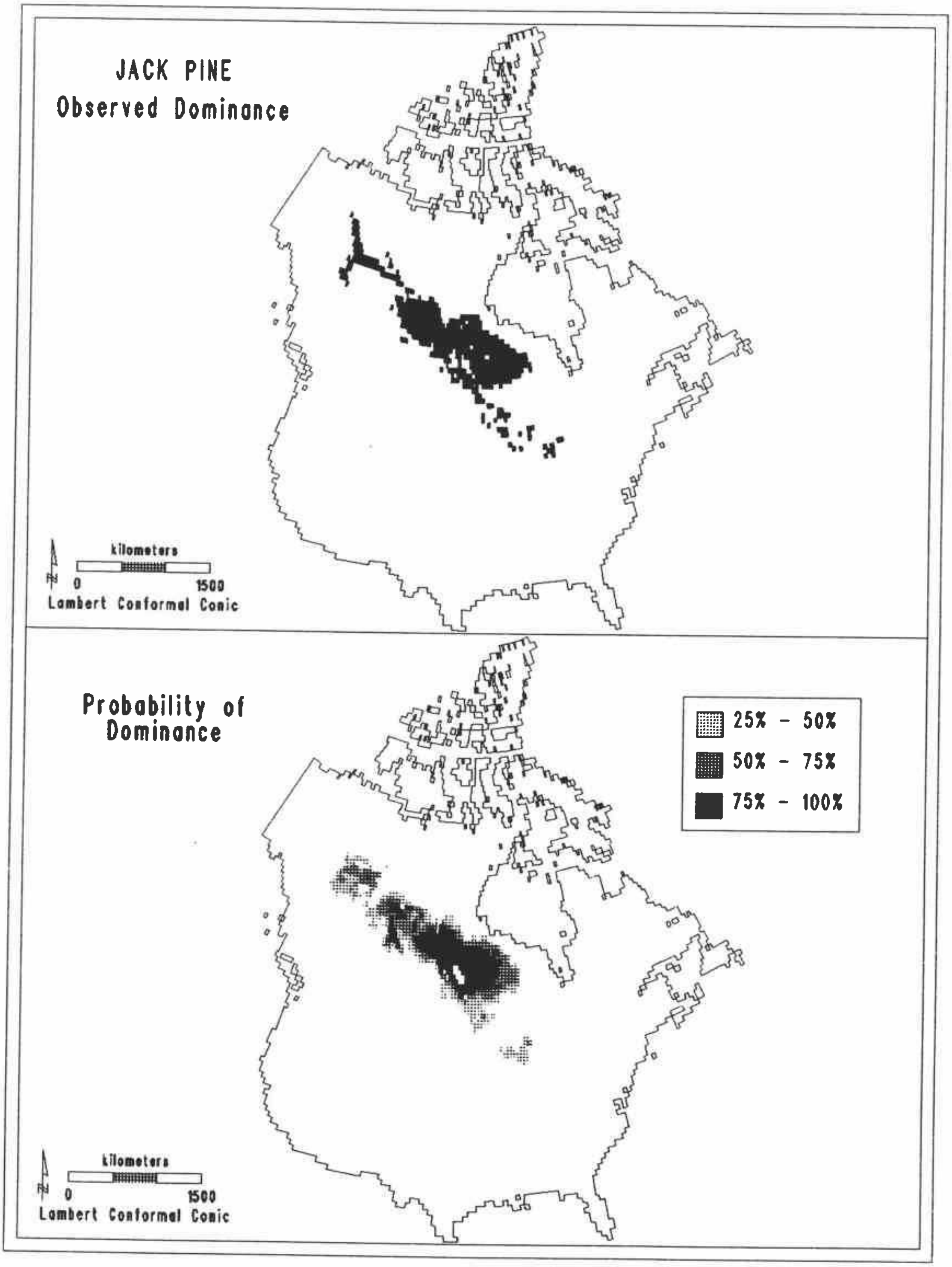


Figure III.1.c

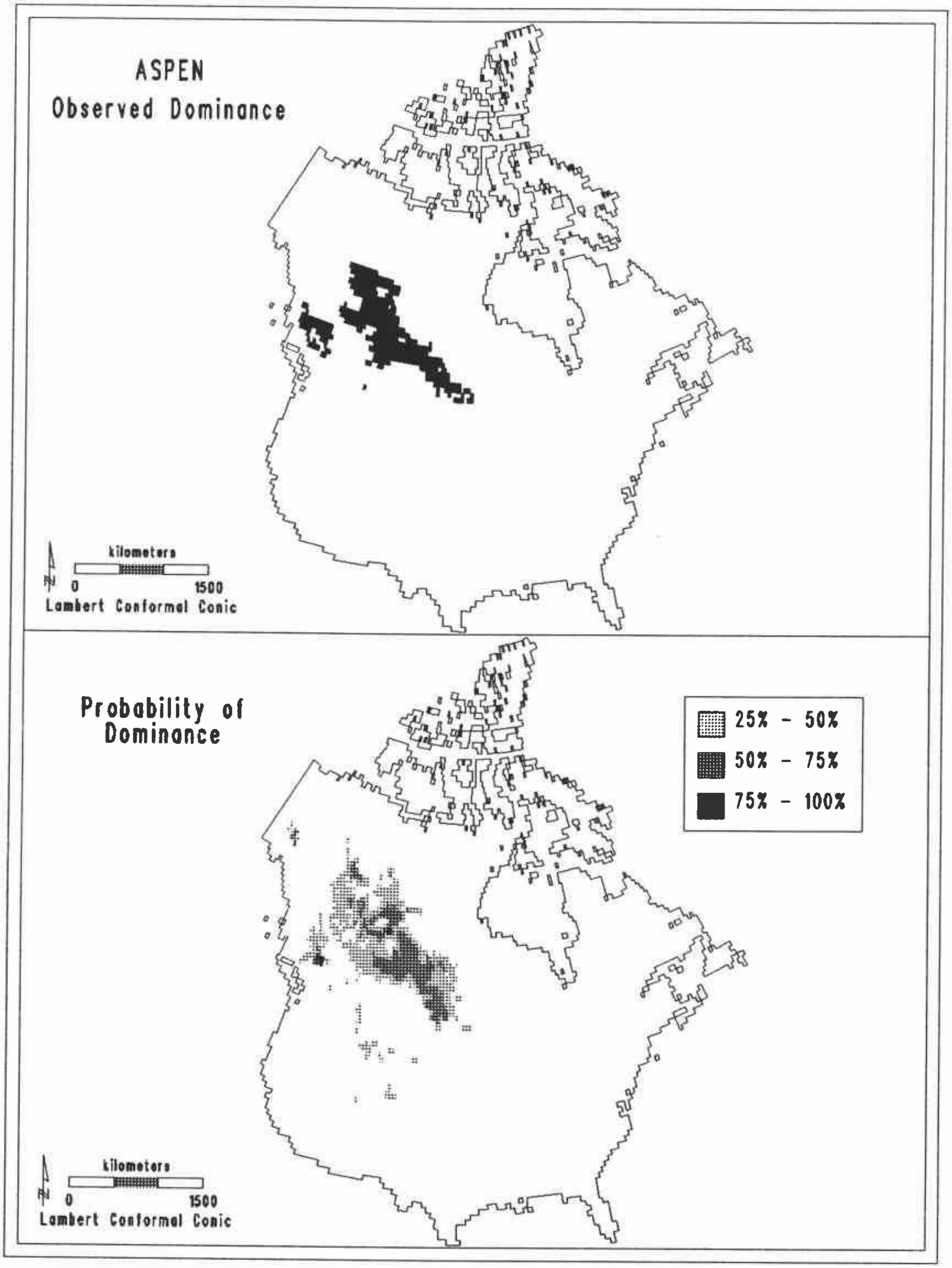


Figure III.1.d

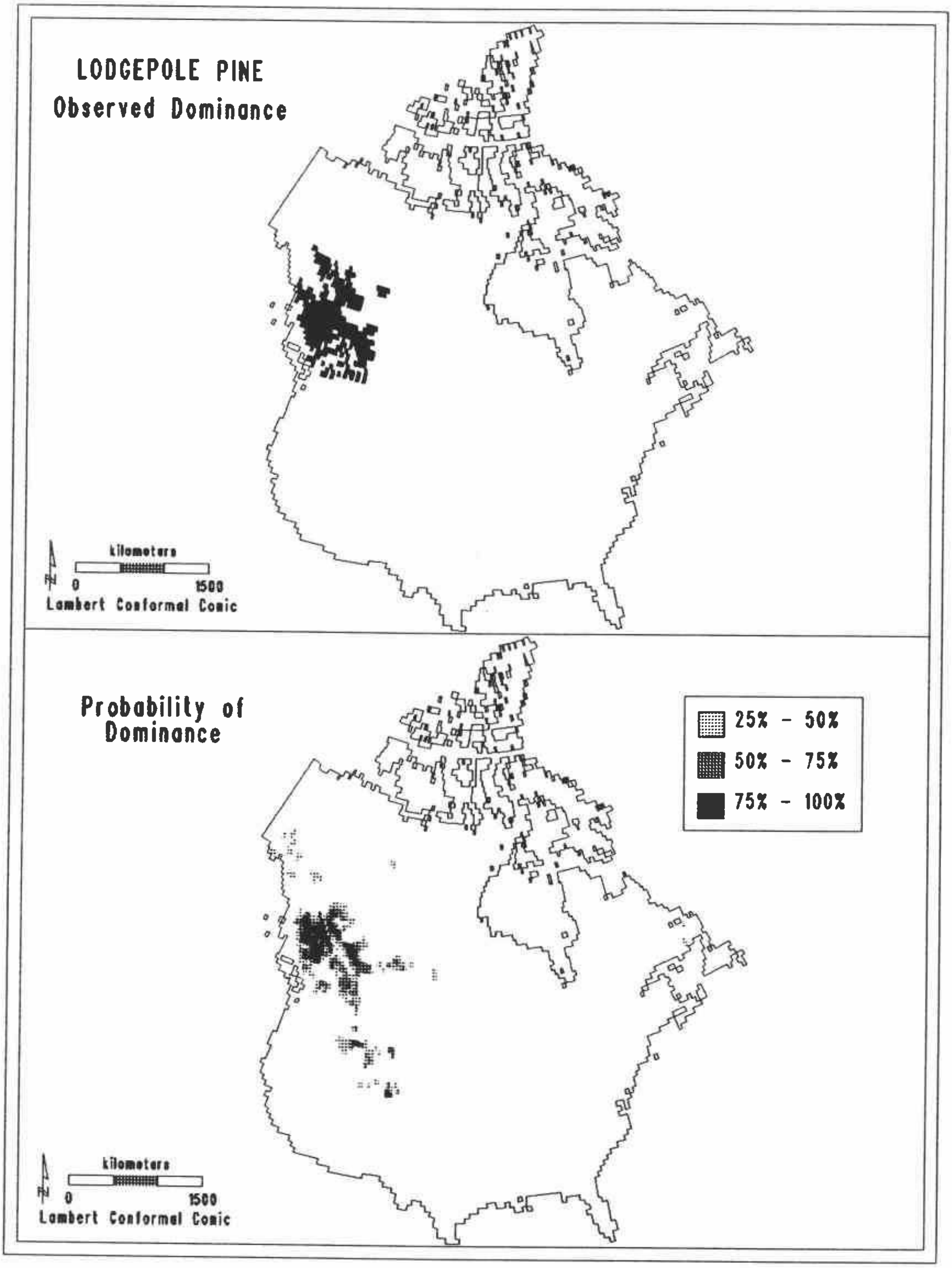


Figure III.1.e

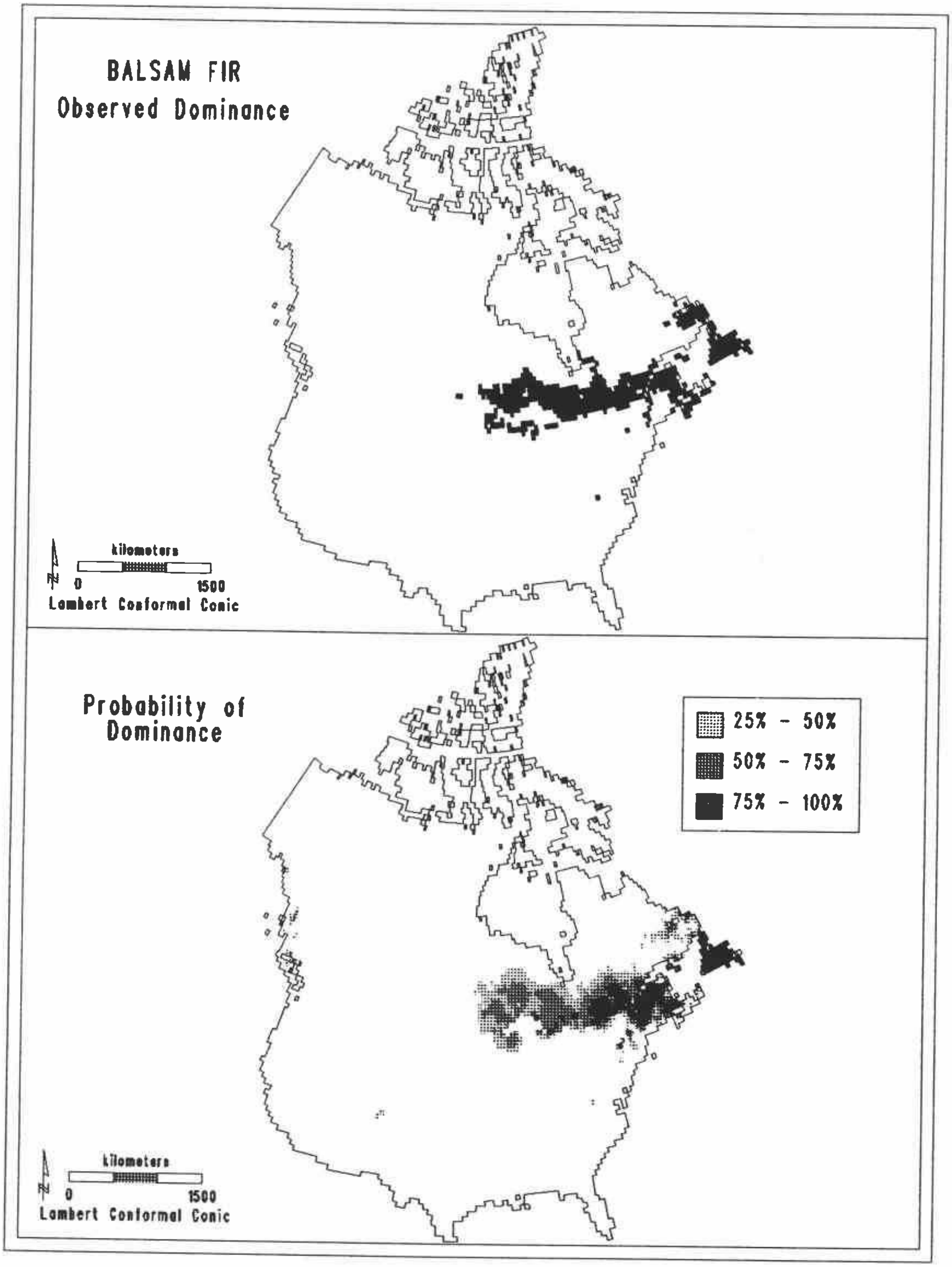


Figure III.1.f

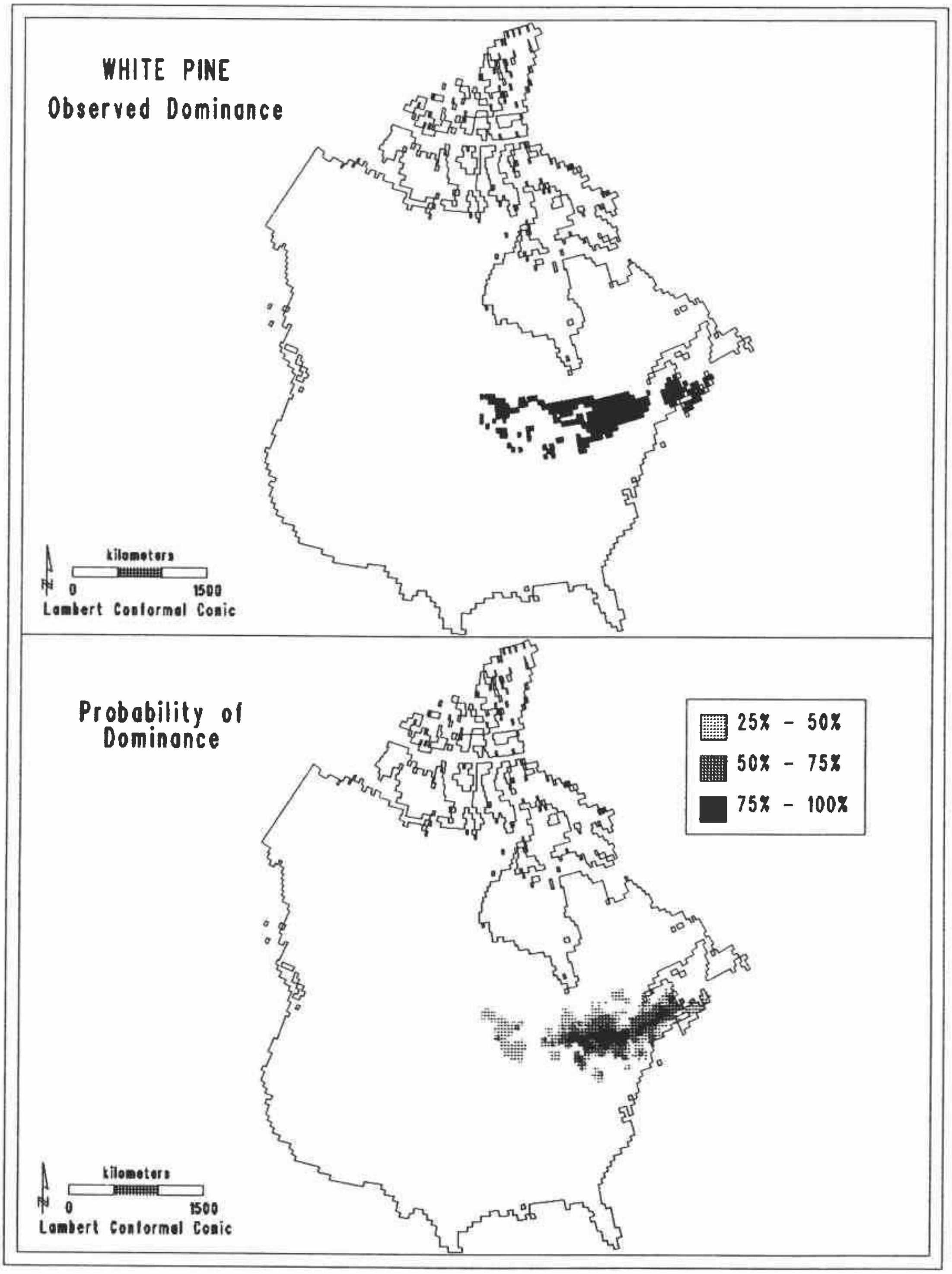


Figure III.1.g

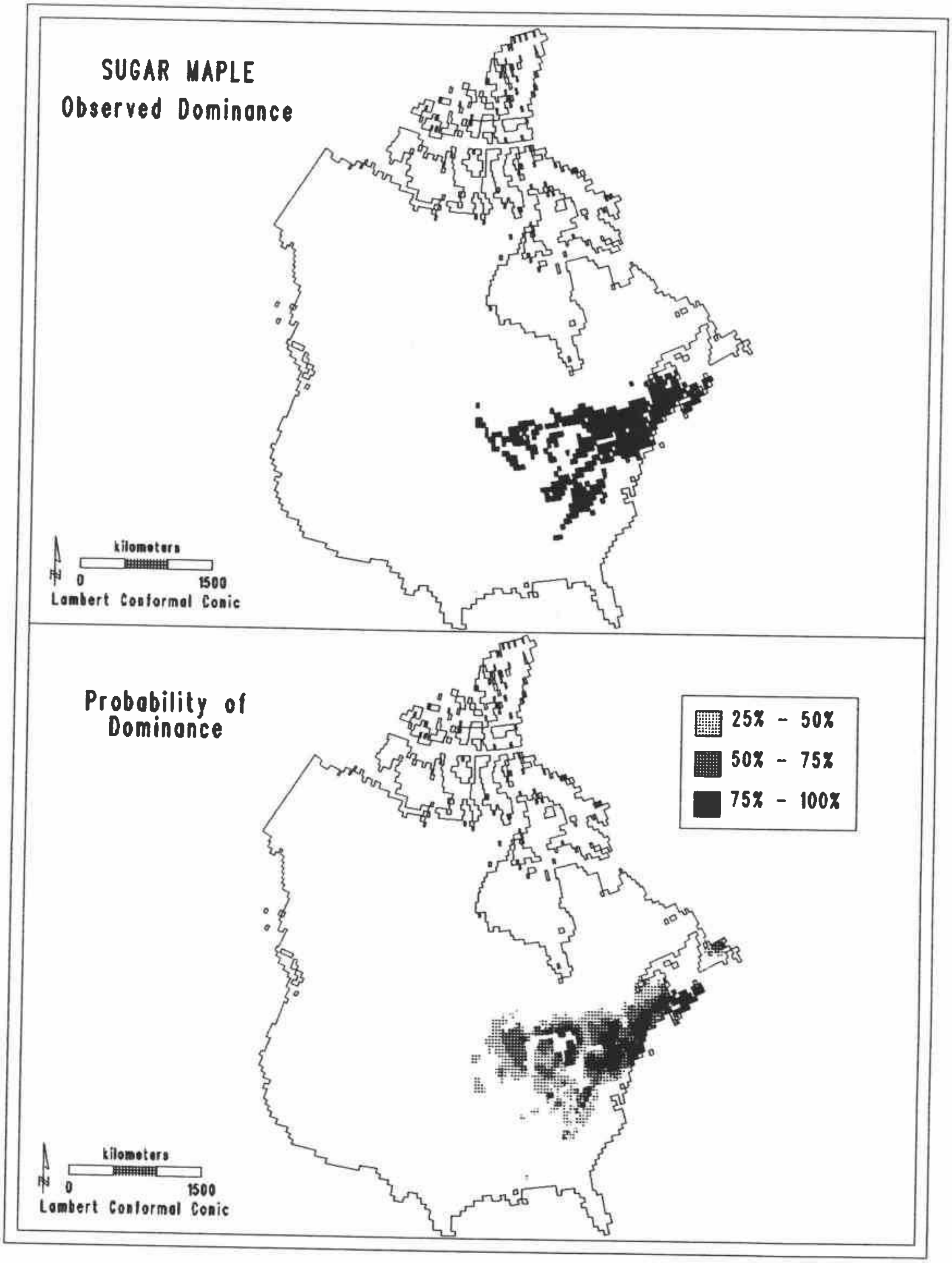


Figure III.1.h

Table III.2. Logistic regression results. "Number of Cells" refers to cells where the species was observed to be dominant (D) or non-dominant (ND). "Number Correct" refers to cells where the species was dominant (non-dominant) and was predicted as dominant (non-dominant). "Number Incorrect" refers to cells where the species was dominant (non-dominant) and was predicted as non-dominant (dominant). "Percent Correct" is the total number of correctly predicted cells expressed as a percentage of the total number of cells. A 50% probability level was taken as the threshold between dominance and non-dominance.

