



Possible Changes in Natural Vegetation Patterns due to Global Warming

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WORKING PAPER

**POSSIBLE CHANGES IN NATURAL VEGETATION
PATTERNS DUE TO A GLOBAL WARMING**

Rik Leemans

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PUBLICATION NUMBER 108 of the Biosphere Dynamics Project

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FOREWORD

IIASA's projects within the Environment Program are devoted to investigating the interaction of human development activities and the environment, particularly in terms of the sustainable development of the biosphere. The research is policy-oriented, interdisciplinary, international in scope and heavily dependent on collaboration with a network of research scientists and institutes in many countries. The importance of IIASA's Environment Program stems from the fact that the many components of the planetary life-support systems are being threatened by increasing human activity, and that these problems are not susceptible to solution by singular governments or even, international agencies. Instead, resolution of the difficulties will demand concerted and cooperative actions by many governments and agencies, based on valid understanding of the earth's environmental systems. Establishment of a basis for international cooperation, and production of accurate global environmental perceptions are both hallmarks of IIASA's Environment Program.

Foremost among the global environmental issues of concern are those involving increasing concentrations of greenhouse gases and changing climate. Problem solutions will only become apparent after collection and analysis of pertinent data, testing of relevant hypotheses, genesis of mitigation strategies and investigation of the efficacy of the strategies which are developed. All of these activities can support development of, or be supported by, the appropriate mathematical models of the biosphere. Therefore, the Biosphere Dynamics Project has been focused on the creation of models which can describe the processes in the biosphere which result in vegetation dynamics. The models are being designed to define the biotic and ecological results of measures suggested to slow or stop increases in greenhouse gases. The models must be capable of documenting whether, and if so by how much, vegetational communities would benefit from mitigation actions, as well as describing how the terrestrial biosphere will respond in its role as carbon source and sink.

One such study is aimed at examining the potential future geographic configurations of the world's vegetation biomes under specified, steady-state distributions of global climate variables. The first step we have chosen is to document the data sets and classification systems available for modification to fit our needs, exemplified by the content of this working paper. This paper appeared as pages 105 to 122 in *Der Treibhauseffekt. Das Problem - Mögliche Folgen - Erforderliche Massnahmen*, edited by A. Hackl and published in 1989 by the Akademie für Umwelt und Energie, A-2361 Laxenburg, Austria. The progress in modifying the models and data sets to fit the peculiar characteristics of global environmental change, supported by the present work, will be examined in subsequent working papers.

B.R. Döös
Leader
Environment Program

ABSTRACT

The distribution of global vegetation patterns is strongly related to climate patterns. Local differences in soil characteristics and water availability, which are in turn also partly determined by climate, force the global vegetation patterns to become even more pronounced and the local patterns more diverse. The predicted global climate change, due to the increased levels of greenhouse gases, will thus have large impacts on broad-scale vegetation patterns. The Holdridge life zone classification is based on biotemperature (a heat sum), annual mean precipitation and a potential evapotranspiration ratio; it was used in the current paper to create an objective global vegetation (life zone) map. The map was created by interpolation of a large data base of weather stations to a grid of land cells with a resolution of 0.5° . The climate scenario for future climate under double CO_2 concentrations is based on results of the U.K. Meteorological Office general circulation model. Large changes in vegetation patterns are observed between the life zone classifications of present and future climate. The polar regions decrease most in their extent, and all boundaries between the different latitudinal regions move toward their poles. Most sensitive to climatic warming are the borders between the latitudinal regions. Changes are most clearly observable at the southern and northern edges of the boreal forest region. Limitations of the Holdridge classification to study impacts of climate change are discussed and improved approaches are proposed.

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POSSIBLE CHANGES IN NATURAL VEGETATION PATTERNS DUE TO A GLOBAL WARMING

Rik Leemans

INTRODUCTION

Regional vegetation is the result of a close network of interrelations between the characteristics of the local environment, natural vegetation succession, and several other factors with human management/influence being one of the most important. On a global scale, climate is the leading factor in differentiating vegetation. The broad-scale distribution of major vegetation types or biomes is roughly in equilibrium with the present climate. The notion that the physical environment largely determines the observed vegetation patterns, can be found in many textbooks on ecology and geography. Although human societies have used local flora and fauna intensively, limitations on the choice of crops and maximum limits to productivity are heavily determined by the local environment. Climate maps of the world are often based on continental and regional vegetation patterns, which were much easier to observe, locate and measure than climatic parameters. And reliable networks of meteorological measurement stations were, until recently, not available in large parts of the world.