	Number of Cells			Number Correct			Number Incorrect			
Species	D	ND	Total	D	ND	Total	D	ND	Total	Percent Correct
black spruce	2704	7313	10017	2423	6851	9274	281	462	743	92.6
white spruce	2006	8011	10017	1381	7444	8825	625	567	1192	88.1
lodgepole pine	339	9678	10017	143	9619	9762	196	59	255	97.5
trembling aspen	421	9596	10017	147	9493	9640	274	103	377	96.2
jack pine	542	9475	10017	377	9374	9751	165	101	266	97.4
balsam fir	511	9506	10017	343	9376	9719	168	130	298	97.0
white pine	276	9741	10017	132	9664	9796	144	132	276	97.8
sugar maple	483	9534	10017	295	9418	9713	188	116	304	97.0

In response surface studies, the response of taxa at different levels of the climatic predictors is often illustrated by plots of the response surfaces themselves (e.g., a contour plot showing the percentage of a pollen taxon as a function of two climatic predictor variables, sometimes at a specific level of a third predictor, as in Anderson et al. (1991)). In this study, the use of five different climatic predictors makes this interpretative approach very unwieldy. To motivate the following discussion of how the climate variables control the distribution of species dominance, histograms were generated for each species (Figure III.2) in which the mean values of each climatic predictor are plotted for five probability classes. This relatively simple interpretative approach illustrates some of the main features of the response surfaces, but does not account for the importance of interactions among climatic predictors represented by cross-product terms (Appendix 1).

Those aspects of the response surfaces illustrated by the histograms (Figure III.2) can be interpreted as the individualistic response of the species to climatic constraints within different seasonal airmass regimes. These regimes are readily distinguished by the different

Figure III.2

Histograms for each species showing the mean values of the individual climatic predictors in five classes of the predicted probability of species dominance. ABS MIN TEMP is absolute minimum temperature, AES is actual evapotranspiration summed over the summer months, SNOWPACK is total annual snowfall in water equivilents, SMD is total annual soil moisture deficit. Class 5 probabilities were not predicted for aspen.