Vegetation and soil have large effects on microclimate and local climates. Climate operates on vegetation in an indirect way, namely through competition between neighboring individuals, probably of different species. This means that a plant will appear only as close to its absolute climatic limit when it can overcome the competition with individuals of other species, which are often better adapted to the local environment. Any direct effect of climate on vegetation or species distribution should be regarded as an exceptional phenomenon, such as those during critical parts of a species life-cycle, like germination and establishment.

In this paper, I use a static equilibrium model, a climate classification, which objectively links climate to vegetation and may provide plausible projections of changes in global vegetation patterns. I will visualize these changes in the distributions as a result of climate change by using a climate scenario based on a Global Circulation Model (GCM). By studying the extent of these patterns, areas with potential large vegetation changes can be recognized.

I will not take into account any other impacts of climate change, like sea-level rise, the thawing of permafrost in high latitude soils, and changes in local soil characteristics like increased decomposition rates, increased leaching and an accelerated degradation, when vegetation cannot take up the extra amount of released nutrients. These impacts can, of course, locally be of major importance. An impressive compilation of such local impacts on agriculture and forestry is given by Parry et al. (1988).

HOLDRIDGE LIFE ZONE CLASSIFICATION

Climate consists of a complex mixture of many elements, like temperature, moisture, precipitation, wind, etc. Practically any climatic element or combinations of those elements could influence a single plant's life. Climate can be quantified in terms of various parameters, like means, extreme values, durations. Many simple and complex ways have been proposed to relate vegetation to climate and vice versa. Tuhkanen (1980) gives a historical review of the different methods used, their data requirements, and advantages and disadvantages. For this study, I use a combined system of climatic parameters, namely the Holdridge life zone classification (Holdridge 1947, 1967).

This system was used in a climate change impact study by Emanuel et al. (1985a, 1985b). Holdridge's underlying assumption is that the differentiation and physiognomy of vegetation under relatively undisturbed conditions reflect the effects of climatic factors on vegetation. This means that any climax vegetation in an area can be defined objectively by its climate. Topographic, biotic and edaphic factors also depend to a certain extent upon climate, and

these lead only to a secondary differentiation (Holdridge 1967). Tests of the Holdridge life zones have revealed that the system can fit tropical vegetation zones (e.g. Holdridge 1967), mediterranean zones (Steila 1966), as well as the boreal zones, but that it is less applicable to cold oceanic or cold arid climates (Hämäl-Ahti et al. 1974) where moisture becomes the determining factor. The ease at which the Holdridge classification can be used in determining the life zones objectively from frequent available climate data (monthly temperature and precipitation) makes this system more suitable for climate change impact studies at a global scale than other well known systems, like the Köppen (1936), Thornthwaite (1948) and Box (1981) classifications which are far more data demanding and dependent or are more difficult to relate to actual vegetation patterns.

The Holdridge life zone classification is based on three climate parameters: biotemperature, mean annual precipitation and a potential evapotranspiration (PET) ratio. The biotemperature is a temperature sum, related to growing degree days, and is here defined as the sum of daily mean temperatures between 0° and 30° C divided by 365. Biotemperature defines the latitudinal or altitudinal belts of life zones. Mean annual precipitation is the sum of the mean monthly values. PET is a simple empirical linear function of biotemperature, and adds no extra information to the model. The PET-ratio is defined as PET divided by annual precipitation. The PET ratio defines different humidity provinces. The three climatic indices are displayed graphically in a logarithmical system, so that each separate life zone becomes equivalent in significance (Figure 1). Each life zone is named to suggest a vegetation association.

I have made use of the Holdridge classification to create a global life zone map by using monthly temperature and precipitation values of weather stations scattered around the world. The data base was compiled at the International Institute for Applied Systems Analysis (IIASA), based on published (Weather Bureau 1959; Walter and Lieth 1960-67; Meteorological Office 1972; Müller 1982) and unpublished (China, USSR) sources. The different source data sets were separately screened for errors, outliers and unreliable stations, and for doublets. An observation record of between 10 and 40 years (if possible 1931-60) was required for the computation of mean monthly temperature and precipitation values. The final data set contained ca. 5500 stations worldwide, characterized by longitude, latitude and altitude.

This array of selected stations was then used to create a global monthly temperature and precipitation data base for land areas on a grid with a resolution of 0.5° (grid cell of about 55 x 55 km at the equator). The interpolation scheme used for each variable is a smooth surface fitting on a triangulation network, based on all stations (Akima 1978). Temperature values were corrected for changes in altitudes between the stations by applying a moist adiabatic lapse-rate of 0.6° C/100 m. Before the interpolation, the altitudes of all stations values were calculated as sea-level temperatures and after the interpolation all grid cell values were calculated as the modal height of that cell, using a topography data set (National Geophysical Data Center 1988). Mean annual precipitation was computed as the sum of all monthly values. The biotemperature was computed by using daily values and generated by fitting a quadratic spline function through the monthly values. The specific PET-ratio was computed from the biotemperature and total annual precipitation. These three climate indices in each land cell (total 62,483 without Antarctica) generated a world life zone map (Figure 2).

The life zone patterns (Figure 2) roughly compare with existing vegetation patterns when compared with, for example, the digitized vegetation map of Olson et al. (1982). Precise comparison is difficult, however, because of differences in the number and definition of vegetation classes. However, the overall global pattern is clearly visible in both schemes. In Northern areas, where temperature is much more important than precipitation, spurious classes appear in life zones in comparison with natural vegetation. In addition, in areas where soil and soil-moisture characteristics strongly determine vegetation, differences between life zones and actual vegetation are encountered, e.g. the extended pampa-grasslands in Argentina (G. Rush, personal communication). Such discrepancies can only be overcome if more soil parameters are taken into account, which leads to a more complex approach and many other problems, like defining the most important factor. Due to the use of a moist adiabatic lapse rate, this map reflects the life zones of mountainous