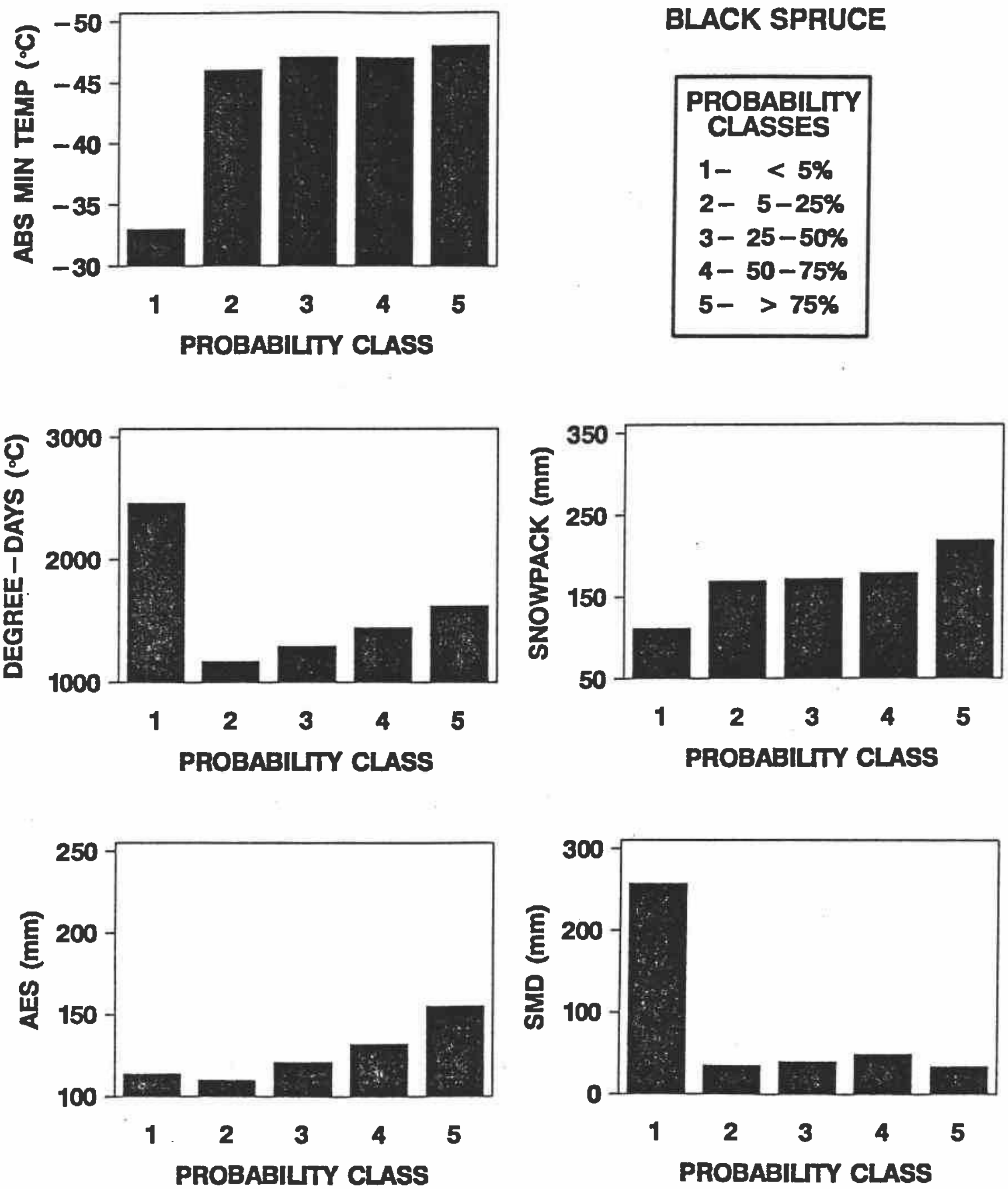


Figure III.2.a

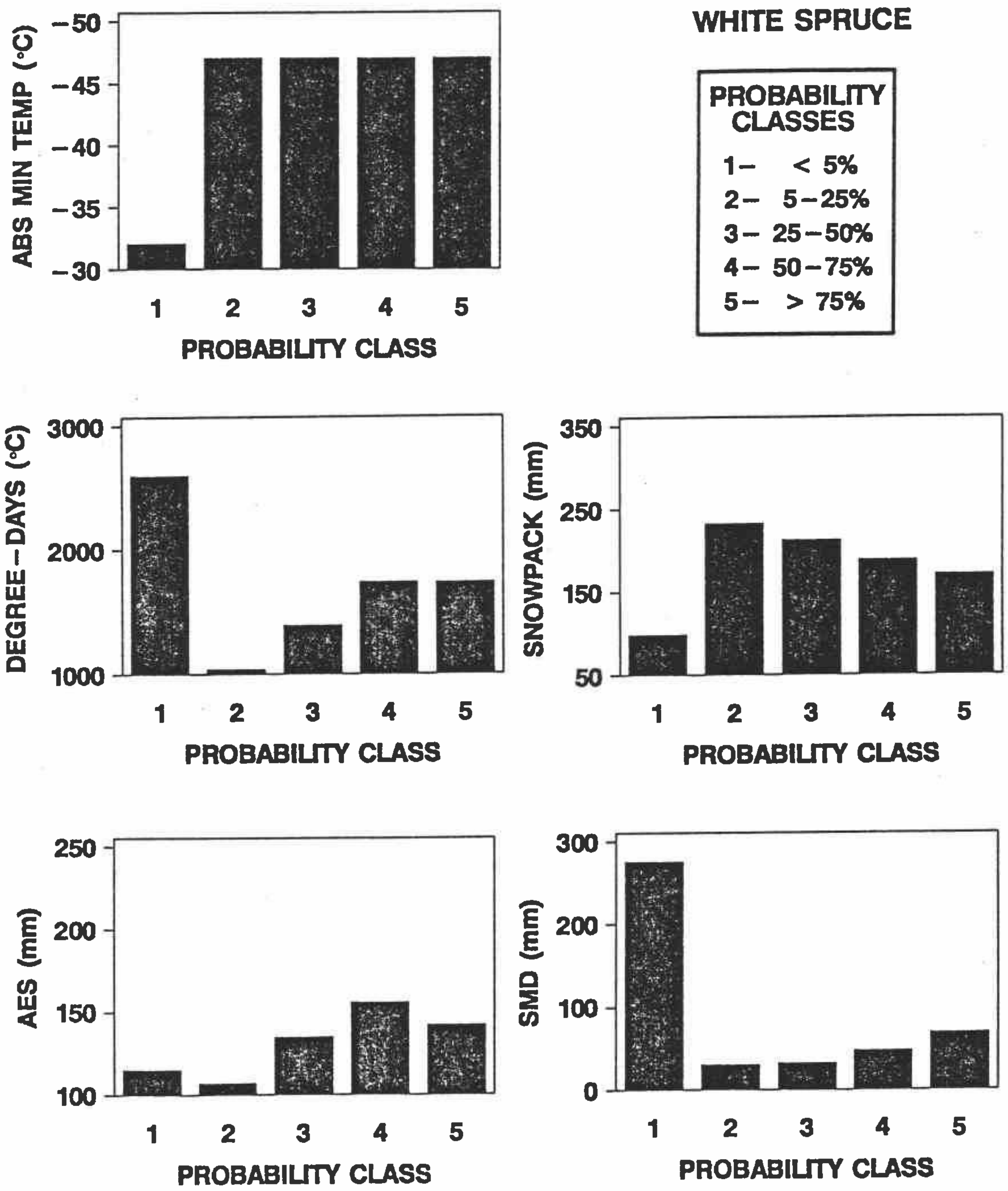


Figure III.2.b

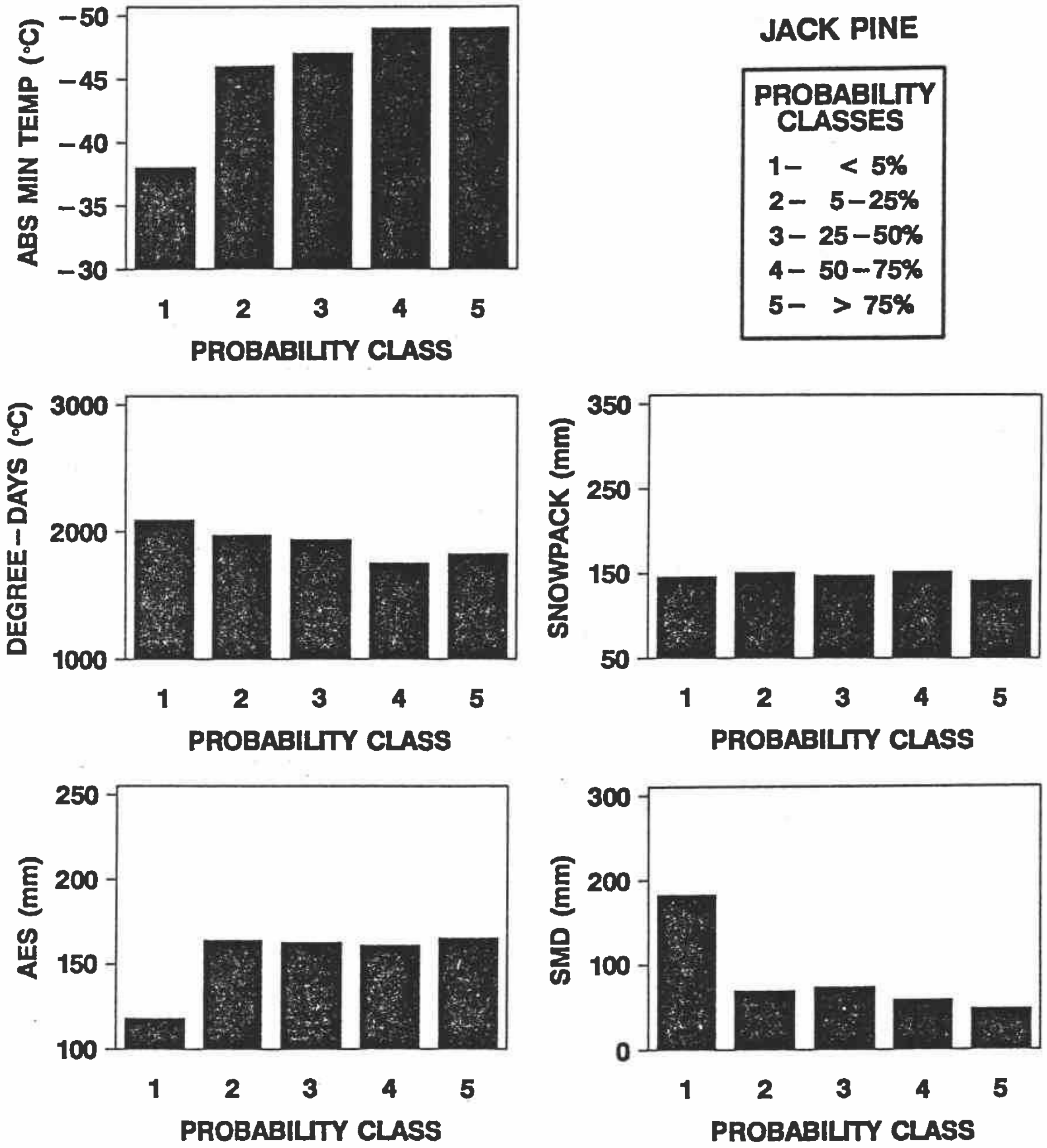


Figure III.2.c

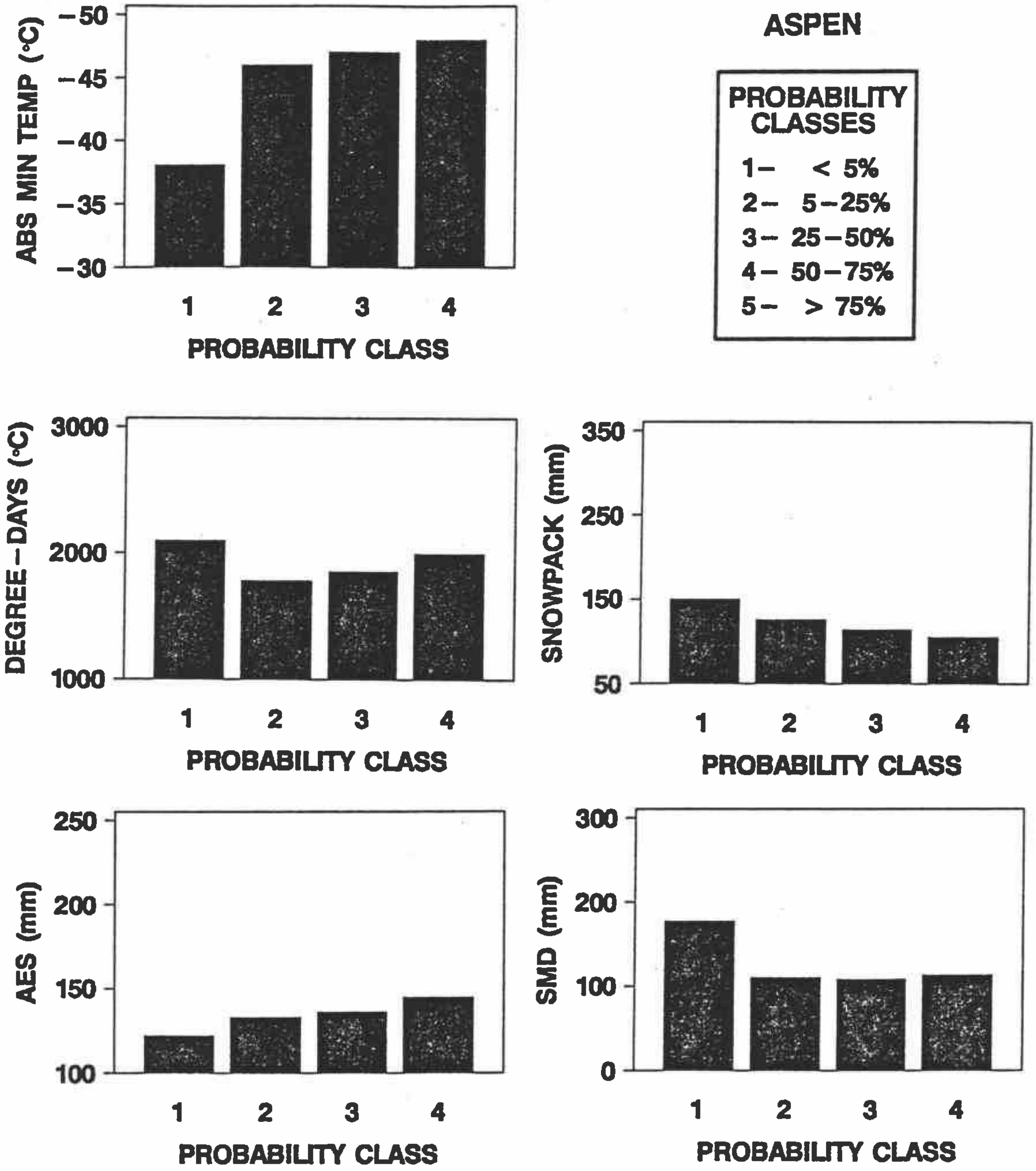


Figure III.2.d

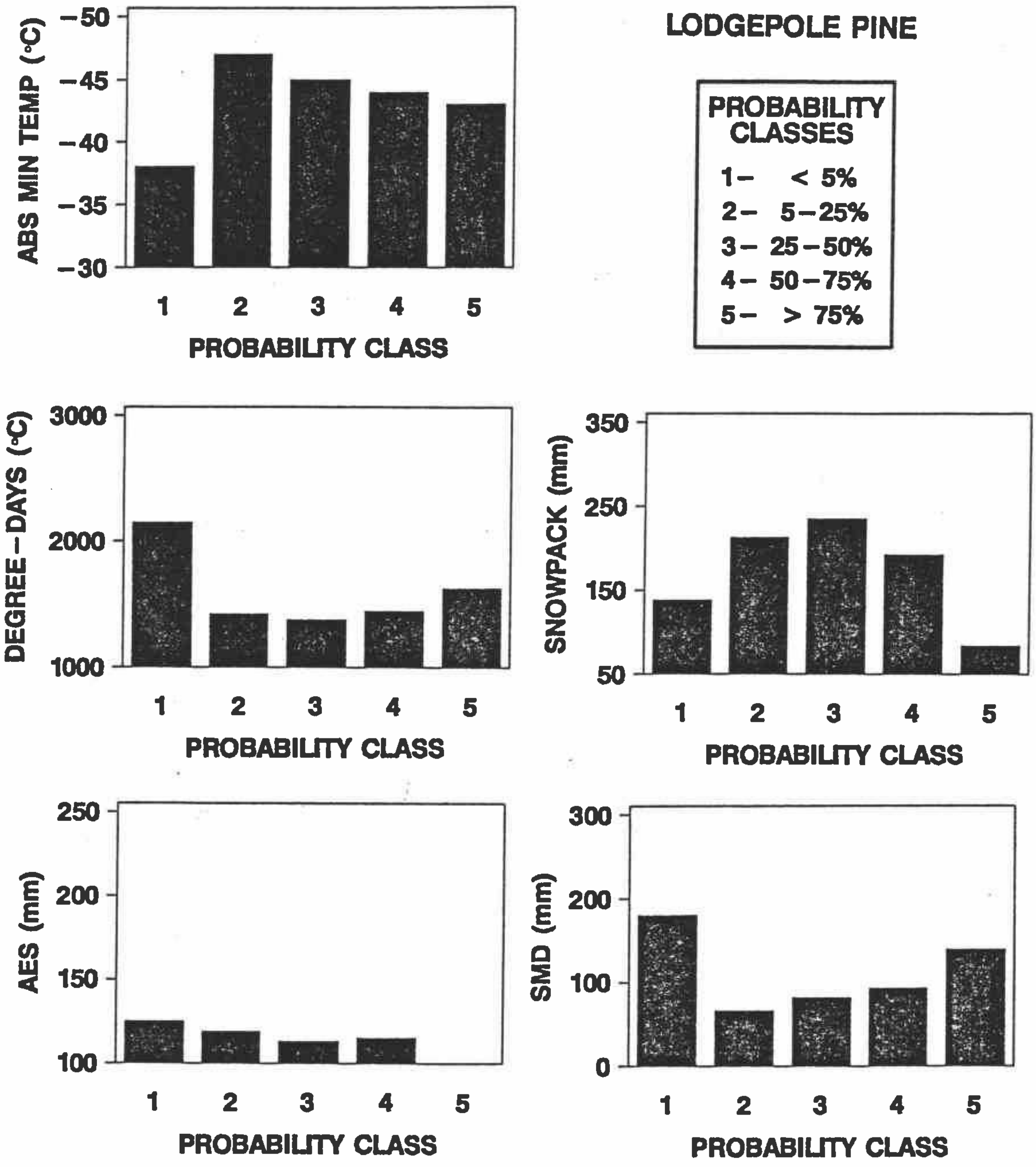


Figure III.2.e

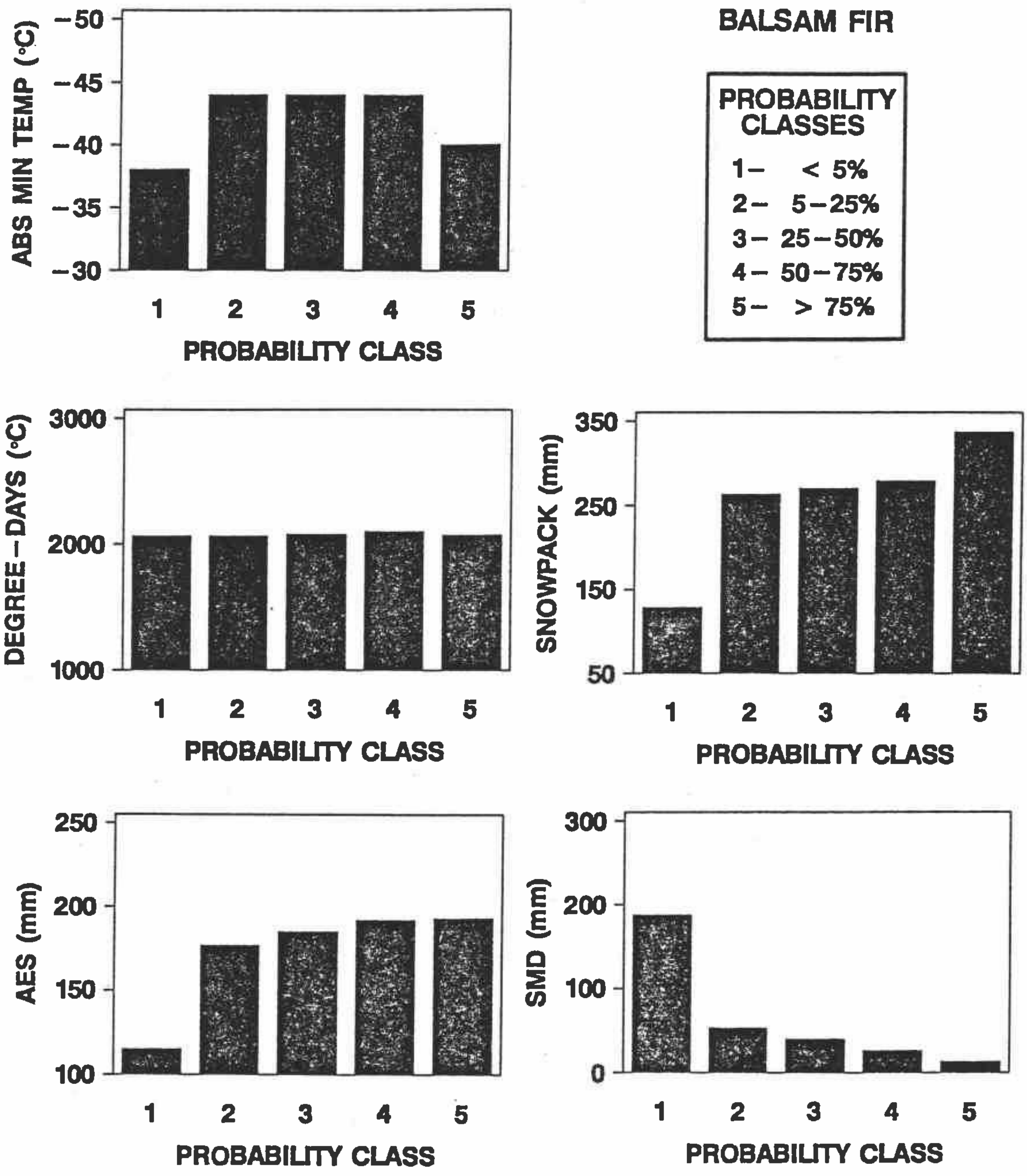
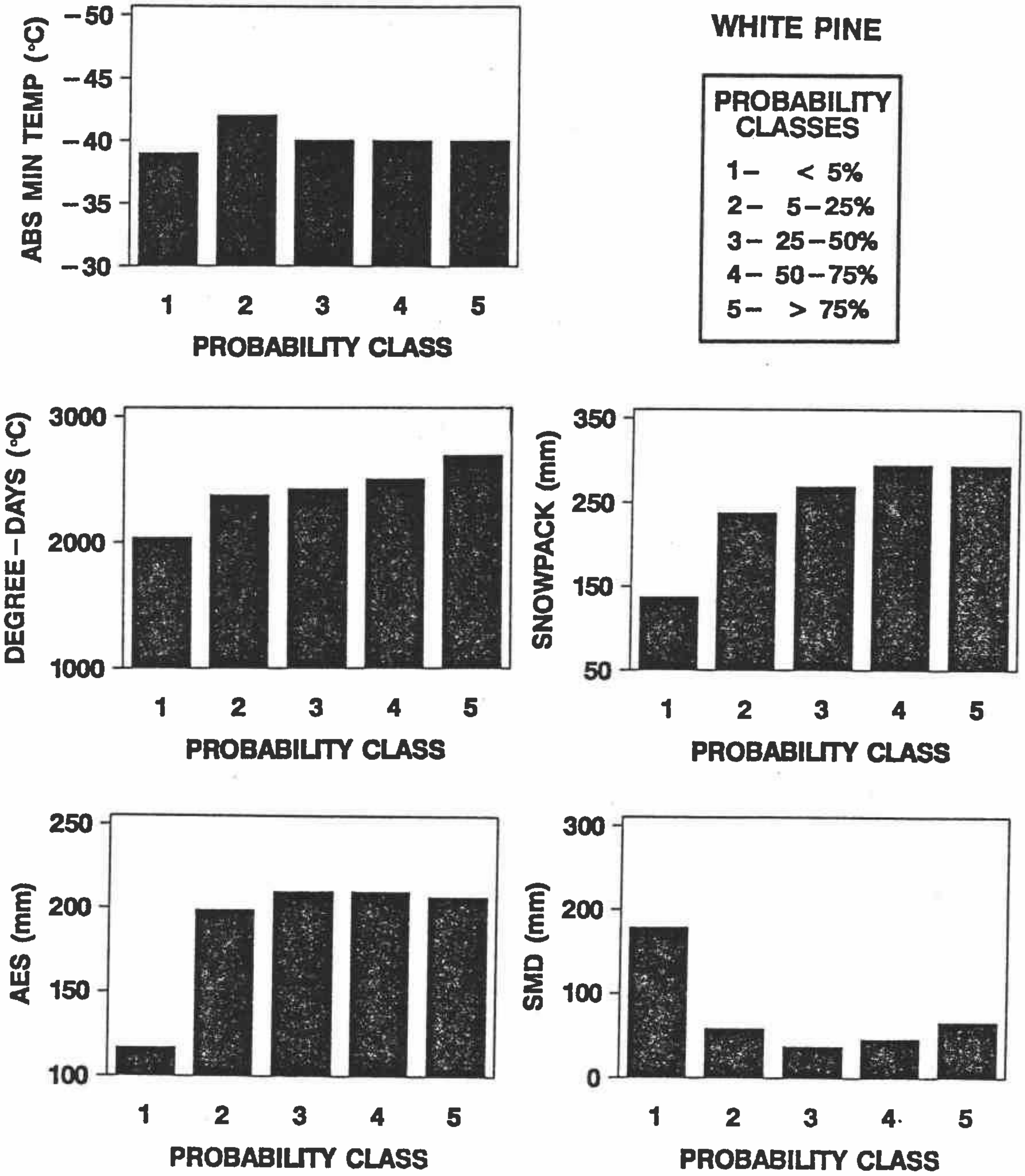


Figure III.2.f



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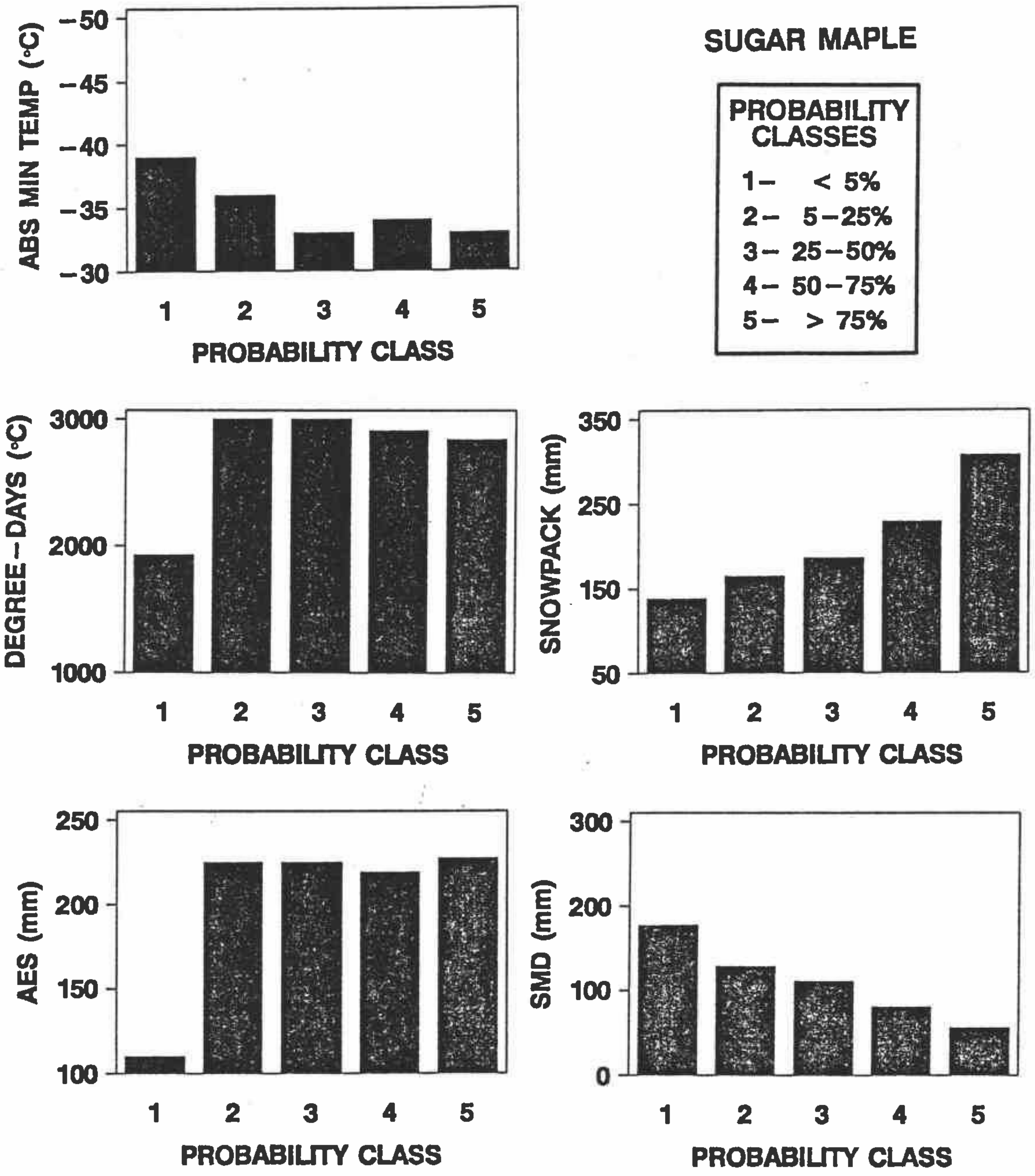

Figure III.2.h

levels of the climatic predictors. For instance, the histograms for the two spruce species (Figure III.2.a,b) illustrate the probability of their dominance is highest in a climatic regime characterized by frigid winters (indicated by relatively low absolute minimum temperatures) and by a cold, mesic growing season (indicated by the relatively low levels of degree-days, AET, and soil moisture deficit and by moderate levels of snowpack which is a major source of moisture early in the growing season). In North America, this seasonal regime is characteristic of one in which Arctic airmasses are important year-round (Hare and Thomas 1974). Within the region where the spruce species are predicted to have at least a five percent probability of dominance (i.e., probability classes 2-5 in Figure III.2), the decreasing probability of dominance with a decrease in degree-days and AET is indicative of climatic constraints to the north where the growing season is insufficient to support reliable sexual reproduction (Black and Bliss 1980) or the full leaf expansion necessary for protection against severe winter desiccation (Tranquillini 1979). The relatively low probabilities of spruce dominance associated with higher absolute minimum temperatures is indicative of constraints along the southwestern and southeastern edges of the predicted region of dominance where Pacific and subtropical airmasses (Bryson and Hare 1974) produce both higher winter temperatures and warmer growing seasons. Here the spruce species are probably constrained by competition with temperate tree species that are more susceptible to frost damage and winter desiccation (Sakai and Weiser 1973, George et al. 1974). The low probabilities of spruce dominance with high soil moisture deficits are indicative of climatic constraints in south-central Canada. Here dry Pacific airmasses during the growing season produce drought and drought-induced fire (Flannigan and Harrington 1988, Clark 1989) which limit the dominance of trees at the forest-prairie ecotone (Coupland 1958).

The response of white spruce dominance within the climatic regime characterized by the year-round importance of Arctic airmasses is complicated by the species' intolerance of poorly drained and/or base-deficient soils (USDA Forest Service 1990a), non-climatic factors which occur at a macroclimatic-scale in Canada. Differences in the observed ranges of dominance for black and white spruce west of the Cordillera (Figure III.1.a,b) are largely related to the distribution of wetlands in the Hudson Bay lowlands and the central interior (National Atlas of Canada

1986) and the prevalence of base-deficient humo-podzolic soils throughout much of interior Labrador (Ritchie 1987).

The histograms for jack pine and aspen (Figure III.2.c,d) illustrate the probability of their dominance is highest under a frigid winter regime (indicated by relatively low absolute minimum temperatures) and a cool, dry growing season (indicated by relatively moderate levels of degree-days, low snowpack, and fairly high soil moisture deficits). This climatic regime, typical of the central interior of Canada (Kendrew 1955), is produced by the dominance of Arctic and cold Pacific air in the winter months and relatively warm, dry Pacific air in the spring and summer months (Borchert 1950, Bryson and Hare 1974). Both aspen and jack pine are relatively drought tolerant and well adapted to fire (Bonan 1988, Ritchie 1987), and their dominance is probably promoted by the relatively high soil moisture deficits and high frequency of fire (Wein 1983) under this climatic regime (Rowe 1972). And in a manner similar to the spruce species, the regions of aspen and jack pine dominance are probably thermally limited to the north and moisture limited to the south (Ritchie 1987). Competition with late successional tree species probably constrains the dominance of these extremely shade intolerant species (U.S.D.A. Forest 1990a, b) in the more humid and less fire-prone regions to the east and west.

The region of aspen dominance is distinguished climatically from that of jack pine by a drier growing season (indicated by lower snowpack, lower AET, and higher soil moisture deficits). The dry Pacific air that is dominant in both regions during the growing season is modified by frequent influxes of moist subtropical air in the region of jack pine dominance, allowing for a more humid climate (Hare and Thomas 1974). The greater AET supported by the moister growing season may be important to the evergreen species in providing resistance against winter desiccation (Tranquillini 1979) under the harsh winter conditions of the continental interior. But the segregation of the areas of dominance for these two species may also be a response to properties of the substratum, as the boundary between the two regions is nearly coincident with the boundary between two major physiographic regions (National Atlas of Canada 1973c). Jack pine is more tolerant of the nutrient-poor, coarse-grained soils derived from glacial outwash on the interior margin of the Canadian Shield (Ritchie 1987), while the richer, finer-textured soils derived from the sedimentary rocks of the Interior Plains support good aspen growth (USDA Forest Service 1990b).

The histograms for lodgepole pine (Figure III.2.e) illustrate that the dominance of the species is highest under a somewhat less frigid winter regime than those previously discussed (indicated by higher absolute minimum temperatures than those shown in Figure III.2.a-d) and under a cool and dry growing season regime (indicated by low levels of degree-days, very low AET, and relatively high soil moisture deficits). This climatic regime, typical of the North Interior upland region of British Columbia (Kendrew and Kerr 1955), is characterized during the growing season by cool maritime Pacific air and during the winter months by Pacific air that is relatively warm compared to the frigid Arctic airmasses that occasionally flow into this region from the source regions to the north. The dryness of the region, which is largely a rainshadow effect (Hare and Hay 1974), is to conducive to fire (Flannigan and Harrington 1988, Clark 1989). Lodgepole pine, being well adapted to fire and extremely shade intolerant (U.S.D.A. Forest Service 1990a), maintains dominance in this region largely due to repeated fires (Rowe 1972).

The histograms for balsam fir (Figure III.2.f) indicate the probability of the species' dominance is highest under a less frigid winter regime than that occupied by the other predominately boreal species (indicated by higher absolute minimum temperatures than those shown in Figure III.2.a-d). The growing season can be characterized as cool and moist (as indicated by relatively moderate levels of degree-days, high levels of snowpack, and low soil moisture deficits). In eastern Canada, this seasonal regime is produced by the dominance of Arctic air modified by influxes of warmer Pacific, subtropical, and Atlantic air in the winter, and by the near dominance of subtropical and Atlantic airmasses during the growing season (Bryson and Hare 1974, Hare and Thomas 1974). The very drought-intolerant balsam fir (Bonan 1988) is probably moisture limited at the western and southern limits of it's dominance range, and thermally limited to the north (Bakuzis and Hansen 1965). The high susceptibility of balsam fir to severe damage and mortality from fire (U.S.D.A. Forest Service 1990a) may be another factor which constrains dominance of the species to the west in the more fire-prone interior of the continent.

The histograms for white pine (Figure III.2.g) illustrate a response similar to that of balsam fir, but white pine dominance is highest under a somewhat milder winter regime (indicated by higher absolute minimum temperatures) and a warmer, drier growing season (indicated by higher levels of degree-days and soil moisture deficit). This reflects the greater importance throughout the year of warmer Pacific, subtropical, and Atlantic airmasses in the region of white pine dominance (Bryson and Hare, 1974, Hare and Thomas 1974). Like balsam fir, white pine is regarded as being moisture limited at the western and southern limits of it's dominance range and thermally limited to the north (Jacobson 1979, Ritchie 1987). A low resistance to fire (U.S.D.A. Forest Service 1990) may likewise constrain white pine dominance at the western edge of it's range. The more southerly position of the range of white pine dominance relative to that of balsam fir is probably reflective of the greater drought tolerance of white pine and the importance of a warmer growing season given pine's greater susceptibility to winter desiccation (Sakai and Weiser 1973).

The histograms for sugar maple (Figure III.2.h) illustrate its dominance is highest under an even warmer winter regime (indicated by significantly higher absolute minimum temperatures) and a warmer and drier growing season (indicated by higher levels of degree-days and soil moisture deficit) than those of balsam fir and white pine. This reflects the position of the range of sugar maple dominance at the southern end of a north-to-south gradient in eastern Canada along which the year-round dominance of Arctic air decreases and that of the warmer Pacific, subtropical, and Atlantic airmasses increases (Bryson and Hare, 1974, Hare and Thomas, 1974). The critical factor constraining sugar maple dominance to the north and northwest is almost certainly absolute minimum temperature as the species is susceptible to frost damage when temperatures fall below about -40° C (Sakai and Weiser 1973). To the west and south, the dominance of the species is probably moisture-limited (Ritchie 1987).

The Classification of Forest-Types

The maximum value of the Calinski and Harabasz (1974) index (Figure III.3) indicated the presence of five clusters in the probability data for grid cells in the boreal forest domain. The mean probability of dominance for the eight tree species in each of the five clusters is shown in Table III.3. Species with mean probabilities of 25% or greater were used to name the cluster groups as derived forest-

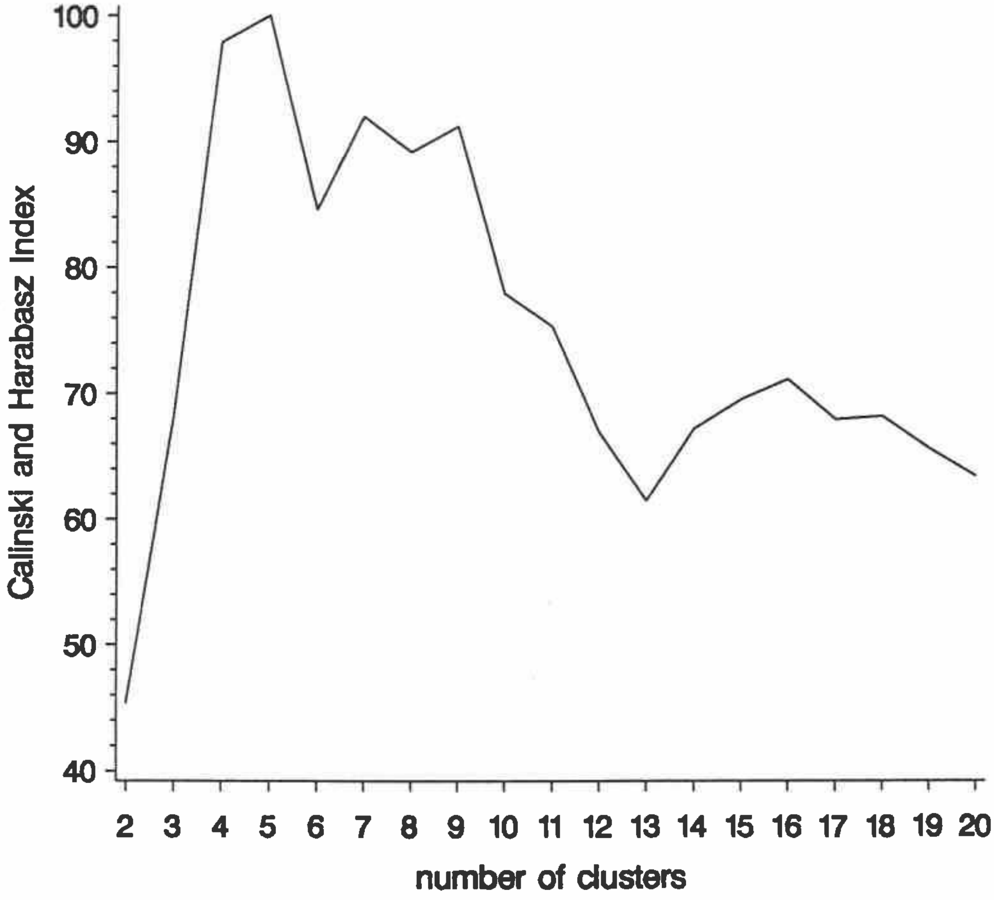

Figure III.3. Standardized values of the Calinski and Harabasz (1974) index as a function of the number of clusters. The highest value of the index indicated the "true" number of clusters (i.e., five) in the set of probability estimates.

Table III.3. Mean probability of species dominance by cluster. All table entries are in percent. Mean values >25% in bold.

	Cluster Number				
Species	1	2	3	4	5
black spruce	**81**	**89**	**47**	**87**	**62**
white spruce	**37**	**64**	**67**	**63**	**63**
jack pine	3	**68**	5	4	1
trembling aspen	1	20	**34**	0	0
lodgepole pine	3	1	**26**	0	0
balsam fir	3	4	0	**61**	**50**
eastern white pine	0	0	0	13	**60**
sugar maple	0	0	0	9	**58**

types in Figure III.4 where the cluster membership of the grid cells is mapped. The vegetation regions identified as members of the subarctic woodland, boreal forest, and mixed forest formation-types on the Canadian vegetation map (National Atlas of Canada 1973a) were aggregated to produce the five types shown on the observed forest-type map in Figure III.5.

A visual comparison shows much of the disagreement between the two maps (Figures III.4 and III.5) occurs west of the Canadian Shield where factors other than climate, especially topographic complexity and disturbance by fire, are important determinants of the vegetation mosaic. However, more detailed vegetation maps of Alberta (University of Alberta 1969), Saskatchewan (Richards and Fung 1969), and the Yukon Territory (Rowe 1972) show a more complex forest-type mosaic in these regions compared to that portrayed on the observed forest-type map. In some instances, the map of derived forest-types is in greater accord with the more detailed maps than is the observed forest-type map.

Moreover, the analysis based on the kappa statistic (Table III.4) indicates there is a large degree of correspondence between the observed and derived forest-type

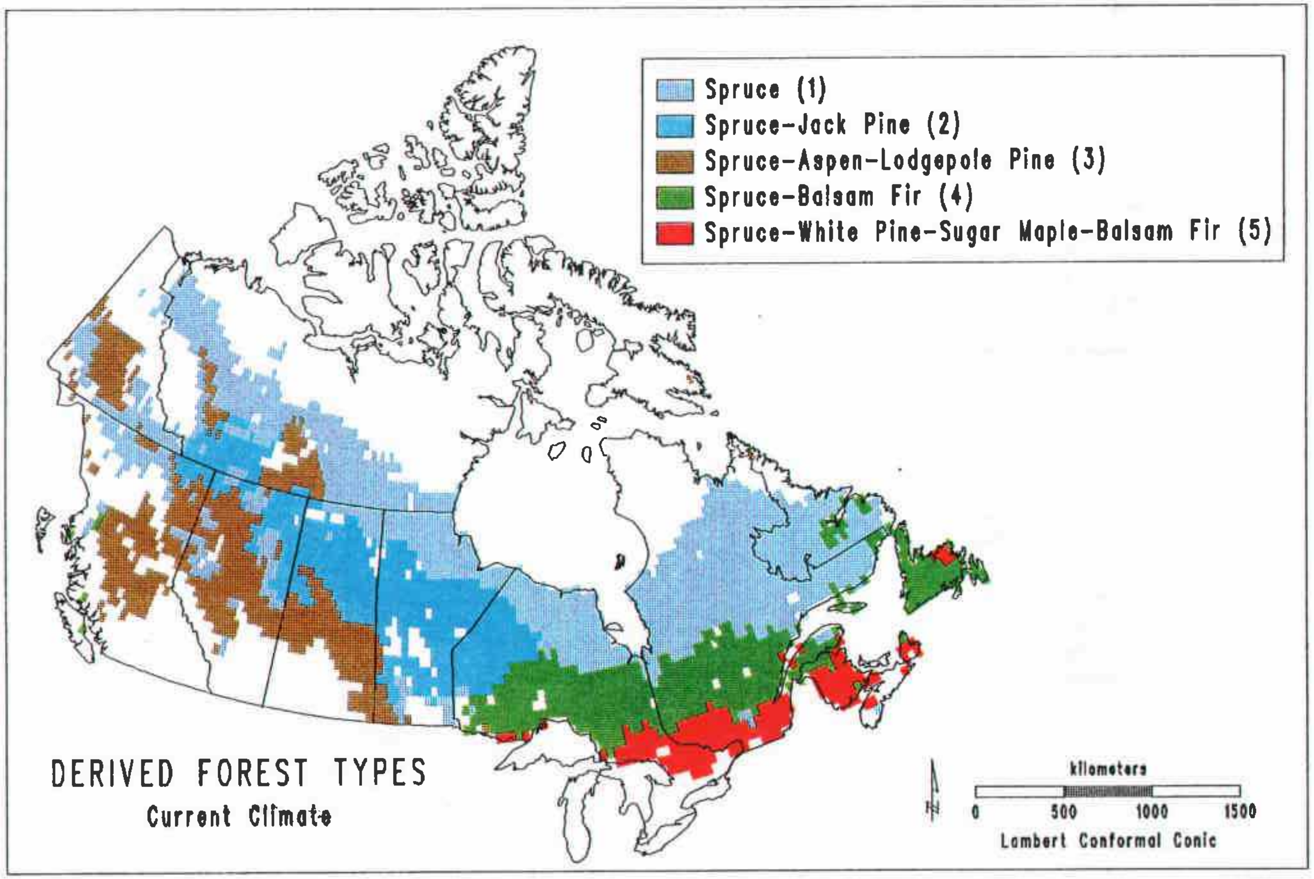

Figure III.4. The distribution of forest-types in the boreal forest region derived by cluster analysis of probabilities of species dominance. Numbers in parenthesis are cluster numbers in Table III.3.

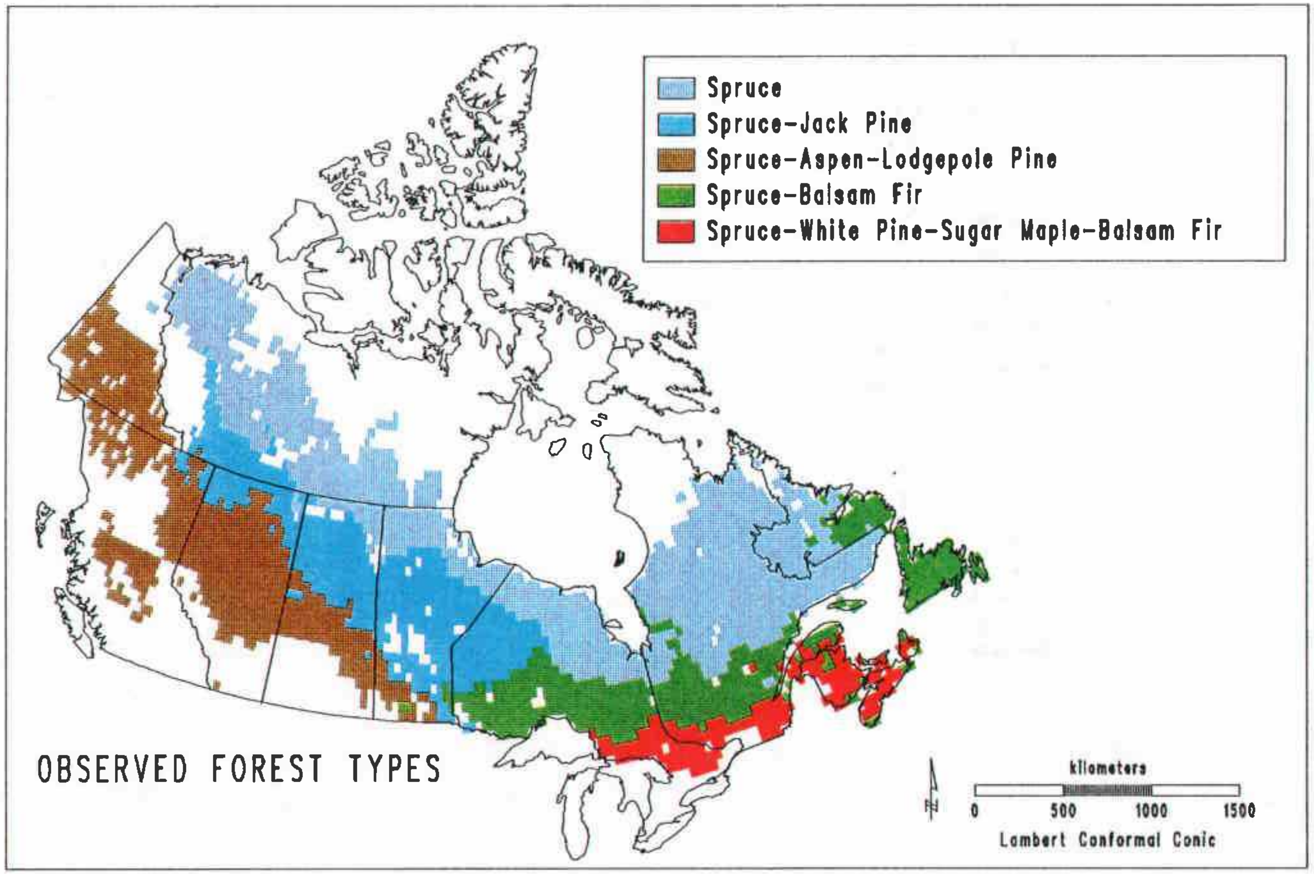

Figure III.5. The distribution of the observed forest-types in the boreal forest region. Vegetation regions on the National Atlas of Canada (1979a) map were aggregated to produce this map.

Table III.4. Kappa statistics for the comparison between the observed areal extent of the boreal forest-types and the areal extent of the forest-types derived by cluster analysis. Distribution of observed forest-types based on vegetation regions map in the National Atlas of Canada (1973a). "Spruce" refers to black and white spruce. Class limits for the assessment scale (Monserud 1990) are: <.40, poor; .40-.55, fair; .55-.70, good; .70-.85, very good; >.85, excellent.

Forest Type	Kappa	Assessment
Spruce	.72	very good
Spruce-Jack Pine	.80	very good
Spruce-Aspen-Lodgepole Pine	.58	good
Spruce-Balsam Fir	.74	very good
Spruce-White Pine-Sugar Maple-Balsam Fir	.71	very good
Boreal Forest Boundary	.89	excellent
Overall	.79	very good

maps. According to a subjective scale of assessment (Table III.4, Monserud 1990), the overall kappa statistic indicates very good overall agreement between the distribution of observed and derived types, and there is excellent agreement for the position of the boundary around the boreal forest region. The assessments of kappa statistics for the individual forest-types range from good to very good (Table III.4).

The division of the boreal forest into five major forest-types captures the broad-scale pattern of the vegetation mosaic (National Atlas of Canada 1973a), and is similar to other regional vegetation classifications of the boreal forest region (e.g., Hare 1950, Rowe 1972, Larsen 1980). The five-group structure also bears a direct relationship to seasonal airmass dynamics. For example, the black spruce-white spruce type in the subarctic sector of the boreal forest occurs just north of the mean summer position of the Arctic front (Bryson 1966, Barry 1967). The spruce-balsam fir type is situated north of the mean winter position of the Arctic front and south of the front's mean summer position (Bryson 1966, Barry 1967), and thus receives warmth and moisture from Atlantic and Gulf of Mexico airmasses throughout much of the late spring and summer

(Bryson and Hare 1974). The spruce-white pine-sugar maple-balsam fir type is just south of the mean winter position of the Arctic front (Bryson 1966, Barry 1967), and is under the influence of southern airmasses even earlier in the growing season (Bryson and Hare 1974).

The boundary in southern Ontario between the two eastern and two continental forest-types lies near the eastern extent of a region dominated by relatively dry Pacific airmasses for at least four months a year (Bryson and Hare 1974). The Canadian portion of this fire-prone region is largely co-incident with the combined distributions of the spruce-jack pine and spruce-aspen-lodgepole pine types east of the Cordillera. These two forest-types are distinguished climatically by the spring incursion of dry Pacific air behind the arctic front which occurs at least a full month earlier in the spruce-aspen-lodgepole pine type (Bryson and Hare 1974). The Pacific air is also modified by frequent influxes of moist subtropical air during the growing season in the spruce-jack pine region (Hare and Thomas 1974). These distinctions are reflected in the semiarid to subhumid soil moisture regime in the spruce-aspen-lodgepole type compared to the more humid regime in the spruce-jack pine type (National Atlas of Canada 1973b).

The contrast in soil moisture regimes, in turn, probably accounts for the greater dominance of the more drought-tolerant white spruce in the spruce-aspen-lodgepole type as compared to the greater dominance of black spruce in the spruce-jack pine type. As previously discussed, the relative importance of aspen and jack pine as the primary pioneer species in the two continental forest types may be more a response to properties of the substratum than to the climatic parameters in this study.

CONCLUSION

The results of the response surface analysis indicate that, at the continental-scale of this study, the dominance of eight important boreal tree species is largely a reflection of climate, and that much of the variation in the probability of dominance is apparently related to the species' individualistic response to climatic constraints within different airmass regions. Furthermore, because the climatic predictors are more directly related to the response of plants than those used in other response surface analyses, the results of this study are more interpretable in terms of the mechanisms by which climate exerts control over species dominance (e.g, in terms of the interactions between absolute minimum temperature and the species' resistance to frost damage, or between soil moisture deficits and species' tolerance of drought or drought-induced fire).

Well-defined forest-types can be distinguished on the basis of the relative probabilities of dominance, notwithstanding the species' individualistic response to climate. The geographic distribution of the forest-types in relation to seasonal airmass dynamics in the boreal forest region suggests the species assemblages are also primarily controlled by climate. Non-climatic factors which partly determine floristic composition at the scale of the stand or patch (e.g., interspecific competition, succession, time since disturbance) are apparently averaged out at the much larger scale of the study, as suggested by Huntley et al. (1989). A shift in the relative dominance of aspen and jack pine across a distinct boundary between substrate types in the central interior of Canada may be an exception to this general principle of broad-scale climatic control.

CHAPTER IV:

CANADIAN VEGETATION RESPONSE TO PROJECTED CLIMATIC CHANGE AT THREE ORGANIZATIONAL LEVELS

INTRODUCTION

In this chapter, the equilibrium models developed in the preceding chapters are used to predict the response of Canadian vegetation under two future climatic scenarios at three organizational levels of the vegetation mosaic. The results from doubled-CO_2 experiments produced by the Goddard Institute for Space Studies (GISS) GCM (Hansen et al. 1988) and the Geophysical Fluid Dynamics Laboratory (GFDL) GCM (Manabe and Wetherald 1987) are used to prescribe the future climates. Changes in the areal extent and distribution of the vegetation formations predicted by CCVM and in species dominance predicted by the response surfaces are described in relation to changes in the climatic parameters under both doubled-CO_2 scenarios. Boreal forest-types derived from future probabilities of species dominance under each climatic scenario are compared to current forest-types to identify future types with no modern analog. A linkage between the formation-level vegetation scenarios generated by CCVM and the species dominance and boreal-forest type scenarios generated by the response surfaces is sought at the common organizational level of the boreal forest domain.

METHODS AND APPROACH

The five climatic parameters used as model drivers in CCVM and the climatic response surfaces are calculated from monthly values of mean temperature, total precipitation, and mean relative humidity. The number of degree-days are calculated from daily temperatures (estimated by linear interpolation between monthly values) using a 0° C threshold. Absolute minimum temperatures are estimated from the coldest mean monthly temperatures by regression. A water balance algorithm was developed to estimate snowpack, soil moisture deficits, and actual evapotranspiration. The algorithm includes a decreasing soil moisture availability function and provisions for the accumulation and melting of snow. Potential evapotranspiration was estimated using Eagleman's (1967) empirical function which accounts for the influence of vapor pressure on PET. The methods employed in estimating the values of the climatic drivers, and their relationship to the survival, growth, and reproduction of dominant plant life-forms in Canada are more fully described in Chapter II.

The current Canadian normals for temperature and precipitation were extracted from a global database distributed over a 0.5° latitude x 0.5° longitude (i.e., half-degree) grid

(Leemans and Cramer 1990). Relative humidities at airport meteorological stations (WeatherDisc Associates 1990) were interpolated to the same grid using an inverse distance-squared algorithm. Output from the GCM $2xCO_2$ and "control" (i.e., $1xCO_2$) experiments were used to calculate temperature anomalies ($2xCO_2$-$1xCO_2$) and precipitation and relative humidity anomalies ($2xCO_2/1xCO_2$). The anomalies were interpolated from the center points of the GCM cells to the half-degree grid, and then combined with the current normals to arrive at $2xCO_2$ "normals" for monthly temperature, precipitation, and relative humidity. This is the most commonly-used procedure for generating regional climatic change scenarios from GCM information (Giorgi and Mearns 1991), and it is the simplest approach to problems posed by the coarse resolution of the GCM data and the rather poor simulation of the "control" climate at the regional-scale.

The five model drivers were estimated from the $2xCO_2$ "normals" on the half-degree grid and then processed by the CCVM rule-base to predict the equilibrium distribution of Canadian vegetation formations under each of the future climate scenarios. Coupling the same climatic estimates with the climatic response surfaces yielded future probabilities of dominance for the eight tree species. The geographic extent of the boreal forest domain under a given scenario was then defined as the subset of grid cells where at least one of the five predominately boreal species (i.e., the first five species listed in Table IV.1) had a future probability of dominance greater than 50%. The probabilities associated with this subset of grid cells were entered into a non-hierarchical clustering procedure in which two to twenty clusters were formed, and the Calinski and Harabesz (1974) index was employed as a stopping rule to indicate the "true" number of clusters. The group membership of grid cells at the clustering level indicated by the stopping rule was supplied to a GIS to produce a map of derived forest-types. Chapter III provides a more detailed explanation of the methods used to derive a forest-type classification from the probabilities of species dominance. Pairwise comparisons between forest types derived for current conditions and those derived under the $2xCO_2$ scenarios were made using the squared chord distance coefficient (Overpeck et al. 1985) to identify future forest-types with no modern analogs.

RESULTS AND DISCUSSION

The Climatic Scenarios

The seasonal progression of precipitation, temperature, relative humidity, and potential evapotranspiration under current conditions and under the $2xCO_2$ scenarios is shown for Canada as a whole in Figure IV.1. Total annual precipitation increases by just less than 20% under both scenarios. The

Table IV.1. Boreal tree species represented by ecological response surfaces.

Common Name	Scientific Name
black spruce	*Picea mariana* (Mill.) B.S.P.
white spruce	*Picea glauca* (Moench) Voss
jack pine	*Pinus banksiana* Lamb.
trembling aspen	*Populus tremuloides* Michx.
balsam fir	*Abies balsamea* (L.) Mill.
eastern white pine	*Pinus strobus* L.
sugar maple	*Acer saccharum* Marsh.
lodgepole pine	*Pinus contorta* Dougl. var. *latifolia* Engelm.

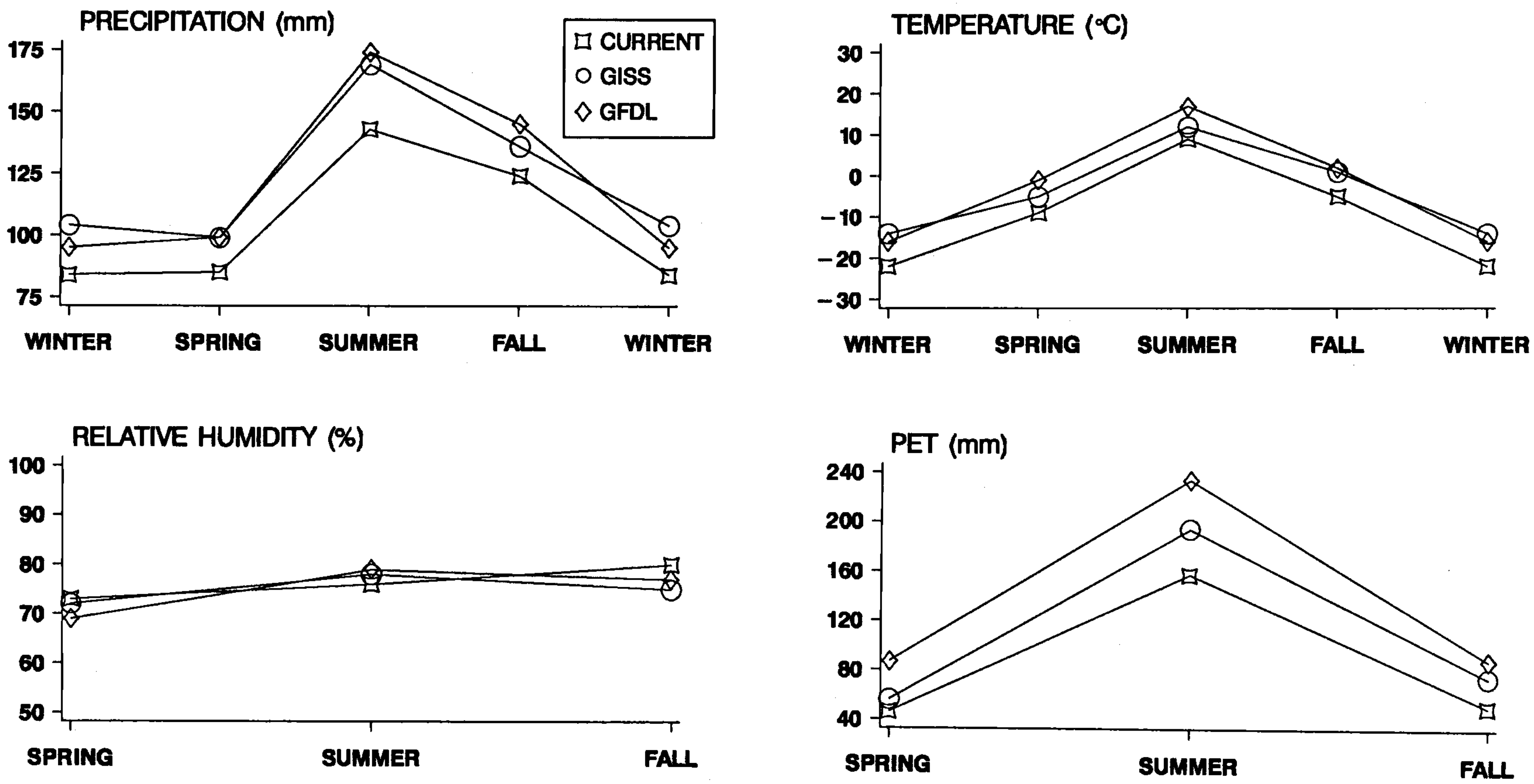

Figure IV.1. Seasonal values of four climate parameters for Canada under current conditions and under the Goddard Institute for Space Studies (GISS) and the Geophysical Fluid Dynamics Lab (GFDL) 2xCO_2 climatic scenarios. Seasonal values are the sum or average of the three monthly values for the season at each grid cell averaged across all cells in the database. Relative humidity and potential evapotranspiration (PET) are near zero in the winter.

increase in winter precipitation under the GISS scenario is almost double the increase in the GFDL scenario, but this relationship is reversed in the case of fall precipitation. The increase in temperature is substantial in all seasons under both scenarios, especially in the winter under the GISS scenario and in the spring and summer under the GFDL scenario where there is an eight degree increase over current seasonal norms. The relative humidity is lower in the spring and fall and higher in the summer under both scenarios, but these changes are relatively small. The increases in potential evapotranspiration (PET), on the other hand, are very substantial under both scenarios. This is especially true under the GFDL scenario where changes in PET range from a 90% increase over normal in the spring to a 50% increase in the summer. The large increases in PET are driven by higher temperatures in the absence of any compensating increases in relative humidity.

The values of the climatic drivers averaged across Canada are shown in Table IV.2. Snowpack decreases under both scenarios as a function of warmer temperatures. Warmer winter temperatures are responsible for the increase in absolute minimum temperature under both scenarios, while the large increases in degree-days are driven by warmer spring, summer, and fall temperatures. The increase in degree-days is particularly dramatic under the GFDL scenario where there is a

Table IV.2. Mean values for Canada of the climatic parameters used in the Canadian Climate-Vegetation Model and the climatic response surfaces. Shown are mean values under current conditions and under the Goddard Institute for Space Studies (GISS) and the Geophysical Fluid Dynamics Lab (GFDL) $2xCO_2$ climatic scenarios. Snowpack is in water equivalents. The base temperature for calculating degree-days was 0° C. Total summer AET is actual evapotranspiration for June to August. SMD is soil moisture deficit.

Climatic Parameter	Current	GISS	GFDL
total annual snowpack (mm)	176	117	133
absolute minimum temperature ($^{\circ}$C)	-45	-41	-42
degree-days ($^{\circ}$C)	1240	1809	2493
total summer AET (mm)	100	118	125
total annual SMD (mm)	63	88	139

100% increase over the current norm. Increases in summer actual evapotranspiration (AET) are reflective of greater summer precipitation, but the latter is not sufficient to offset the large increases in PET which produce very substantial increases in soil moisture deficit (SMD) under both scenarios. This is especially true under GFDL conditions where there is a 120% increase in this index of drought stress.

The mean values of the model inputs and drivers represent the predicted consequences of an enhanced greenhouse effect on the climate of Canada as a whole, but they cannot represent the considerable regional variation within and between the two scenarios. Much of this geographic variation is evident in the vegetation simulations described below, and will be discussed in that context.