DIAGRAM FOR THE CLASSIFICATION OF WORLD LIFE ZONES OR PLANT FORMATIONS

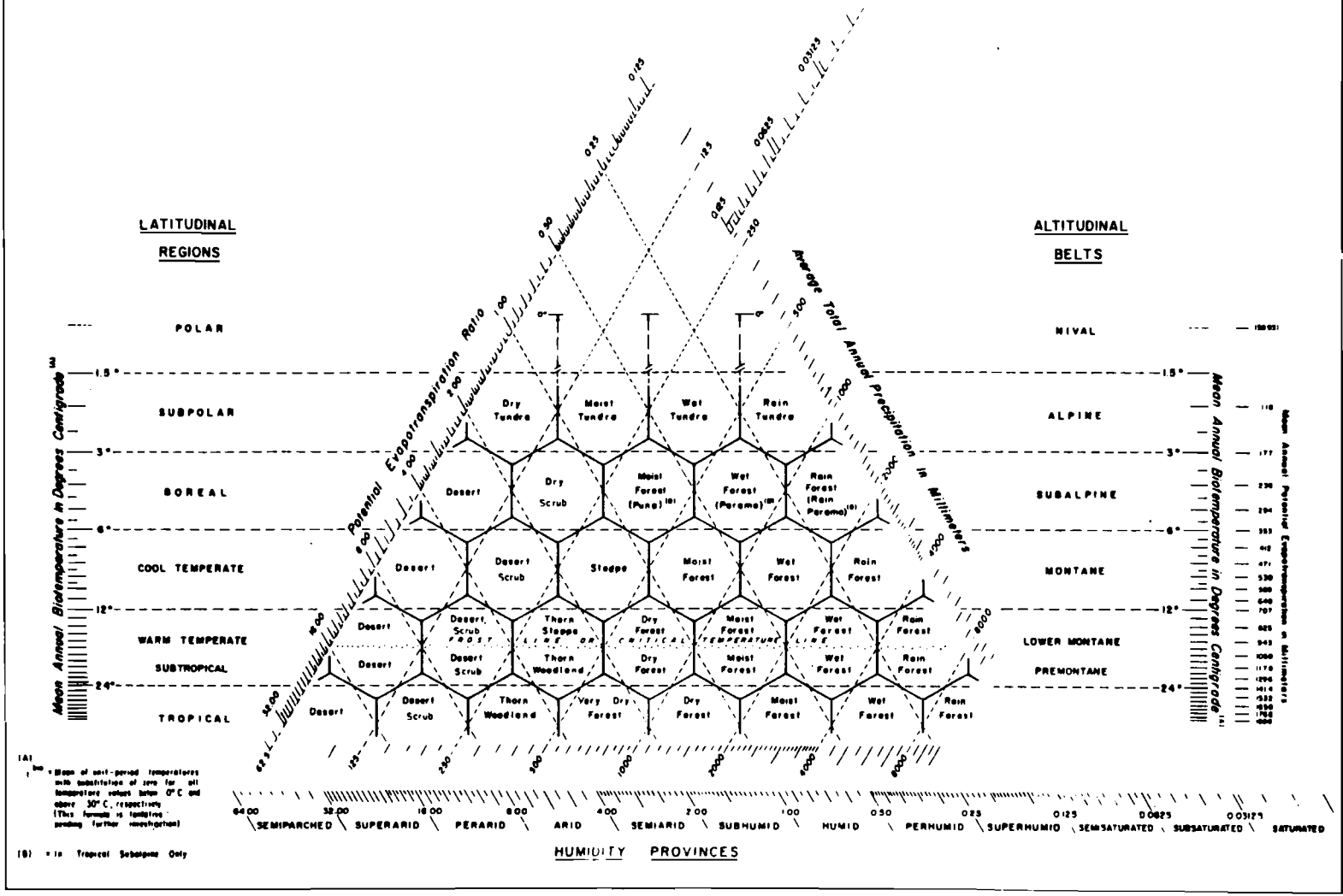


Figure 1. The Holdridge classification of world life zones (Holdridge 1967).