The Formation-Level Scenarios

The distributions of the Canadian vegetation formations as predicted by CCVM under current conditions and under the 2xCO_2 climatic scenarios are shown in Figures IV.2 - IV.4. CCVM does not include provisions for boggy terrain and glaciers, so the area occupied by these units under current conditions is mapped as "unclassified" (Figures IV.2 - IV.4) and was excluded from the quantitative evaluation of the simulation results. Table IV.3 lists the predicted areal extent of the vegetation formations in each simulation, and changes in

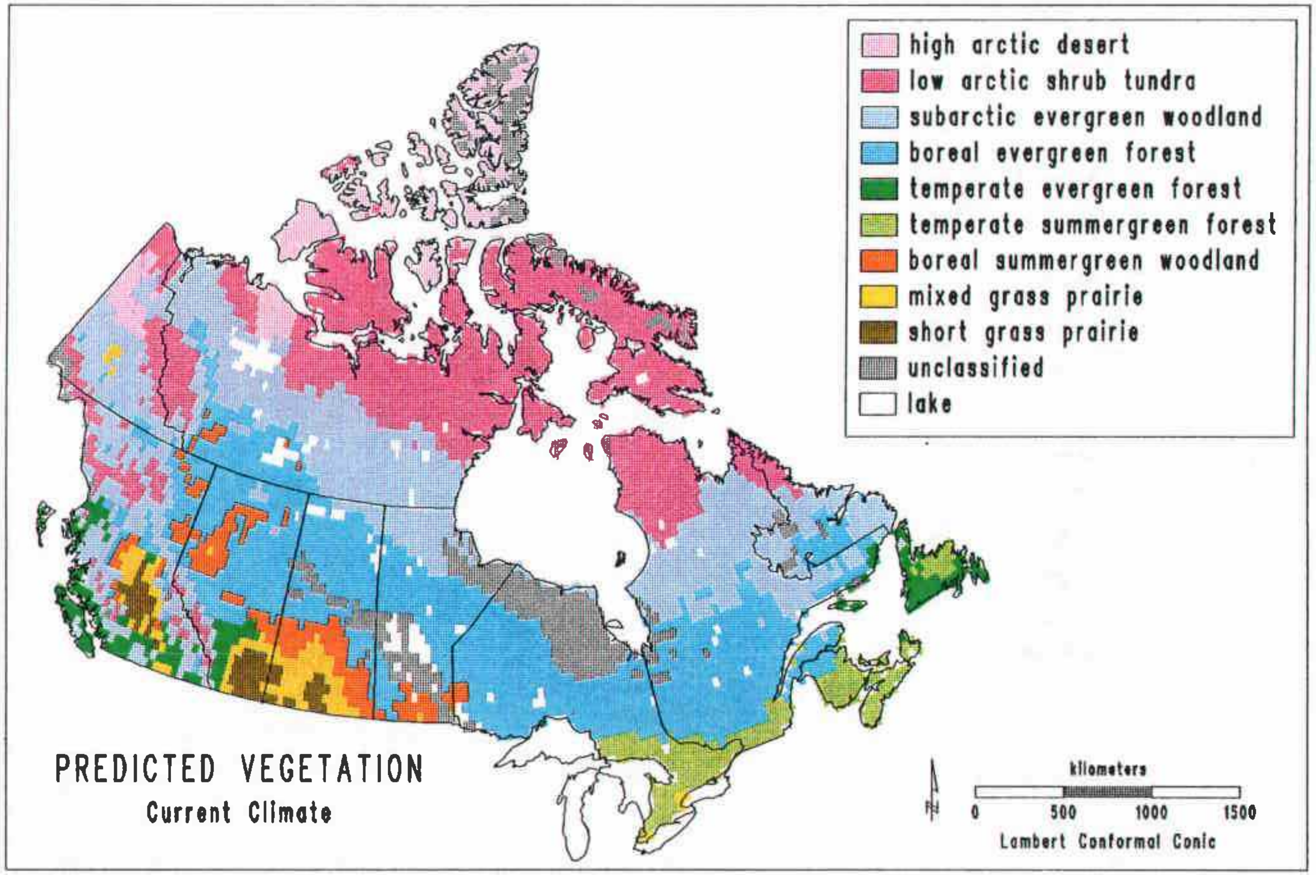

Figure IV.2. Formation-level vegetation predicted by the Canadian Climate-Vegetation Model under current climatic conditions

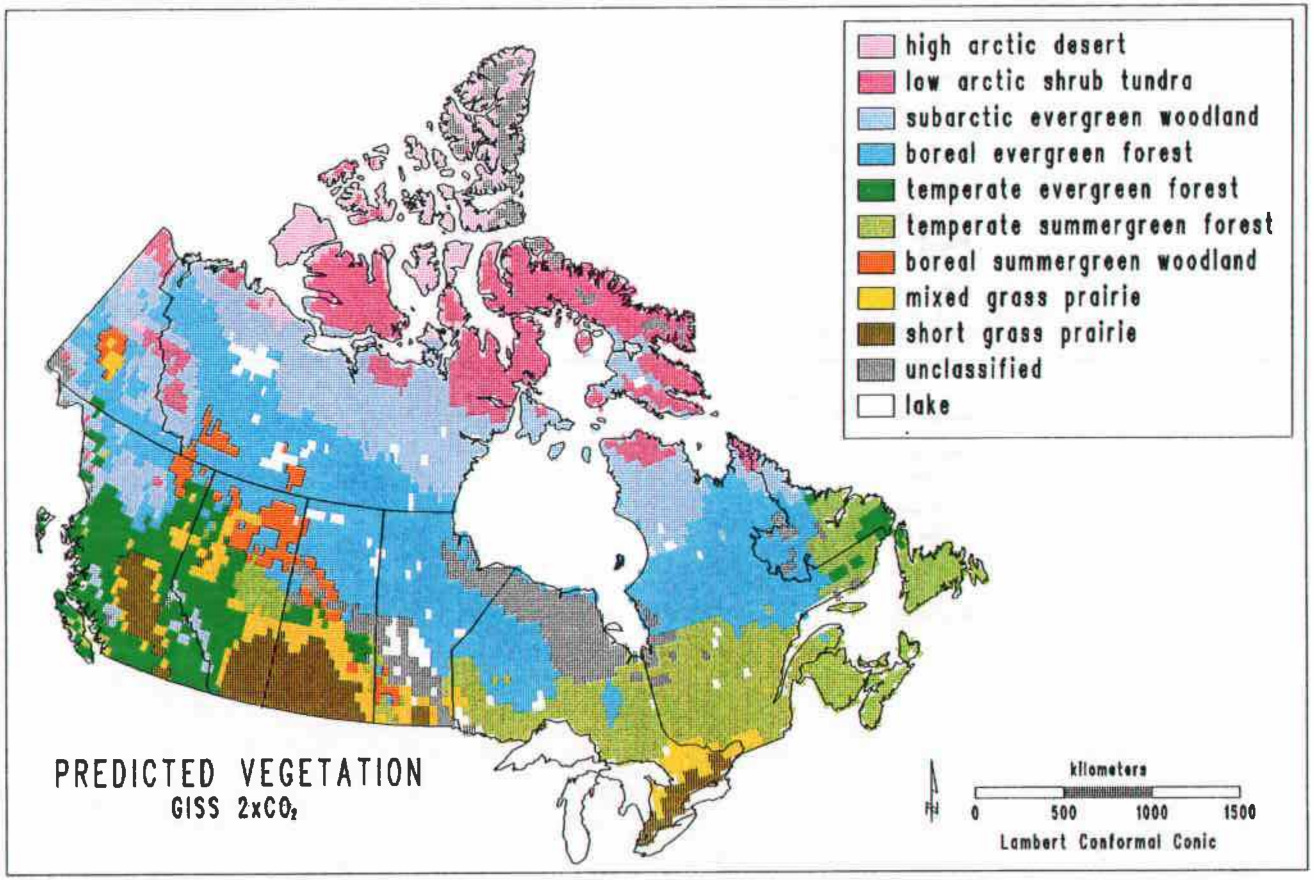

Figure IV.3. Formation-level vegetation predicted by the Canadian Climate-Vegetation Model under the Goddard Institute for Space Studies (GISS) $2xCO_2$ climatic scenario

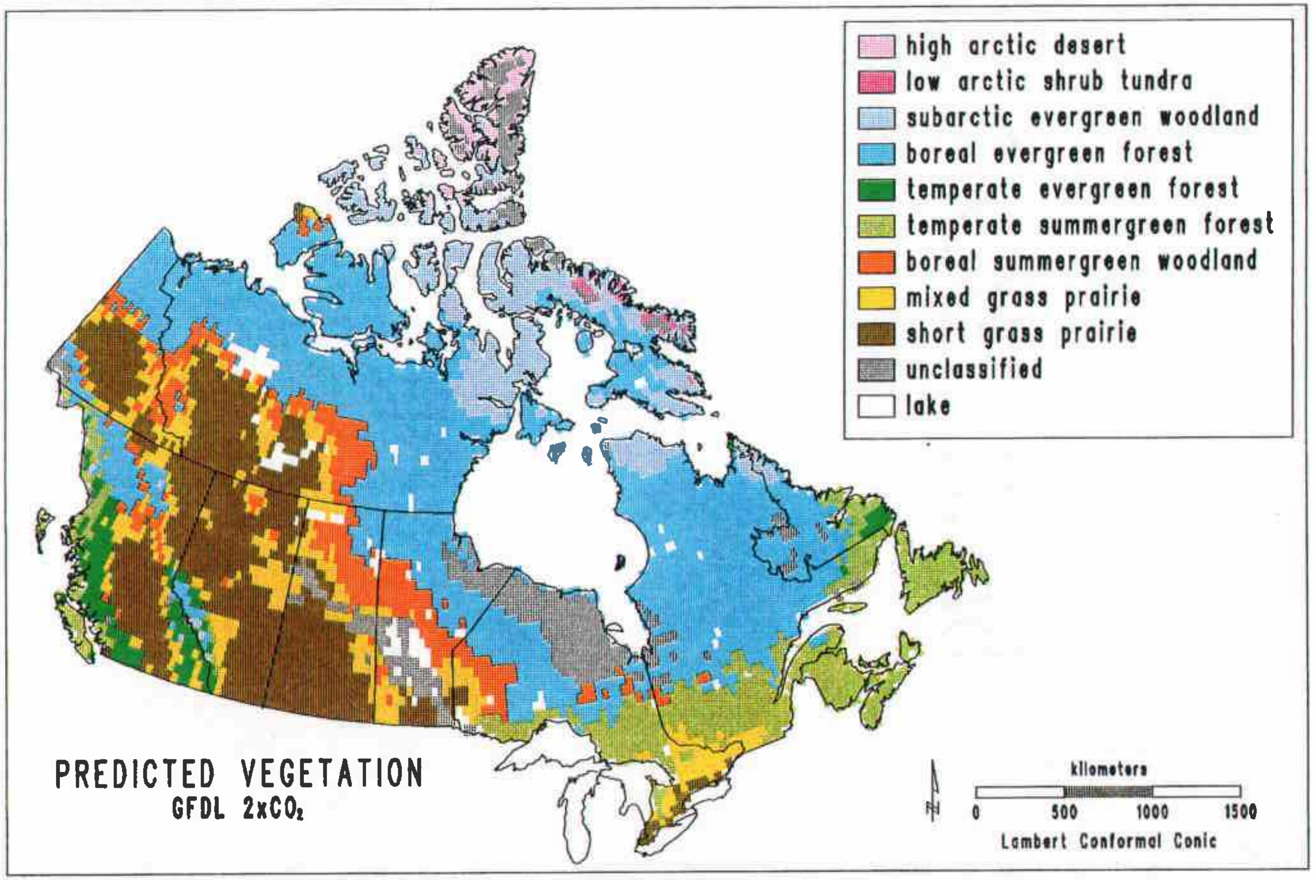

Figure IV.4. Formation-level vegetation predicted by the Canadian Climate-Vegetation Model under the Geophysical Fluid Dynamics Lab (GFDL) 2xCO_2 climatic scenario

Table IV.3. The areal extent of Canadian vegetation formations predicted by the Canadian Climate-Vegetation Model under current conditions and under the Goddard Institute for Space Studies (GISS) and the Geophysical Fluid Dynamics Lab (GFDL) 2xCO_2 climatic scenarios. Table entries are square kilometers x 10^4.

Vegetation Formation	Current	GISS	GFDL
high arctic desert	51	52	15
low arctic shrub tundra	227	105	3
subarctic evergreen woodland	226	163	83
boreal evergreen forest	247	254	356
temperate evergreen forest	29	70	32
temperate summergreen forest	37	135	95
boreal summergreen woodland	33	24	65
mixed grass prairie	21	37	78
short grass prairie	13	45	167

the area occupied by each formation under the future climatic scenarios (i.e., relative to their extent in the simulation for current conditions) are portrayed in Figure IV.5. As discussed in Chapter II, the CCVM simulation for current conditions is an accurate representation of the actual distribution of vegetation formations in Canada.

The features common to both 2xCO_2 scenarios are the expansion of nearly all the boreal and temperate formations at the expense of the arctic and subarctic types. The predicted increase in degree-days, which would enhance resistance to winter desiccation near the tree-line (Wardle 1974, Tranquillini 1979), results in a northward migration of the subarctic woodland in both scenarios. In the GISS scenario, the northern shift of the subarctic woodland reduces the extent of low arctic shrub tundra, which in this simulation remains constrained on its northern margin by the scant snowpack of the high arctic region which leaves erect shrubs exposed to winter desiccation (Saville 1972, Edlund 1983). The reduction of low arctic tundra is almost complete in the GFDL simulation, and under this scenario the encroachment of subarctic woodland restricts even the high arctic desert to a relatively small portion of its current range.

The predicted migration of the tree-line into the limited land area of the far north is accompanied by an even greater poleward movement of the forest-line produced by the

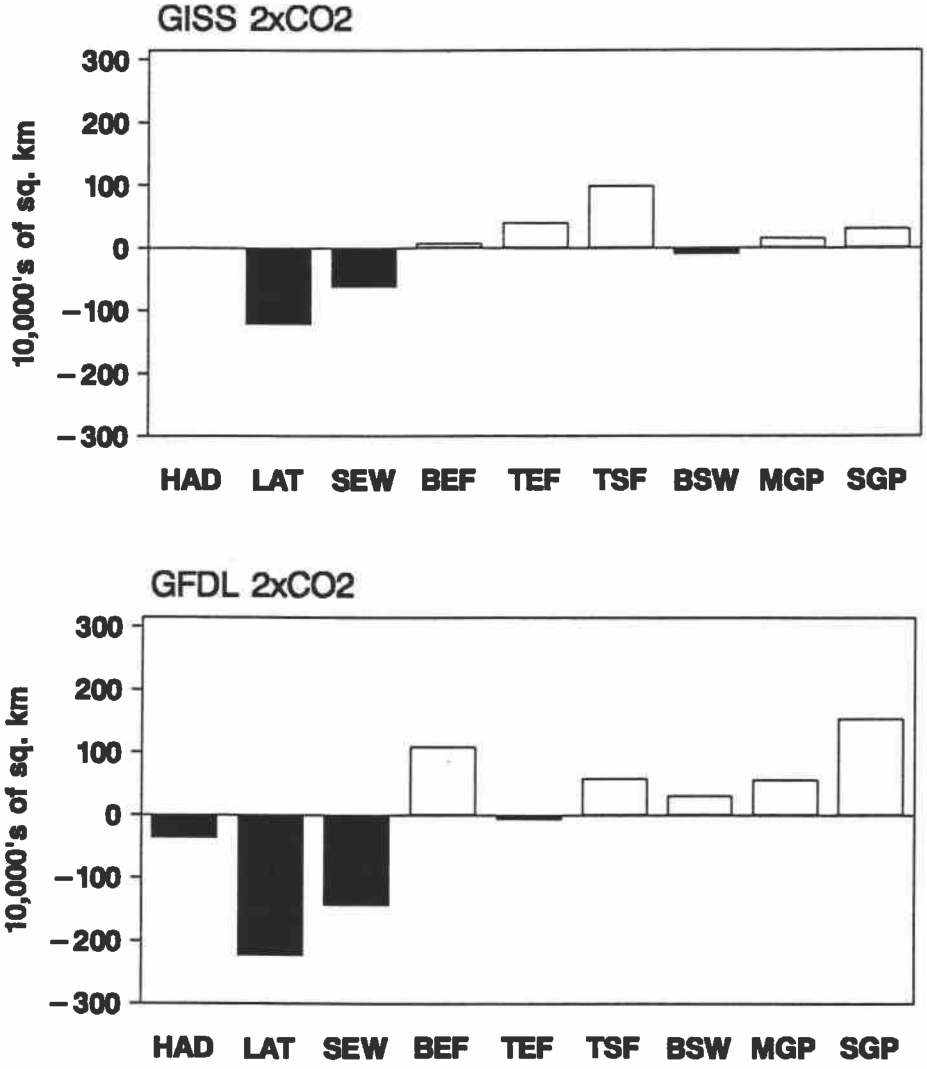

Figure IV.5. The change in the areal extent of vegetation formations predicted by the Canadian Climate-Vegetation Model (CCVM) under the Goddard Institute for Space Studies (GISS) and the Geophysical Fluid Dynamics Lab (GFDL) $2xCO_2$ climatic scenarios. Changes were calculated relative to the areal extent of vegetation formations predicted by CCVM under current climatic conditions. Vegetation Formations: HAD, High Arctic Desert; LAT, Low Arctic Shrub Tundra; SEW, Subarctic Evergreen Woodland; BEF, Boreal Evergreen Forest; TEF, Temperate Evergreen Forest; TSF, Temperate Summergreen Forest; BSW, Boreal Summergreen Woodland; MGP, Mixed Grass Prairie; SGP, Short Grass Prairie.

increase in degree-days. The net effect is a predicted reduction in the areal extent of subarctic woodland, especially under GFDL conditions where the increase in degree-days is the greatest. The basis for the shift in the position of the forest-line is the observed increase in sexual reproduction and establishment of trees with an increase in the length and warmth of the growing season near the upper margin of the boreal evergreen forest (e.g., Black and Bliss 1980).

In the GISS scenario, the area gained by the boreal forest in it's northward expansion is largely offset by the expansion of temperate summergreen forest in southeastern Canada. CCVM predicts expansion of the temperate forest formations as a result of the increase in absolute minimum temperature. The mechanistic basis behind such an expansion is a lowering of constraints imposed by low temperatures on the ranges of many temperate tree species with a relatively low tolerance to freezing (Sakai and Weiser 1973, George et al. 1974). In western Canada, the increase in the evergreen temperate forest in western Canada under GISS conditions occurs because the total summer AET is less than a calibrated threshold set in CCVM. Below this threshold it is inferred that summergreen hardwoods cannot fix enough carbon to maintain their competitiveness with evergreen conifers (Waring and Franklin 1979).

In the GFDL simulation, the temperate summergreen forest of southeastern Canada does not migrate as far north due to a smaller increase in absolute minimum temperature under this climatic scenario. There is a small decline in the extent of temperate evergreen forest in western Canada, in part because an increase in total summer AET results in a prediction of temperate summergreen forest along the Pacific coast. Temperate evergreen forest is also reduced by the expansion of mixed grass and short grass prairie in western Canada under GFDL conditions. CCVM predicts a sizable expansion of the boreal summergreen woodland and the prairie types in response to the large increases in soil moisture deficits. In the GISS simulation, the smaller increases in the moisture deficit compared to those in the GFDL simulation produce a smaller increase in extent of the two prairie formations. The predicted expansion of dry woodland and prairie in the two vegetation scenarios is based on the causal-relationship between soil moisture deficits and vegetation structure when vegetation exists in dynamic equilibrium with the water balance (Woodward 1987).

The Species-Level Scenarios

Maps of the probabilities of species dominance (i.e., probability surfaces) generated by the response surfaces for current and 2xCO_2 conditions are shown in Figure IV.6. To

Figure IV.6

The observed distribution of species dominance and the distribution of the climatically-determined probabilities of species dominance under current conditions and under the Goddard Institute for Space Studies (GISS) and the Geophysical Fluid Dynamics Lab (GFDL) 2xCO_2 climatic scenarios. The observed distribution of species dominance (in black) is the combined extent of regions in which the species was listed as a dominant on the vegetation regions map in the National Atlas of Canada (1973a). The probabilities of species dominance were estimated by the climatic response surfaces from values of the climatic predictors at each grid cell. The shading represents three different probability levels: 25-50% (lightest shading), 50-75% (medium shading), and greater than 75% (black).

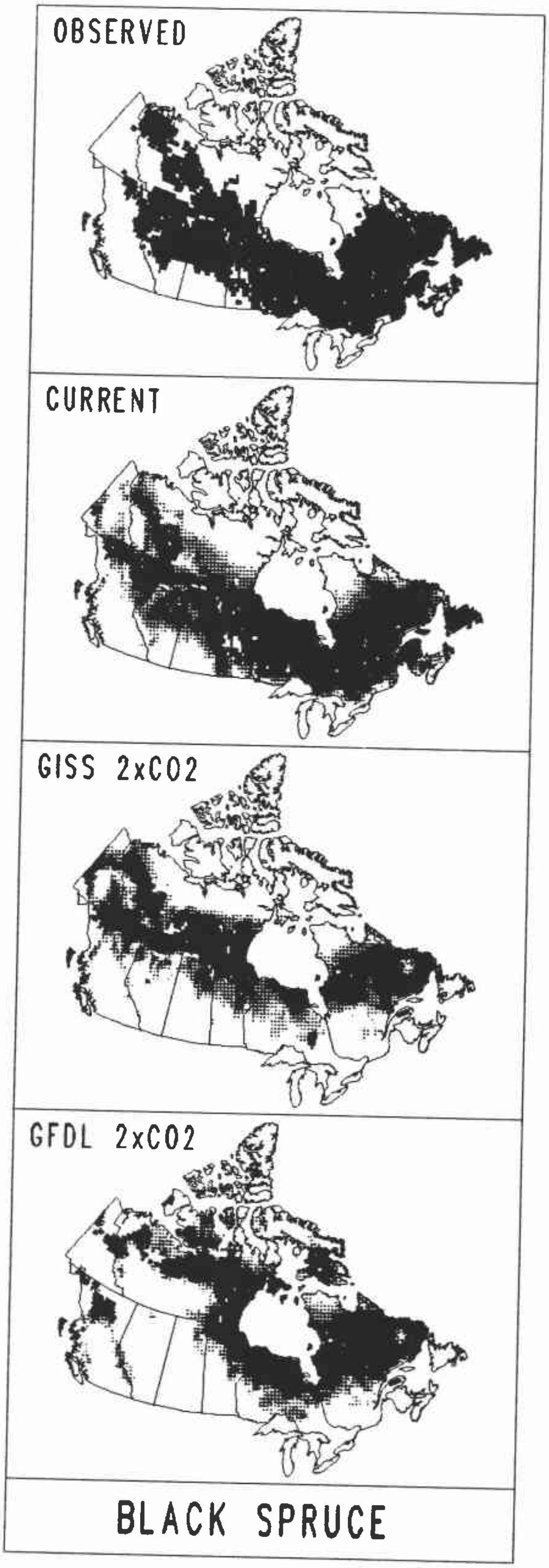

Figure IV.6.a

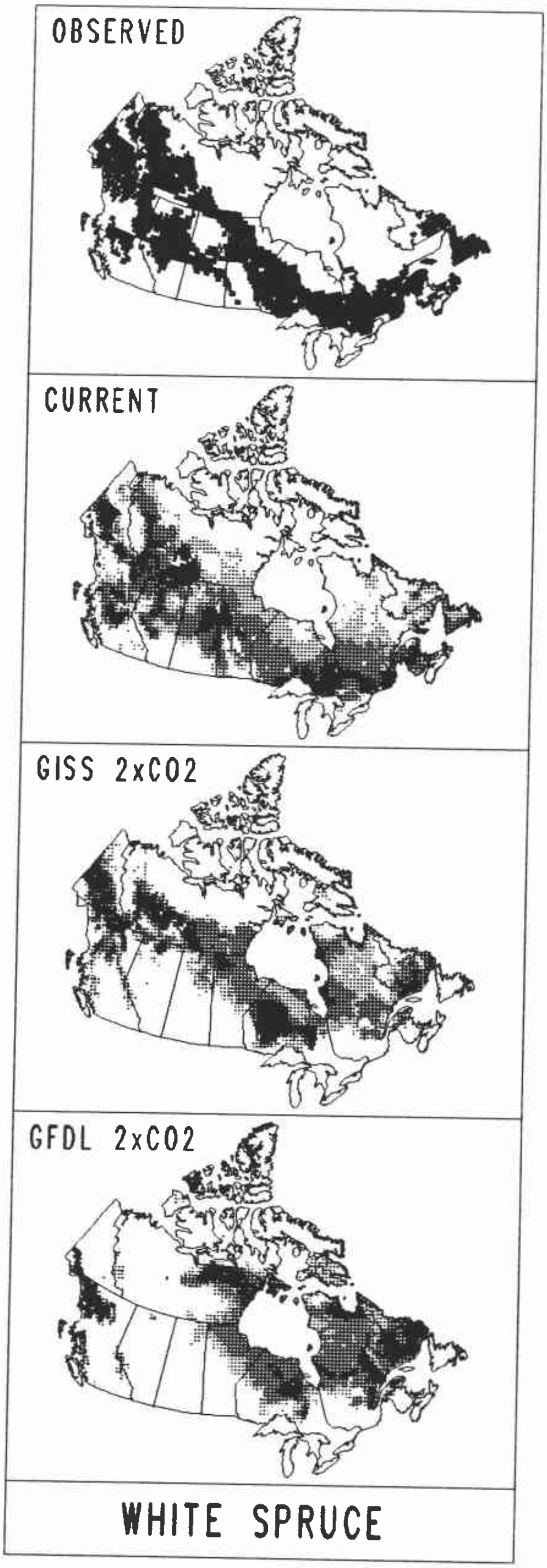

Figure IV.6.b

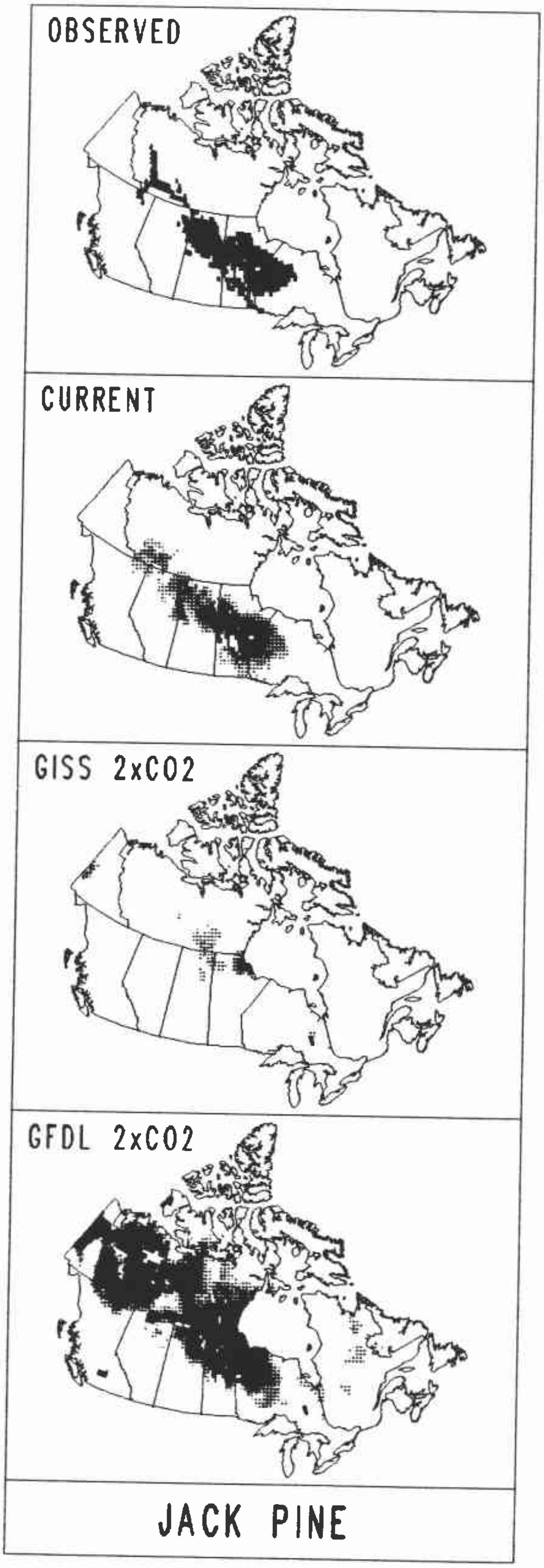

Figure IV.6.c

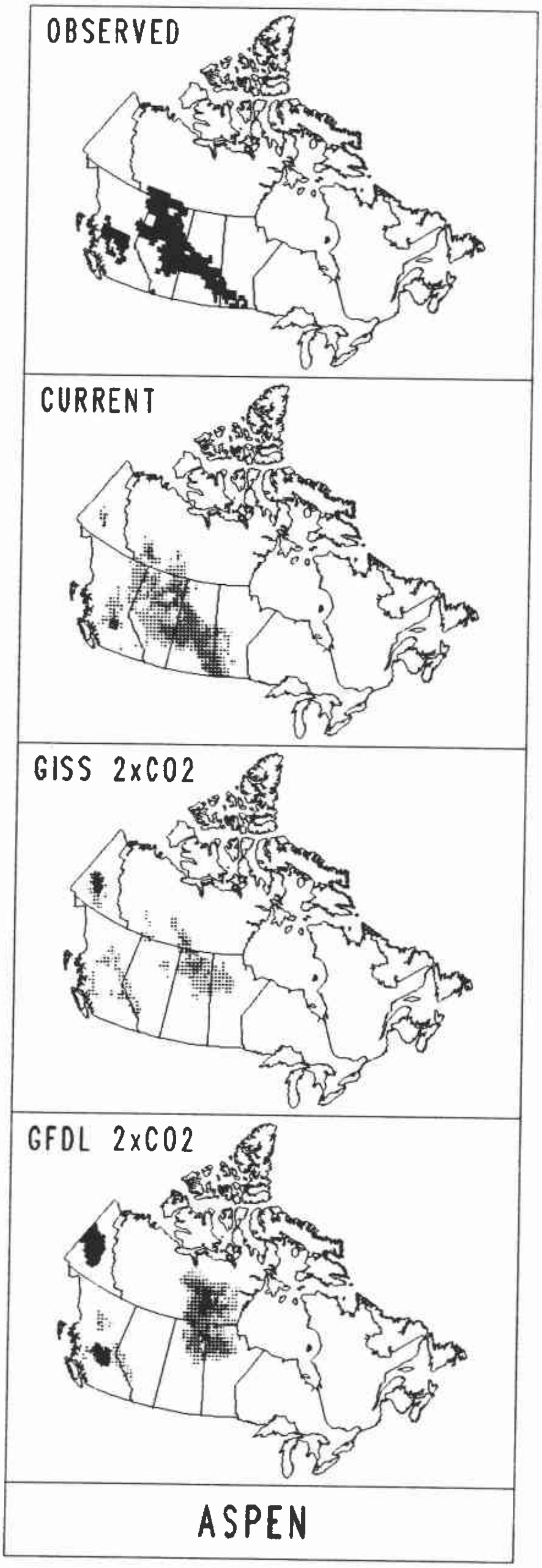

Figure IV.6.d

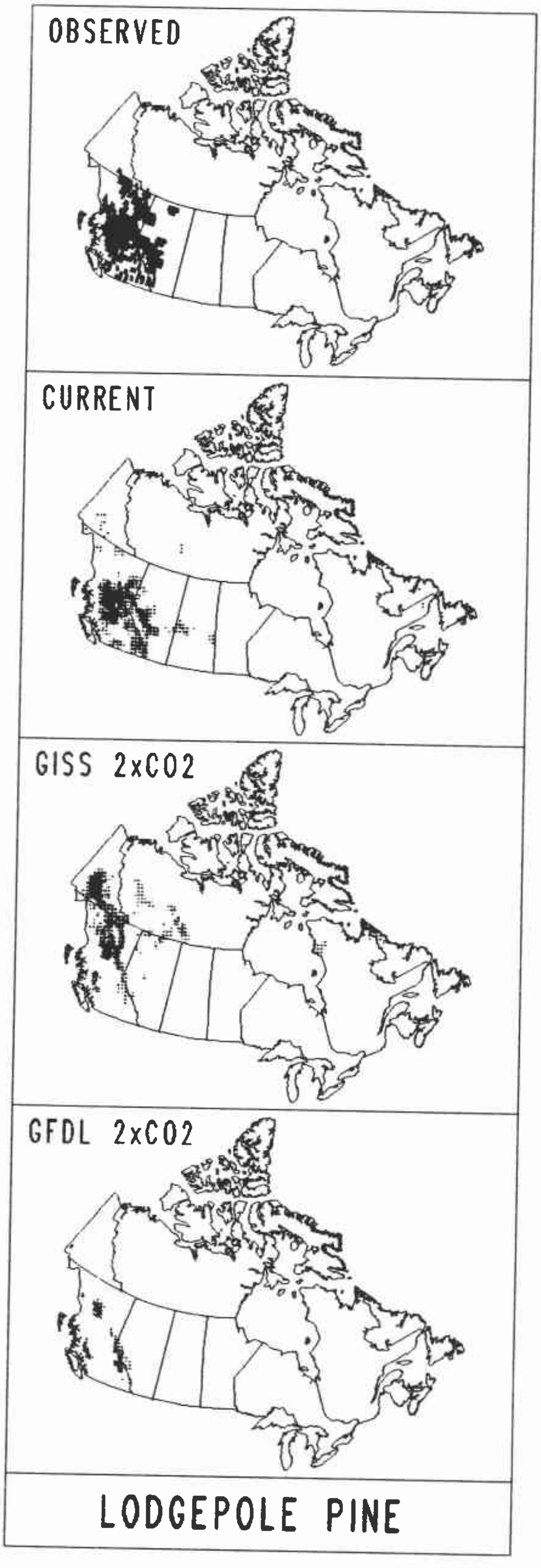

Figure IV.6.e

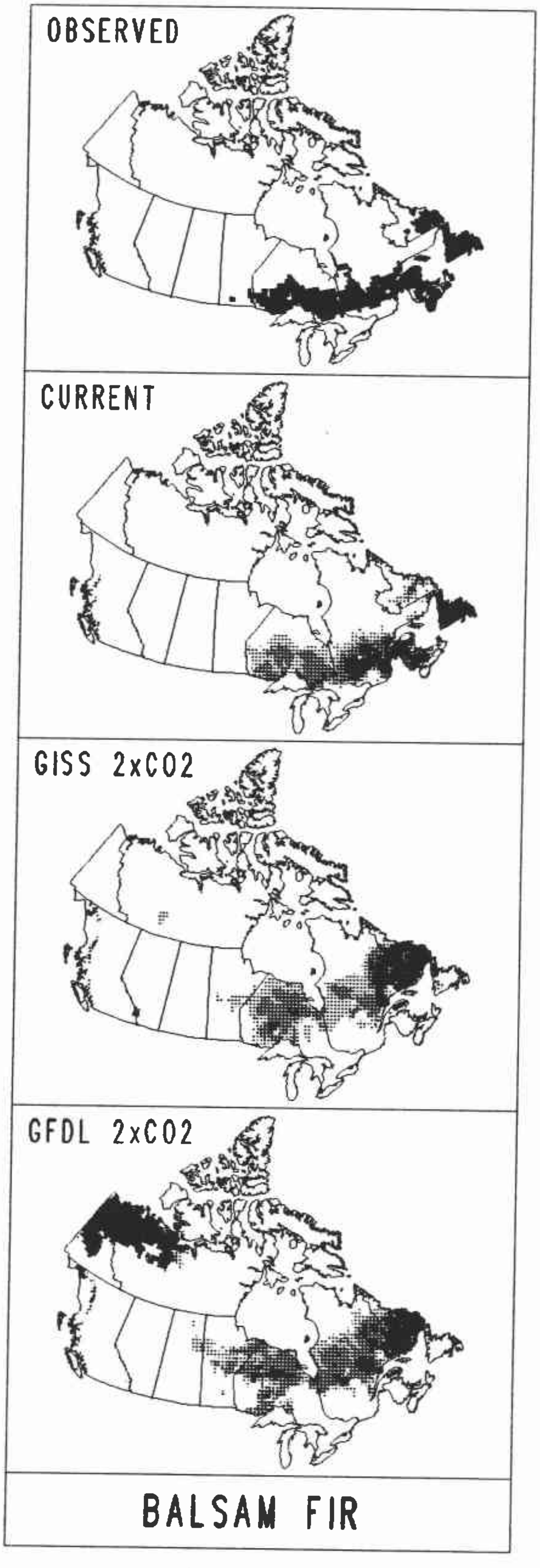

Figure IV.6.f

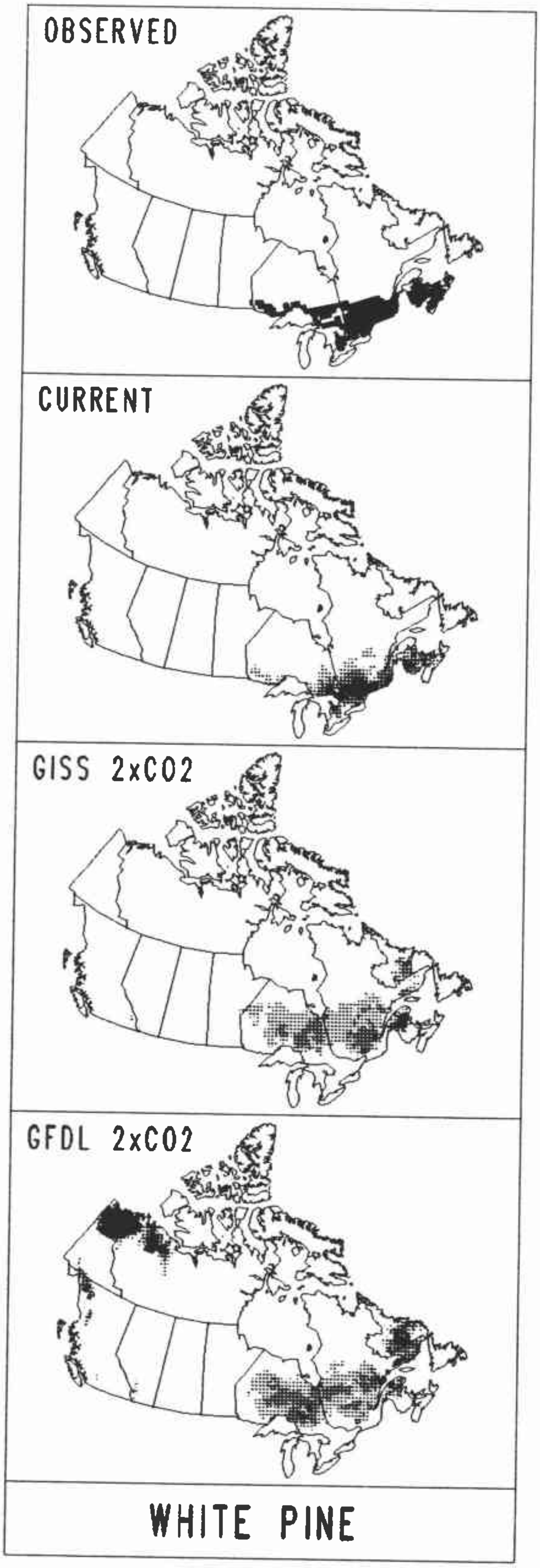

Figure IV.6.g

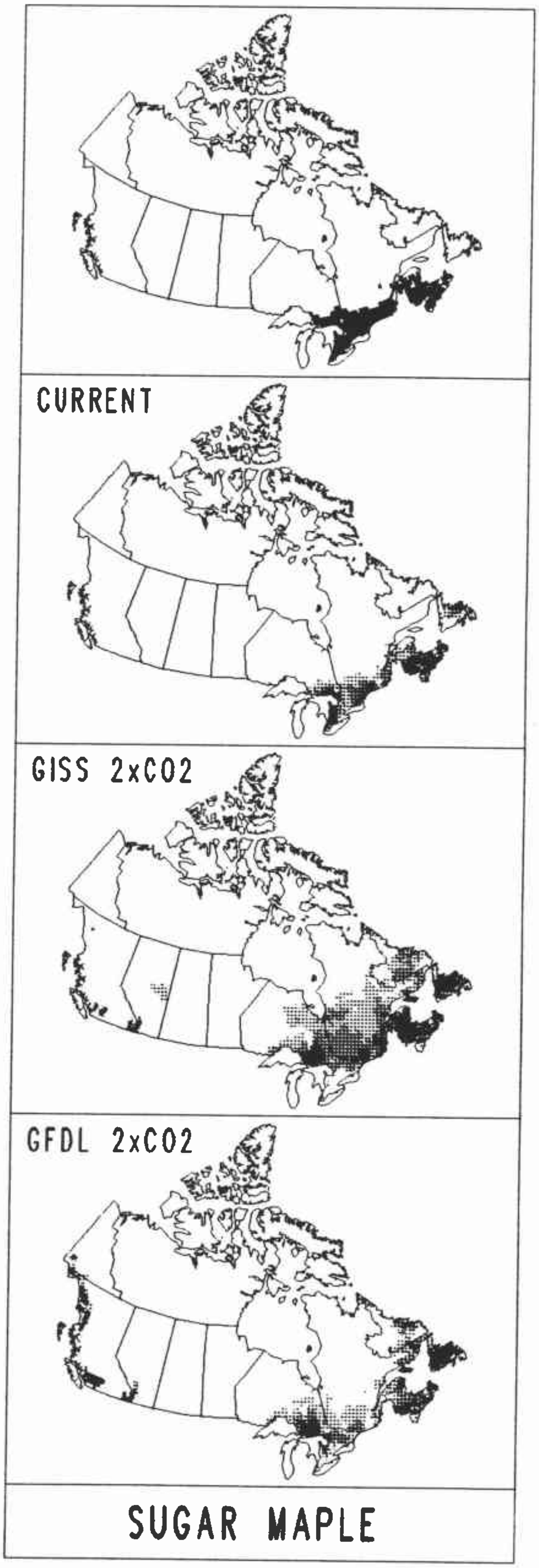

Figure IV.6.h

illustrate the accuracy of the method, the observed ranges of species dominance are also shown for comparison against the current probability surfaces. The observed ranges were determined based on information accompanying a vegetation regions map in the National Atlas of Canada (1973a) as described in Chapter III. The areal extent of predicted dominance for each species in each of the three simulations is shown in Table IV.4. The area of predicted dominance was defined as the total area of grid cells in which the probability of dominance for a given species was greater than 50%.

The probability surfaces generated under the GISS and GFDL climatic scenarios exhibit broad agreement for some species and disagreement for others, but results for both suggest future climatic change could lead to significant changes in the distribution of species dominance. In contrast to changes predicted by the rule-based CCVM, some of the predicted changes in the distribution of species dominance are more difficult to explain in terms of isolated climatic factors given the powers and interactions between predictor variables that are included in the response surface regressions. The results are interpreted below in terms of changes in individual climatic predictors which show the highest degree of geographic relationship to changes in the distribution of species dominance. In all cases, the predictors singled out for their

Table IV.4. The areal extent of species dominance predicted by the climatic response surfaces under current conditions and under the Goddard Institute for Space Studies (GISS) and the Geophysical Fluid Dynamics Lab (GFDL) 2xCO_2 climatic scenarios. Dominance was defined as a greater than 50% probability of dominance. Table entries are square kilometers x 10^4.

Species	Current	GISS	GFDL
black spruce	481	341	365
white spruce	313	263	254
jack pine	78	8	259
aspen	39	8	56
lodgepole pine	32	30	8
balsam fir	84	91	188
white pine	29	31	83
sugar maple	30	86	57

explanatory power are significant variables in the logistic regression equations, either alone or in interaction with other predictors (Appendix I).

The $2xCO_2$ probability surfaces for black and white spruce (Figure IV.6.a,b) indicate the areal extent of their dominance could be reduced by 20-30% under equilibrium conditions (Table IV.4). The predicted range of spruce dominance is displaced northward by at least 600 km in southeastern Canada in both scenarios, and by as much as 800 km in the central interior of the country under GFDL conditions. The predicted shifts in the range of dominance are driven from the south by increases in growing degree-days in southeastern Canada and by increased soil moisture deficits in the central interior of the country, the latter being especially pronounced in the GFDL scenario. Much of the displacement at the northern edges of the dominance ranges is driven by increases in growing degree-days and summer AET. The reduction in the probability of spruce dominance (and especially white spruce dominance) in the Yukon Territory and the western MacKenzie District under GFDL conditions is a function of changes in degree-days, summer AET, and soil moisture deficits and the relatively complex interactions among these parameters in the spruce response surfaces.

Jack pine is the most strictly continental species of the Canadian boreal forest (Ritchie 1987), and high probabilities of dominance (Figure IV.6.c) for the species under current conditions are strongly related to the very low absolute minimum temperatures found in the central interior of Canada. There is also a positive relationship between jack pine dominance and relatively high levels of summer AET which may be related to the species' survivability in the harsh winter conditions of its current range (Wardle 1974). Jack pine's intolerance of deep snowpack (Ritchie 1987) probably limits the dominance of the species at the eastern edge of the range. The predicted redistribution of jack pine dominance, which is very different in the two GCM scenarios, can largely be accounted for by changes in the distributions of these three climatic parameters. Under the GISS scenario, the coincidence of low absolute temperatures, relatively high summer AET, and low snowpack occurs over a very limited area. Consequently, there is a predicted reduction of about 90% in the range of jack pine dominance under these conditions. In the GFDL scenario, the occurrence of this climatic configuration is more extensive than under current conditions, and there is a more than three-fold increase in the extent of jack pine dominance as a result.

Under current conditions, the probability of aspen dominance (Figure IV.6.d) is highest in the boreal summergreen woodland, the broad ecotone between the prairies and the boreal forest of central Canada. Here aspen dominance is strongly related to mid-range levels of soil moisture deficit along a gradient extending from the relatively high deficit levels of the prairies to the low levels of the forest. Under the GISS scenario, this gradient becomes considerably steeper, and there is a reduction in the spatial extent of the mid-range deficit levels related to high probabilities of aspen dominance. As a result, the extent of aspen dominance declines by almost 80% under GISS conditions. A new, relatively large region of mid-level deficits, northeast of the current range of aspen dominance, is predicted in the GFDL scenario. A shift of aspen dominance into this area, together with an expansion in the Dawson region of the Yukon Territory, accounts for most of the predicted 45% increase in the extent of aspen dominance predicted under GFDL conditions.

The probability surface for lodgepole pine under current conditions (Figure IV.6.e) shows a high probability of dominance in the central interior of British Columbia, where absolute minimum temperatures are relatively high and the growing season is relatively cool and short (as indicated by a low number of growing degree-days). Under the GISS scenario, the distribution of this climatic type is displaced to the north and becomes centered on the border between British Columbia and the Yukon Territory. The predicted area of lodgepole pine dominance shifts northward into this area with just a small reduction in it's extent. With the much larger increase in degree-days under the GFDL scenario, the climatic conditions associated with high lodgepole pine probabilities become restricted to just a few small highland areas in British Columbia. As a result, a 75% reduction in the extent of lodgepole pine dominance is predicted under GFDL conditions.

The current probability surfaces for balsam fir and eastern white pine (Figure IV.6.f,g) are similar, as both species are limited by soil moisture deficits at their western and southern boundaries and by the length and warmth of the growing season to the north (Ritchie 1987). Balsam fir is more tolerant of shorter growing seasons (Bonan 1988) and has a higher probability of dominance further north, while white pine is more drought-tolerant (Bonan 1988) and has a higher probability of dominance in southern Ontario and Quebec. The probability surfaces for these two species under 2xCO_2 conditions also show much agreement. In the GISS scenario, the response to an increase in growing degree-days in the north and a drying trend in the south is a simple northward displacement of about 400 km in the range of dominance for balsam fir and about 600 km for white pine. A small net increase in the extent of dominance is predicted for balsam fir and white pine under these conditions. In the GFDL scenario, there is a similar shift northward in southeastern Canada, but under these conditions a new climatic region characterized by relatively high degree-days and low soil moisture deficits appears in northwestern Canada (i.e., in an area centered on the MacKenzie River Delta). Both balsam fir and white pine are predicted to occur here with a high probability of dominance. This new area of species dominance, together with some expansion in southeastern Canada, accounts for a two to three-fold increase in the extent of dominance predicted for each species under GFDL conditions.

The current probability surface for sugar maple (Figure IV.6.h) is very similar to that of white pine. Both species are constrained by soil moisture deficits along their western boundaries (Ritchie 1987), but sugar maple is much less tolerant of low absolute minimum temperatures which limit the species at the northern edge of its range (Sakai and Weiser 1973). The redistribution of sugar maple dominance in both 2xCO_2 scenarios is largely a response to increases in absolute minimum temperature. Under the GISS scenario where winter temperature increases are the greatest, an extension of the northern limit of sugar maple dominance by as much as 700 km results in almost a three-fold expansion in the extent of it’s dominance. In the GFDL scenario, there is less of a northward shift in the dominance range, and the increase in the extent of sugar maple dominance is about twice the current value. In contrast to the GFDL simulations for white pine and balsam fir, sugar maple dominance is not predicted in the northwest sector of Canada because absolute minimum temperatures remain too low in this region under GFDL conditions.

The Forest-Type Scenarios

As described in Chapter III, the stopping rule indicated the presence of five clusters in the probability data associated with the boreal subset of grid cells under current conditions. The mean probability of dominance for each species in each of the five clusters is shown in Table IV.5. Species with mean probabilities of 25% or greater were used to name the cluster groups as forest-types in Figure IV.7 where the cluster membership of the grid cells is mapped. In Chapter III, a high degree of spatial correspondence was found between the derived forest-types and the boreal forest-types in the actual vegetation mosaic of Canada.

The stopping rule indicated the presence of three clusters in the probability data associated with the boreal subset of grid cells under each of the $2xCO_2$ scenarios. The mean probabilities of dominance for the species in the clusters derived under the GISS and GFDL scenarios are shown in Tables IV.6 and IV.7 respectively. As in Figure IV.7, species with mean probabilities of 25% or greater were used to name the cluster groups as forest-types in Figures IV.8 and IV.9.

The squared cord distance coefficents (Overpeck et al. 1985) in Table IV.8 were calculated from the mean probabilities of dominance in Tables IV.5 - IV.7 to measure the pairwise resemblances between forest-types (i.e., clusters) in the current simulation and those in the $2xCO_2$ scenarios. The mean

Table IV.5. Mean probability of species dominance by cluster derived under current conditions. All table entries are in percent. Mean values >25% in bold. See Figure IV.7 for forest-type names corresponding to cluster numbers.

	Cluster Number				
Species	1	2	3	4	5
black spruce	**81**	**89**	**47**	**87**	**62**
white spruce	**37**	**64**	**67**	**63**	**63**
jack pine	3	**68**	5	4	1
trembling aspen	1	20	**34**	0	0
lodgepole pine	3	1	**26**	0	0
balsam fir	3	4	0	**61**	**50**
eastern white pine	0	0	0	13	**60**
sugar maple	0	0	0	9	**58**

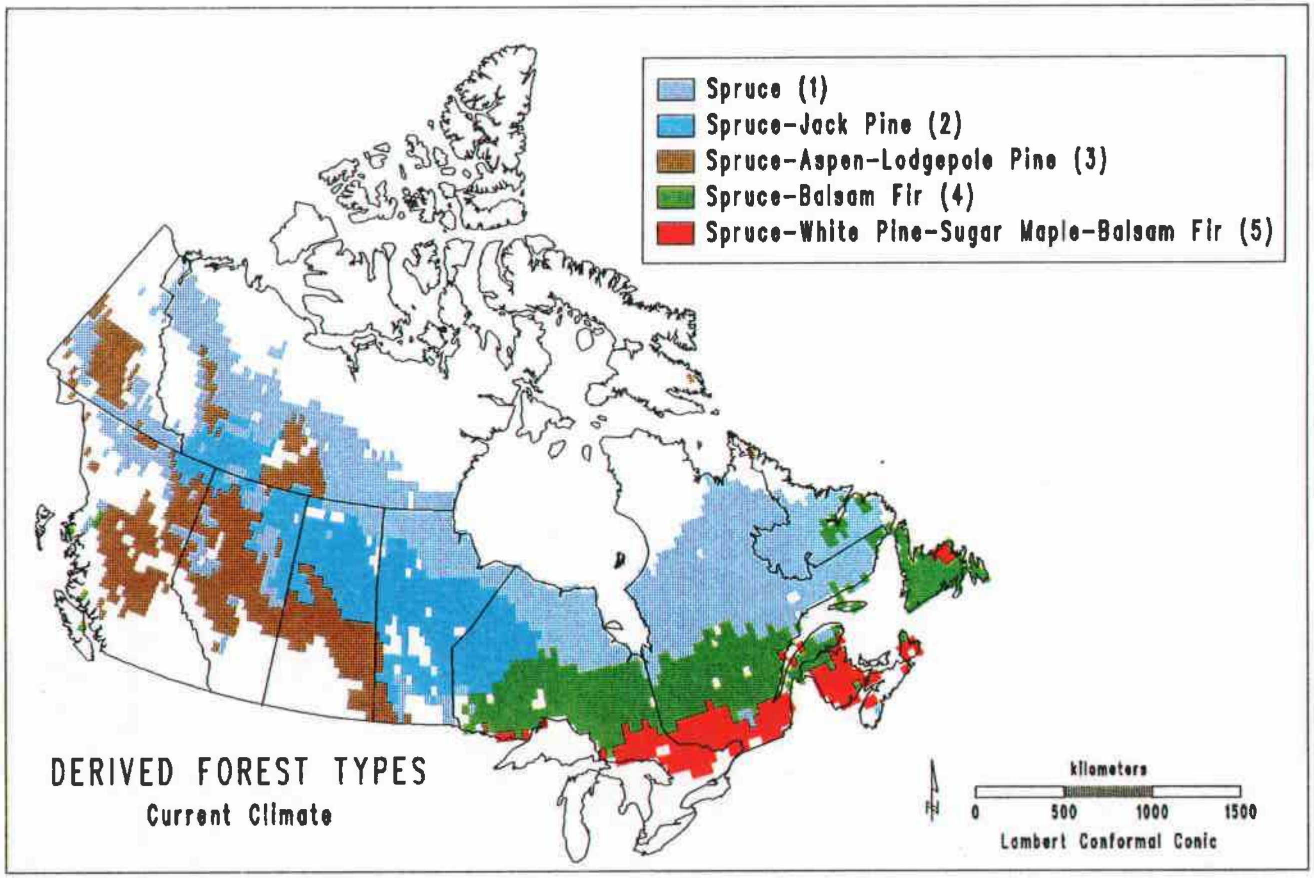

Figure IV.7. The distribution of forest-types in the boreal forest region derived by cluster analysis of probabilities of species dominance under current climatic conditions. Numbers in parenthesis are cluster numbers in Tables IV.5 and IV.8.

Table IV.6. Mean probability of species dominance by cluster derived under the Goddard Institute for Space Studies (GISS) 2xCO_2 climatic scenario. All table entries are in percent. Mean values > 25% in bold. See Figure IV.8 for forest-type names corresponding to cluster numbers.

	Cluster Number		
Species	1	2	3
black spruce	**80**	**44**	**57**
white spruce	**45**	**72**	**57**
jack pine	7	0	2
aspen	7	16	0
lodgepole pine	4	**47**	0
balsam fir	4	1	**58**
white pine	1	0	23
sugar maple	1	0	24

Table IV.7. Mean probability of species dominance by cluster derived under the Geophysical Fluid Dynamics Lab (GFDL) 2xCO_2 climatic scenario. All table entries are in percent. Mean values > 25% in bold. See Figure IV.9 for forest-type names corresponding to cluster numbers.

	Cluster Number		
Species	1	2	3
black spruce	**72**	**35**	**57**
white spruce	**53**	18	**28**
jack pine	9	**85**	**46**
aspen	3	24	4
lodgepole pine	3	0	0
balsam fir	10	8	**83**
white pine	6	0	**44**
sugar maple	4	0	7

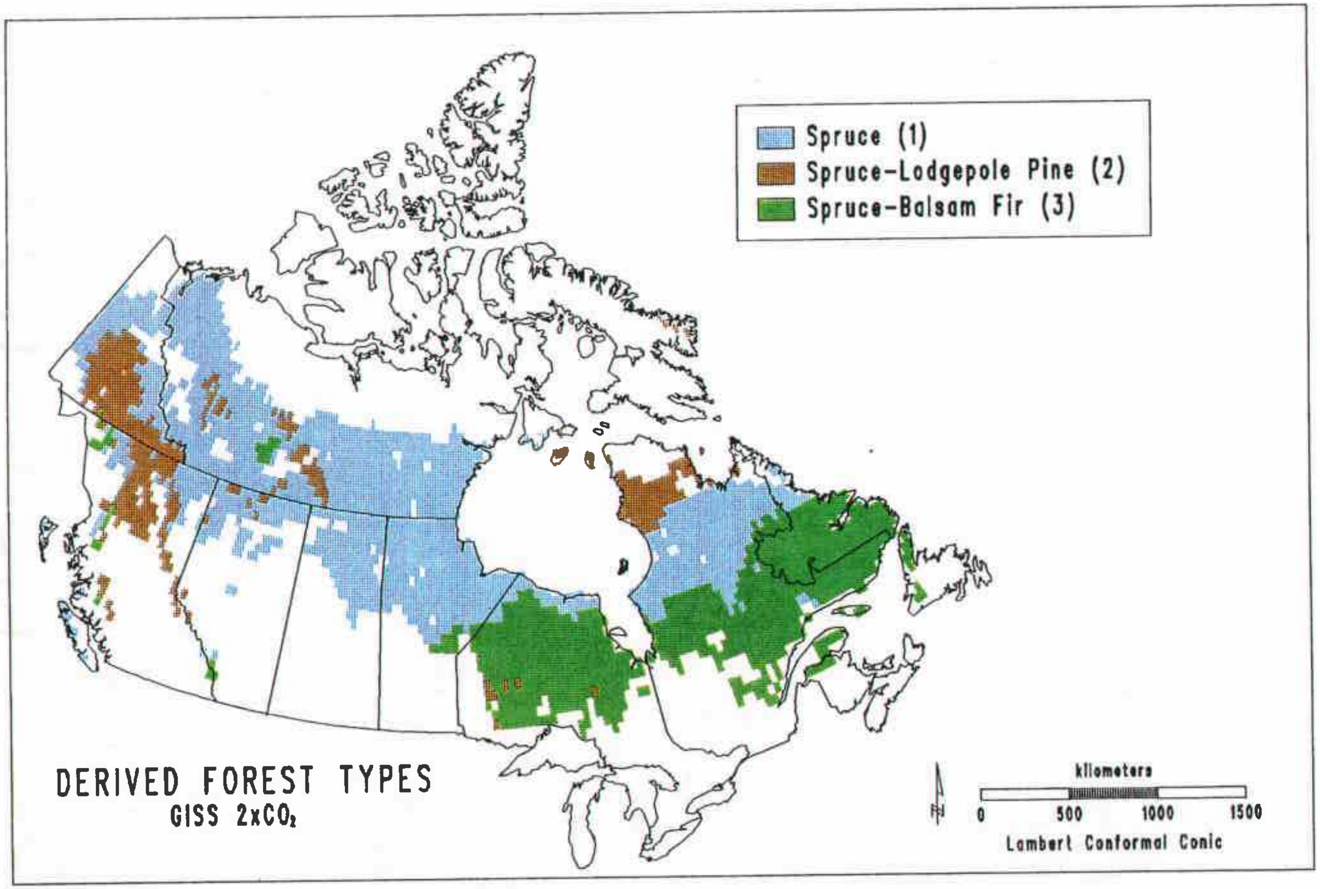

Figure IV.8. The distribution of forest-types in the boreal forest region derived by cluster analysis of probabilities of species dominance under the Goddard Institute for Space Studies (GISS) $2xCO_2$ climatic scenario. Numbers in parenthesis are GISS cluster numbers in Tables IV.6 and IV.8.

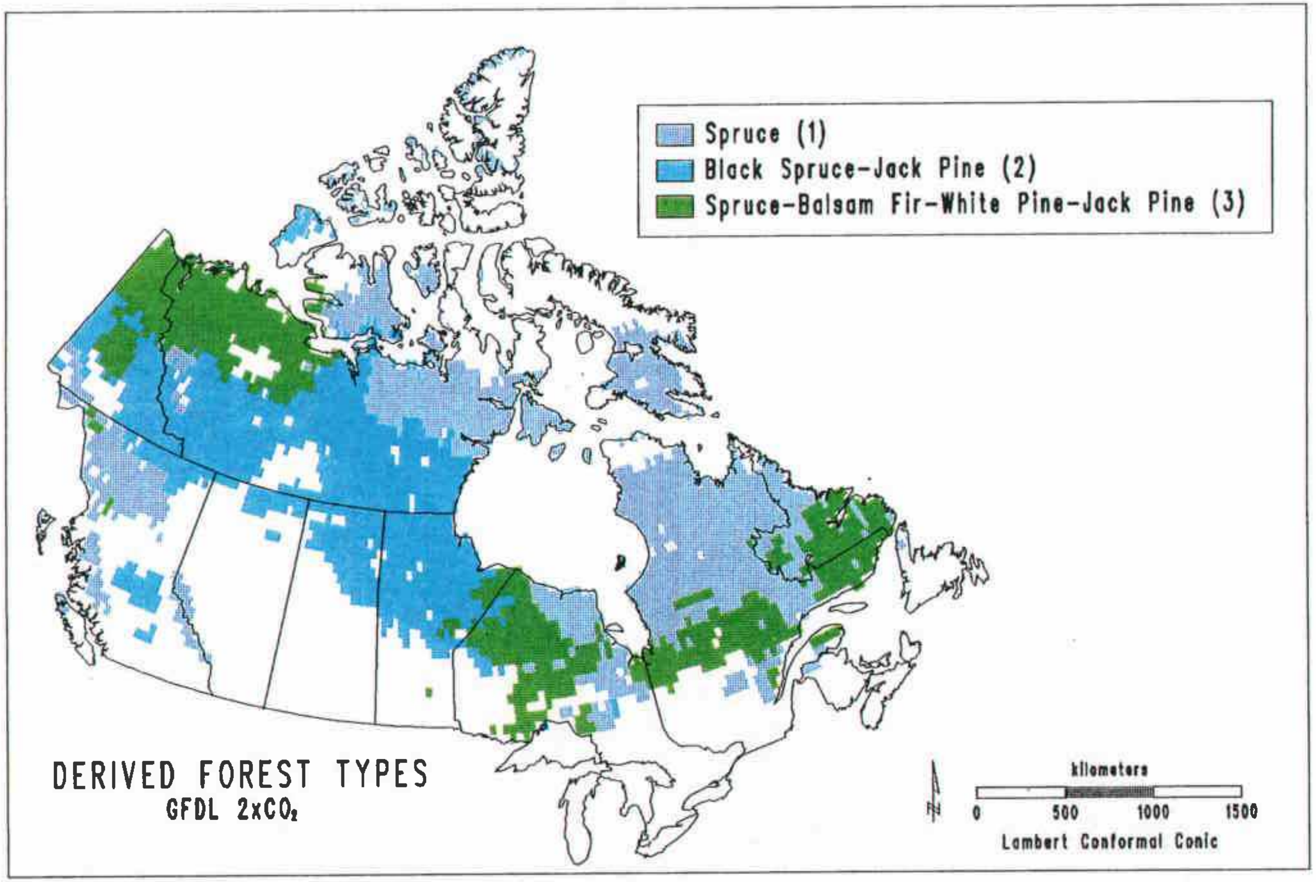

Figure IV.9. The distribution of forest-types in the boreal forest region derived by cluster analysis of probabilities of species dominance under the Geophysical Fluid Dynamics Lab (GFDL) 2xCO_2 climatic scenario. Numbers in parenthesis are GFDL cluster numbers in Tables IV.7 and IV.8.

Table IV.8. Squared cord distance coefficients for pairwise comparisons of clusters derived under current conditions and under the Goddard Institute for Space Studies (GISS) and the Geophysical Fluid Dynamics Lab (GFDL) 2xCO2 climatic scenarios. Calculations based on the standardized values of the mean probabilities in Tables IV.5 - IV.7. The smallest distance coefficent for each 2xCO2 cluster is shown in bold. See Figures IV.7 - IV.9 for forest type names corresponding to cluster numbers.

Current Cluster Number	GISS Cluster Number			GFDL Cluster Number		
	1	2	3	1	2	3
1	**.04**	.30	.46	**.10**	.58	.60
2	.14	.51	.64	.20	**.11**	.47
3	.19	**.07**	.83	.31	.57	.89
4	.25	.67	**.04**	.13	.71	**.19**
5	.51	.90	.05	.30	1.02	.26

probabilities were standardized for each forest-type before the distance coefficents were calculated so that the resulting values would be comparable to those found using proportional data in comparisons of modern and fossil pollen spectra (Overpeck et al. 1985). The forest-type in the current simulation to which a given 2xCO_2 type is most closely related is indicated by the lowest cord distance for the 2xCO_2 type (shown in bold in Table IV.8). These relationships are also indicated in Figures IV.7 - IV.9 where analogous forest-types are mapped in the same color. Overpeck et al. (1985) identify a critical squared cord distance value of .12 below which samples in the pairwise comparison are likely to be from the same forest-type. If the results in Table IV.8 are judged according to this standard, all but one of the 2xCO_2 forest-types has a modern analog in one of the current types.

The spruce type predicted for current conditions (Figure IV.7) persists in the GISS scenario (Figure IV.8) without any significant changes in the relative probabilities of dominance of the two spruce species (Tables IV.5 and IV.6). There is a poleward shift in the northern limit of the spruce type produced by increases in growing degree-days and summer AET, and there is some southward expansion of the type in northern Saskatchewan and Manitoba due to a contraction in the range of jack pine dominance (Figure IV.6.c) which converts spruce-jack pine forest to spruce forest in this region. There is also some reduction in the range of the spruce type in Labrador associated with increases in degree-days along the southern limit of the type.

The spruce-aspen-lodgepole pine type predicted for current conditions (Figure IV.7) also persists in the GISS scenario, but in a modified form characterized as the spruce-lodgepole pine type (Figure IV.8). As under current conditions, the mean probability of white spruce dominance remains higher than that of black spruce, but there is an increase in the mean probability of lodgepole pine dominance, and the mean probability of aspen dominance falls below the 25% threshold for type characterization (Tables IV.5 and IV.6). The reversal in the relative probabilities of dominance of pine and aspen, and the more restricted distribution of the modified type, are a result of the consolidation in the area of lodgepole pine dominance in northwestern Canada and the reduction in the extent of aspen dominance in the central interior of the country (Figure 6.d,e). A relatively high probability of white spruce dominance predicted near the northern end of the Labrador Peninsula (Figure IV.6.b), together with the low probabilities predicted for other species in this region under GISS conditions, produced the eastern outlier in the distribution of the spruce-lodgepole pine type.

The spruce-balsam fir type predicted under current conditions (Figure IV.7) occurs in the GISS scenario (Figure

IV.8) with some changes in the relative probabilities of dominance of the member species (Tables IV.5 and IV.6). There is a moderate increase in the mean probability of balsam fir dominance to a level commensurate with that of the two spruce species. There is also an increase in the mean probabilities for white pine and sugar maple to a level just below the 25% threshold for type characterization. Increases in growing degree-days and summer AET in the north together with increased soil moisture deficits in the south produced the poleward displacement of the spruce-balsam fir type under GISS conditions.

The spruce-white pine-sugar maple-balsam fir type in the simulation for current conditions (Figure IV.7) is not distinguished as a boreal forest-type in the GISS scenario. A relatively high probability of dominance is predicted for white pine and sugar maple in the Great Lakes-St. Lawrence region under the GISS scenario (Figure IV.6.g,h), but the increased soil moisture deficits under GISS conditions produce low probabilities of dominance for the spruce species and balsam fir (Figure IV.6.a,b,f) which exclude this region from the boreal forest domain (Figure IV.8). It should be noted, however, that the spruce-balsam fir type in the GISS scenario is very closely allied to the spruce-white pine-sugar maple-balsam fir forest type in the current simulation (Table IV.8). The spruce-jack pine forest-type is the other type distinguished under current conditions (Figure IV.7) that is absent from the GISS scenario. As mentioned above, climatic conditions under GISS conditions restrict the extent of jack pine dominance to a small area (Figure IV.6.d) that is encompassed within the range of the spruce forest-type under the GISS scenario (Figure IV.8).

Compared to the forest types in the GISS scenario, the GFDL types (Figure IV.9) are less similar to those in the simulation for current conditions (Figure IV.7) as indicated by the larger squared cord distances for the GFDL types (Table IV.8). The spruce type persists in the GFDL scenario, but compared to the relative probabilities of dominance under current conditions, white spruce is more nearly co-dominant with black spruce under GFDL conditions (Table IV.5 and IV.7). Increases in degree-days and summer AET produce some expansion of the spruce type at the northern end of the Labrador Peninsula and at the southern end of Baffin Island. In north-central Canada, these changes in climate also produce some poleward movement of the forest-type, but soil moisture deficits south of this region confine the type to a relatively small mainland area northwest of Hudson Bay and to adjacent islands of the Arctic Archipelago. West of the Cordillera, the spruce type invades high elevation sites in northern British Columbia currently occupied by alpine-tundra communities (National Atlas of Canada 1973a).

The black spruce-jack pine type in the GFDL scenario (Figure IV.9) is a highly modified version of the spruce-jack pine type distinguished under current conditions (Figure IV.7). In the black spruce-jack pine type, the probability of jack pine dominance is considerably higher, black spruce has a much lower probability of dominance, and the probability for white spruce falls below the level of type characterization (Tables IV.5 and IV.7). These changes in relative probabilities of dominance are driven by persistently low absolute minimum temperatures and increases in summer AET under GFDL conditions which result in the predicted expansion of jack pine dominance throughout much of the northern interior (Figure IV.5.c), and by the decreased soil moisture and the interacting changes in climate which reduce spruce dominance in the central-interior and northwestern sectors Canada respectively under the GFDL scenario (Figure IV.6.a,b).

Of all the forest-types distinguished under the 2xCO_2 scenarios, the spruce-balsam fir-white pine-jack pine type in the GFDL scenario (Figure IV.9) has the lowest similarity to forest-types distinguished under current conditions (Table IV.8), and is therefore the nearest equivalent to a "non-analog" assemblage as defined in paleoecological studies (Overpeck et al. 1985). The very high probability of balsam fir dominance distinguishes this forest-type from any of the current types (Table IV.5 and IV.7). In the southeastern portion of it's distribution, the spruce-balsam fir-white pine-jack pine type is also distinguished by the combination of high and low probabilities of white pine and sugar maple dominance respectively. This is a consequence of substantial increases in growing degree-days in the absence of any comparable increase in absolute minimum temperatures in southeastern Canada under GFDL conditions. In the northwestern portion of it's range, the individualistic responses of white pine and jack pine to different aspects of the GFDL climatic scenario result in a nearly equal probability of dominance for these two pine species that is also not found in any of the forest-types in the current simulation.

If the spruce-balsam fir-white pine-jack pine type is taken as a distant relation of the spruce-balsam fir type (Table IV.8), then two of the forest-types in the simulation for current conditions, the spruce-aspen-lodgepole pine type and the spruce-white pine-sugar maple-balsam fir type (Figure IV.7), are unrepresented in the GFDL scenario (Figure IV.9). The probability of dominance for lodgepole pine, one of the characteristic members of the spruce-aspen-lodgepole pine type, is very low throughout almost all of Canada under GFDL conditions (Figure IV.6.e). And the area of aspen dominance in the GFDL scenario (Figure IV.6.d) is incorporated into the black spruce-jack pine type (Figure IV.9) where aspen has a mean probability of dominance just below the threshold for type characterization (Table IV.7). The southeastern portion of the spruce-balsam fir-white pine-jack pine type in the GFDL scenario (Figure IV.9) shows some relationship to the spruce-white pine-sugar maple-balsam fir type distinguished under current conditions (Table IV.8). But the latter type is not distinguished in the GFDL scenario primarily because the probability of dominance for sugar maple, a characteristic member of the mixed forest type, is very low in the boreal forest domain under GFDL conditions (Table IV.7). Under the GFDL scenario, absolute minimum temperatures increase only slightly and continue to restrict the dominance of sugar maple at the northern edge of it's range while increases in degree-days and moisture deficits move the boreal forest domain further to the north.

Linking the CCVM and Response Surface Scenarios

The formation-level vegetation scenarios generated by the rule-based CCVM and the simulations of species dominance and boreal-forest types based on the probabilities generated by the response surfaces can be linked at the common organizational level of the boreal forest domain. The boreal forest domain was defined for the purposes of forest-type classification as the subset of grid cells where at least one of five predominately boreal species had a probability of dominance greater than 50%. Alternatively, the boreal domain could be defined as the combined extent of the boreal evergreen forest and the boreal summergreen woodland formations. Geographic correspondence in the domains defined from these two different standpoints would provide a link between the formation and forest-type simulations under current and future climates.

The kappa statistic (Monserud 1990) was used to assess the geographic correspondence between the formation-based and probability-based definitions of the boreal forest domain in the current, GISS, and GFDL simulations. The values of the statistic were in the range of .55 to .70, which according to a scale of assessment proposed by Monserud (1990), indicates good agreement between the two definitions of the boreal forest domain in all three of the simulations. In general, most of the disagreement occurred in regions of the simulations where CCVM predicted prairie or subarctic woodland. Since CCVM is calibrated against the actual vegetation of Canada to accurately predict the present position of the prairie-forest and forest-tundra ecotones, it is fair to state that there is a tendency for overpredicting the current extent of the boreal forest when the probabilities of species dominance are used to define the boreal forest domain.

Constraints on the Realism of the Vegetation Scenarios

There are several constraints on the realism of the future vegetation scenarios in this study. The wide range of uncertainty involved in climatic projections derived from the output of coarse-scale GCM $2xCO_2$ experiments (Gates 1985, Dickinson 1989) may be the most limiting constraint on the modeling results. The very different results obtained under the two different climatic scenarios illustrate the potential significance of this source of error. The implicit assumption that the climatic parameters used as model drivers constitute a full set of factors determining the potential vegetation of a region is another constraint on the realism of the scenarios. For example, podzolic soils in areas currently occupied by boreal evergreen forest could limit the expansion of the prairie formations in the GFDL scenario. Soils will change in response to changes in climate and vegetation, but generally at a much slower rate, and in some cases parent materials might limit soil development (Emanuel et al. 1985a, Rizzo and Wiken 1992). Permafrost could also act as a constraint on the rate and direction of vegetation change (Bonan et al. 1990). Additional examples of potentially influential processes not modeled in this study are the direct effects of elevated concentrations of CO_2 on plant water use efficiency and rates of carbon gain (Woodward et al. 1991), changes in the magnitude and frequency of extreme climatic events and their impact on disturbance regimes (Overpeck et al. 1990), and the influence of changing day lengths on the timing of phenological events as plant distributions shift northward (Davis 1989).

The consideration of only eight dominant species in the response surface analysis is a significant constraint on the realism of the species and forest-type scenarios. Other boreal tree species (e.g. *Betula papyrifera*, *Populus balsamifera and Larix laricina*), western temperate tree species (e.g., *Abies lasiocarpa*, *A. amabilis*, *Picea engelmannii*, *Psueodotsuga menziesii*, and *Thuja plicata*), and eastern temperate tree species (e.g., *Pinus resinosa*, *Picea rubens*, *Tsuga canadensis*, *Fagus grandifolia*, *Quercus macrocarpa*, and *Acer rubrum*) could attain dominance in the boreal forest domain and under the future climatic conditions as defined in this study. The response of these species may or may not be adequately represented by ecologically-similar species included in the response surface analysis.

Even if there were only minor errors of fact and concept in the climate and vegetation models, there would still be significant uncertainties associated with the transient response of vegetation as it moved towards a state of quasi-equilibrium with the climate prescribed by a given 2xCO_2 scenario. Consider for example the predicted shift in the range of balsam fir in the GFDL scenario (Figure IV.6.f). To reach the new climatic region in northwestern Canada from the closest point in it's current distributional range (Little 1971), the species would have to migrate over a distance of at least 1000 km. Even at the fastest documented rate of migration (i.e, 200 km/century for white spruce in Canada about 9000 years ago (Ritchie and MacDonald (1986)), dispersal over that distance would take at least 500 years. The transient climate is likely to reach equilibrium conditions for doubled-CO_2 levels sometime near the end of the next century (Houghton et al. 1990), but without an effective global policy to curb greenhouse gas emissions, climatic warming is likely to continue beyond this arbitrary equilibrium point. Continued climatic change might produce unfavorable conditions for balsam fir in northwestern Canada prior to the arrival of the species. The transient changes in climate could also create barriers to migration in the form of unfavorable regional climates or disturbance regimes which would block the dispersal of balsam fir into northwestern Canada. And since there is little known about ecotypic variation in balsam fir (USDA Forest Service 1990a), there is also some uncertainty in the implicit assumption that local populations of balsam fir at the edge of it's range closest to the new climatic zone would possess the breadth of environmental tolerance represented in the response surface for the species.

This enumeration of constraints on the realism of the vegetation scenarios is not meant to discount the results of the study, but rather to place them in their proper perspective. The scenarios represent the potential magnitude of vegetation change under specified future climates, and are not intended as a prediction of exact patterns of change. Predictions of the latter sort may be unavailable for some time. They will have to await more reliable projections of transient climatic change at regional-scales and the development of dynamic vegetation models that explicitly account for soil dynamics, direct effects of CO_2, plant migration mechanisms, changing disturbance regimes, ecotypic variation, and a host of other relevant factors.

CONCLUSION

The equilibrium response of Canadian vegetation to an enhanced greenhouse effect was simulated at three different organizational levels using a rule-based model and a series of climatic response surfaces. The climatic parameters used as model drivers influence the response of vegetation more directly than those commonly used in equilibrium models. When run under climatic conditions prescribed by two different doubled-CO_2 GCM experiments, the rule-based model predicts a reduction in the extent of arctic tundra and subarctic woodland formations and a northward shift and some expansion in the distribution of boreal evergreen forest. These changes are driven primarily by increases in the length and warmth of the growing season. The model also predicts some expansion of the temperate forest and prairie formations in response to increases in absolute minimum temperature and soil moisture deficits respectively. Soil moisture deficits are especially pronounced under the GFDL climatic scenarios where potential evapotranspiration during the growing season is much greater than the current norm.

Results of the response surface analysis suggest the potential for significant changes in the probability of dominance for eight important tree species within the boreal forest domain. Most of the species exhibited a unique response to changes in the climatic parameters, and the response of a given species was often significantly different under the two climatic scenarios. Despite the individualistic response of the species to changes in climate, all but one of the forest-types derived by cluster analysis of the dominance probabilities were analogous to extant forest-types in the boreal region of Canada. But there were fewer forest-types distinguished under the 2xCO_2 scenarios, and the were also some differences in the within-type relative dominance of species. The scenarios of species dominance and boreal-forest types can be linked to the formation-level scenarios at the common organizational level of the boreal forest domain.

The vegetation scenarios in this study depict only the potential magnitude of the equilibrium response to an enhanced greenhouse effect. Constraints on the realism of the vegetation scenarios include uncertainties in the regional-scale predictions of climatic change, omission of potentially influential physical and biological factors, and additional uncertainties associated with the transient response of vegetation as it moves towards a state of quasi-equilibrium with conditions prescribed by a given climatic scenario.

CHAPTER V:

SUMMARY AND CONCLUSIONS

In this study, the potential magnitude of the equilibrium response of Canadian vegetation to climatic change was modeled at three organizational levels (i.e., the vegetation formation, the boreal forest-type, and the individual tree species). Several General Circulation Model (GCM) studies suggest an enhanced greenhouse effect will induce significant changes in the earth's climatic system, especially at mid to high latitudes in the Northern Hemisphere. The paleoecological record suggests that the predicted changes are more than sufficient to cause large changes in the composition and distribution of vegetation. The response of Canadian vegetation is of particular concern because many regional economies in Canada are solely dependent on renewable resources provided by natural ecosystems. The active participation of the boreal ecosystem in the dynamics of important greenhouse gases and the potential for biospheric feedbacks during climatic change are another motivation for better understanding the potential sensitivity of Canadian vegetation to an enhanced greenhouse effect.

Predicting the potential impacts of climatic change on natural vegetation requires large-scale ecological and biogeographic modeling. There have been two basic approaches to modeling the vegetation response to altered climates. The dynamic approach is capable of predicting the transient response, but dynamic models require extensive process-level information and the simulations they produce are currently limited to the scale of a gap within forested landscapes. The equilibrium approach is temporally static, but in contrast to dynamic models, equilibrium models require less information and provide an comprehensive estimate of the potential magnitude of the vegetation response at regional to continental scales.

The two principal methods for predicting the equilibrium response of vegetation to climatic change are climate-vegetation classification and climatic response surfaces. Classification models forecast the redistribution of vegetation at the level of the life-form or vegetation formation, while climatic response surfaces are often used for modeling the vegetation response at the level of individual species. To date, nearly all applications of equilibrium models have been alike in their use of annual or monthly measures of temperature and precipitation as model drivers. These aspects of climate and the distribution of plants are not necessarily related in a cause-and-effect manner, so the correlations central to these modeling efforts may not persist under altered conditions. Physiological constraints on the survival, growth, and reproduction of plants will likely persist within the time-frame of the projected climatic warming. The five parameters used as model drivers in this study (i.e., depth of snowpack, length and warmth of the growing season, absolute minimum temperature, soil moisture deficit, and summer actual evapotranspiration) more directly represent aspects of climate which physiologically constrain the distribution of major life-forms and dominant species in Canada.

In the first part of this study, a rule-based climate-vegetation classification model was developed to predict the equilibrium response of formation-level vegetation to the five climatic parameters. The rules in the Canadian Climate-Vegetation Model (CCVM) are critical climatic thresholds which constrain the distributions of the dominant life-forms characterizing the vegetation formations of Canada. The geographic positioning of these thresholds is determined by the large-scale structure and seasonal dynamics of the atmosphere. As judged by comparisons against vegetation maps at regional to continental scales, CCVM accurately predicts the distribution of Canadian vegetation formations under the current climate. The CCVM simulation for current conditions is more detailed and more accurate than those produced by either the Holdridge or Box equilibrium models.

In the second part of this study, climatic response surfaces were derived to predict the probability of dominance of eight important boreal tree species using the same five climatic parameters as predictor variables. The response surfaces provided estimates of the probability of species dominance under current climatic conditions across the spatial extent of North America with a high degree of success. The results of the response surface analysis indicate that, at the continental-scale of this study, the dominance of the tree species is largely a reflection of climate, and that much of the variation in the probability of dominance is apparently related to the individualistic response to climatic constraints within different airmass regions. Furthermore, because the climatic predictors were more directly related to the response of plants than those used in other response surface analyses, the results in this part of the study were more interpretable in terms of the mechanisms by which climate exerts control over species dominance.

A forest-type classification for the Canadian boreal forest region was derived from the probabilities of species dominance under current conditions. The derived forest-types showed a high degree of geographic correspondence with the distribution of forest-types in the actual vegetation mosaic. The distribution of the derived forest types also suggests that the relative dominance of tree species at the scale of the boreal forest domain is controlled primarily by seasonal airmass dynamics. A shift in the relative dominance of aspen and jack pine across a major boundary between substrate types may be an exception to this general principle of broad-scale climatic control.

In the final part of this study, the equilibrium response of Canadian vegetation to an enhanced greenhouse effect was simulated at the three organizational levels. Results of doubled-CO_2 experiments conducted with the Goddard Institute for Space Studies (GISS) and the Geophysical Fluid Dynamics Lab (GFDL) GCMs were coupled with current climate normals to produce two regional-scale climatic scenarios. Under both scenarios, CCVM predicted a reduction in the extent of arctic tundra and subarctic woodland formations and a northward shift and some expansion in the distribution of boreal evergreen forest. These changes were driven primarily by increases in the length and warmth of the growing season. CCVM also predicted some expansion of the temperate forest and woodland/prairie formations in response to increases in absolute minimum temperature and soil moisture deficits respectively. Soil moisture deficits and the consequent expansion of prairie were especially pronounced under the GFDL climatic scenario where potential evapotranspiration during the growing season is much greater than the current norm.

Significant changes in the probability of species dominance were indicated when the climatic response surfaces were coupled with the $2xCO_2$ climatic scenarios. Most of the species exhibited a unique response to changes in the climatic parameters, and the response of a given species was often significantly different under the two climatic scenarios. Despite the individualistic response of the tree species to the changes in climate, all but one of the forest-types derived from future probabilities of species dominance were analogous to extant forest-types in the boreal forest domain of Canada. But there were fewer forest-types distinguished under the $2xCO_2$ scenarios, and there were also some differences in the within-type relative dominance of species. The scenarios of species dominance and boreal-forest types generated by the response surfaces can be linked to the formation-level scenarios generated by CCVM at the common organizational level of the boreal forest domain.

The vegetation scenarios in this study depict only the potential magnitude of the equilibrium response to an enhanced greenhouse effect. Constraints on the realism of the vegetation scenarios include uncertainties in the regional-scale predictions of climatic change, omission of potentially influential physical and biological factors, the consideration of only eight tree species in the response surface analysis, and additional uncertainties associated with the transient response of vegetation as it moves towards a state of quasi-equilibrium with conditions prescribed by a given climatic scenario. Nevertheless, the vegetation scenarios generated in this study are arguably the most reliable and comprehensive equilibrium predictions for Canada to date given the direct relationship between the climatic parameters and the distribution of vegetation and the simulation at three different organizational levels within the vegetation mosaic of Canada. And given the potential magnitude of the vegetation change depicted in these scenarios, serious consideration should be given to the ecological and socio-economic implications of these changes.

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APPENDIX

Appendix I. The maximum-likelihood estimates of the logistic regression parameters for the species response surfaces. The probability of dominance is calculated as $p = 1 - (e^x / (1 + e^x))$ where x is the solution to the regression function.

Parameter	Black Spruce	White Spruce	Aspen	Jack Pine
intercept	52.1587	7.7944	12.0963	325.2
snw	0.	0.	0.	0.
dd	0.	0.	0.	0.0206
min	0.	-0.2699	0.	28.7368
def	1.4485	0.	0.	0.
aes	-0.8111	0.	0.	0.
snw2	0.	-0.00002	0.	0.000175
dd2	0.	0.000022	0.	0.
min2	0.	0.	0.	0.8265
def2	0.	0.	0.	0.
aes2	0.00287	0.000586	0.	0.
snwXdd	0.	0.00003	-0.0001	-0.00005
snwXmin	0.00216	0.	0.	-0.00100
snwXdef	-0.0009	-0.00043	-0.00069	0.
snwXaes	-0.00006	0.	0.	0.
ddXmin	0.000111	0.	0.	0.000431
ddXdef	-0.00009	-0.00016	0.	0.
ddXaes	0.	-000079.	0.	-0.00007
minXdef	0.0646	0.	0.	0.
minXaes	-0.0128	0.0168	0.00047	0.
defXaes	0.	0.00500	0.	0.
snw3	2.065e-7	1.082e-8	6.614e-8	0.
dd3	0.	-0.0857e-8	0.	0.
min3	0.000357	0.	0.	0.00759
def3	0.	3.672e-7	0.	0.
aes3	-1.52e-6	-0.00002	0.	1.921e-6
snw2Xdd	0.	0.	1.015e-7	4.136e-7
snw2Xmin	4.187e-6	0.	3.687e-6	0.
snw2Xdef	2.676e-6	3.456e-7	1.518e-6	-2.17e-6
snw2Xaes	0.	0.	0.	-3.91e-6
dd2Xsnw	0.	-1.09e-8	3.44e-8	0.
dd2Xmin	-2.63e-8	0.	0.	0.
dd2Xdef	1.146e-8	0.	0.	0.
dd2Xaes	0.	0.	0.	0.
min2Xsnw	0.000068	0.	0.00004	0.
min2Xdd	0.	9.335e-6	-1.33e-6	0.
min2Xdef	0.00078	-0.0001	-0.00001	0.000013
min2Xaes	0.	0.000087	0.	0.
def2Xsnw	0.	1.904e-6	2.985e-6	0.
def2Xdd	0.	0.	0.	0.
def2Xmin	0.	-4.7e-6	0.	0.
def2Xaes	3.583e-6	0.	0.	0.
aes2Xsnw	0.	0.	0.	0.
aes2Xdd	0.	1.524e-6	0.	0.
aes2Xmin	0.000038	0.	0.	0.
aes2Xdef	0.	-0.00001	0.	1.739e-6

Appendix I. (continued)

Parameter	Balsam Fir	Sugar Maple	Lodgepole Pine	White Pine
intercept	20.1326	36.6082	-463.7	-15.2531
snw	-0.1085	0.	0.	0.
dd	0.	0.	0.2253	0.
min	0.	0.	-31.5266	-3.2189
def	0.	0.	0.	0.
aes	0.	0.	-0.4846	0.
snw2	0.00006	0.	0.	0.
dd2	0.	0.	-0.00004	0.
min2	0.	0.	-0.6966	-0.1036
def2	0.	0.	0.	0.
aes2	0.	-0.00042	0.00162	0.
snwXdd	0.	0.	0.	0.
snwXmin	0.	0.	0.	0.
snwXdef	0.	0.	-0.00033	-0.00004
snwXaes	0.	0.	0.	-0.00017
ddXmin	0.	0.	0.00822	0.000244
ddXdef	0.	0.	-0.0001	0.
ddXaes	0.	0.	0.000212	0.
minXdef	0.	0.	0.	0.
minXaes	0.	0.0121	0.	0.
defXaes	0.	0.	0.	-0.00016
snw3	0.	0.	-3.08e-9	0.
dd3	0.	0.	8.831e-9	3.15e-10
min3	-0.00015	-0.00023	-0.00526	-0.00111
def3	0.	0.	0.	0.
aes3	0.	0.	0.	5.38e-7
snw2Xdd	8.224e-8	0.	0.	0.
snw2Xmin	-0.02e-4	0	0.	-1.31e-6
snw2Xdef	4.149e-7	-1.31e-7	3.412e-7	0.
snw2Xaes	-1.13e-6	0.	0.	0.
dd2Xsnw	0.	-4.61e-10	0.	0.
dd2Xmin	0.	0.	-6.25e-7	0.
dd2Xdef	0.	0.	0.	0.
dd2Xaes	0.	0.	-1.14e-7	0.
min2Xsnw	0.	0.	0.	0.
min2Xdd	-5.62e-6	0.	0.000076	0.
min2Xdef	0.	0.	0.	0.000035
min2Xaes	0.	0.	0.	0.
def2Xsnw	2.251e-6	0.	2.179e-6	0.
def2Xdd	0.	0.	0.	0.
def2Xmin	0.	0.	0.	0.
def2Xaes	0.	0.	6.306e-6	0.
aes2Xsnw	9.751e-7	0.	0.	0.
aes2Xdd	0.	0.	0.	0.
aes2Xmin	0.	-0.00004	0.	0.
aes2Xdef	0.	2.364e-7	1.994e-6	0.