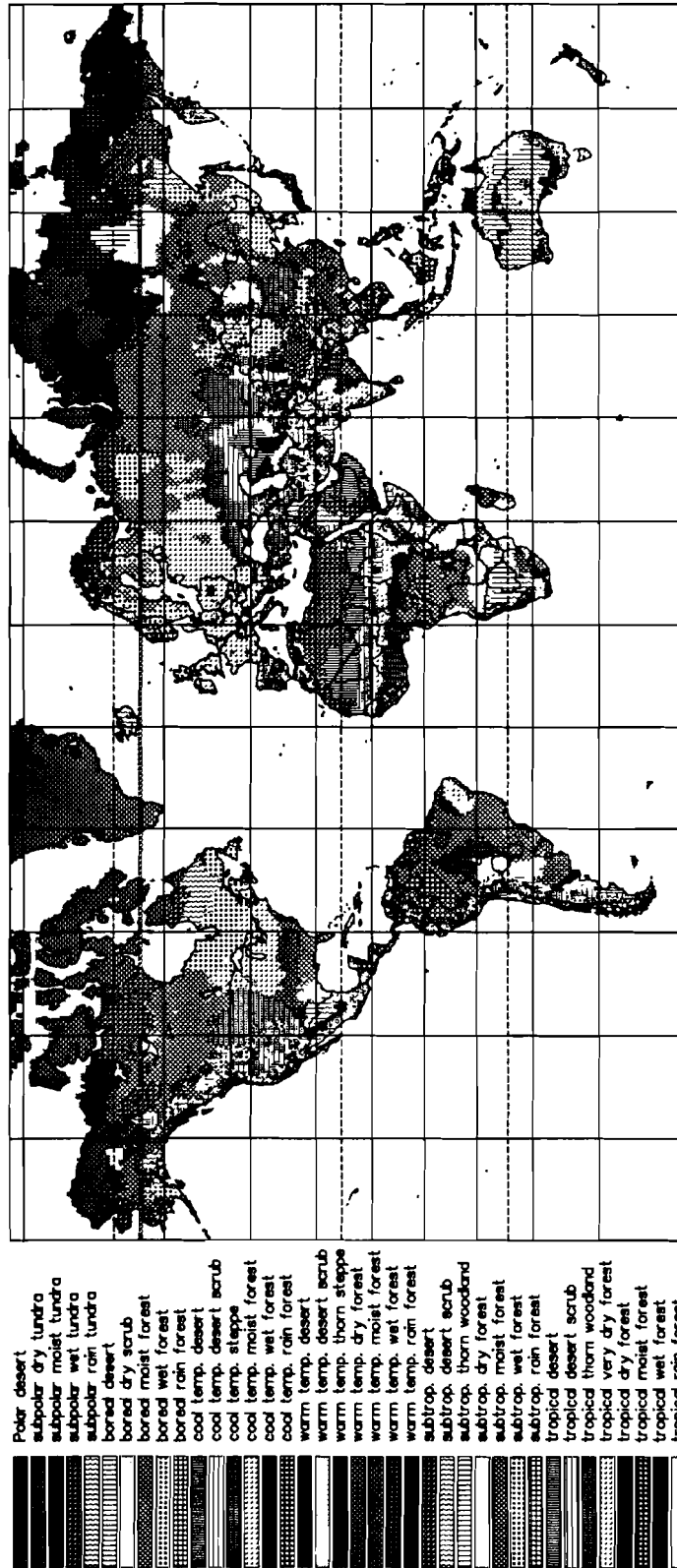


Figure 2. A world map with the Holdridge life zone classification based on a 0.5° gridded temperature and precipitation data base.

areas much better than does the life zone map published by Emanuel et al. (1985a).

The impact of climate change was determined by using results of simulated climate by a general circulation model of the atmosphere (GCM). At present there are several scenarios of climate change available. Most available GCMs indicate similar climate change trends, although major differences may occur in the magnitude of change and in local patterns. I used the output of the model developed by the U.K. Meteorological Office (UKMO), and for a present climate and a doubled CO₂ (Mitchell 1983). This model was chosen because it has a higher horizontal spatial resolution than most other models. This leads to more reliable regional patterns (Mitchell, personal communication) needed to give a realistic scenario of vegetation change.

The differences in monthly mean temperature and monthly mean precipitation between the two different model runs were used to define the amount of climate change. This quantity was then added to the present climate data base to give a doubled CO₂ future climate. The combination of the change, simulated by the UKMO GCM-model, and an authentic climate data base has the advantage that existing regional differences in the climate parameters are included, and that imperfections in the GCM-model are reduced. The simulated global climate change scenario thus becomes more realistic.

The "climate change" data base was used to determine a Holdridge life zone classification for the future climate under a doubled CO₂. The maps shown here mark only the areas undergoing a change; the portions of present life zones which would change (Figure 3) and portions of future life zones which vegetation could potentially change into (Figure 4). Changes are apparent between the two maps: only little more than 50% of the world's vegetation does not change from one life zone to another between present and future climate (Table 1 and Table 2). The climatic warming is obvious in the pattern of life zone changes. The latitudinal belts are markedly replaced polewards. This results in the largest vegetation change being in the polar regions. This vegetation decreases in area by 33%. Given that Greenland remains as a large polar desert (land ice), the largest part of the change occurs in the tundra ecosystems. There boreal life zones largely replace the tundra which is limited at its northern border by the polar ice-sea, and thus cannot expand poleward. The boreal forest, in turn, is replaced at its southern edge by temperate forests, but its total area remains almost equal, due to its northward extension. This result contrasts that of Emanuel et al. (1985a, 1985b), who found a larger decrease in the area of the boreal forest. A complex pattern of changes occurs at the borders between the temperate and subtropical regions. The range of most tropic life zones increases. In Africa, the Sahara desert expands toward the south and the transitions toward the tropical life zone becomes much less gradual than in the present climate.

DISCUSSION

Vegetation Change

The changes in potential life zones as shown here are large, and affect directly or indirectly the whole globe with all its ecosystems. For example, the tundra systems are important for many migrating birds, like geese, for their reproduction and summer foraging. If these grounds disappear or even largely decrease, this will have a catastrophic effect on the populations of these birds, and probably many other ecological impacts along their migratory path. During the creation of large biosphere reserves, possible effects of climate change should be considered; these reserves should not be created in areas with a high probability of change. Unfortunately, the most diverse systems are located in the transitions between ecosystems or biomes.

The actual impacts of climate change on vegetation will probably not be observed immediately after the climate change has occurred. There will be a time lag, ranging from decades to decennia. Species and their propagules are not available immediately if the circumstances become appropriate. Especially plants are rather immobile and have slow migration rates. Boreal species, for example, have an estimated natural migration capacity of 1 to 40 kilometers per century (Davis 1981). Massive, practically impossible, new

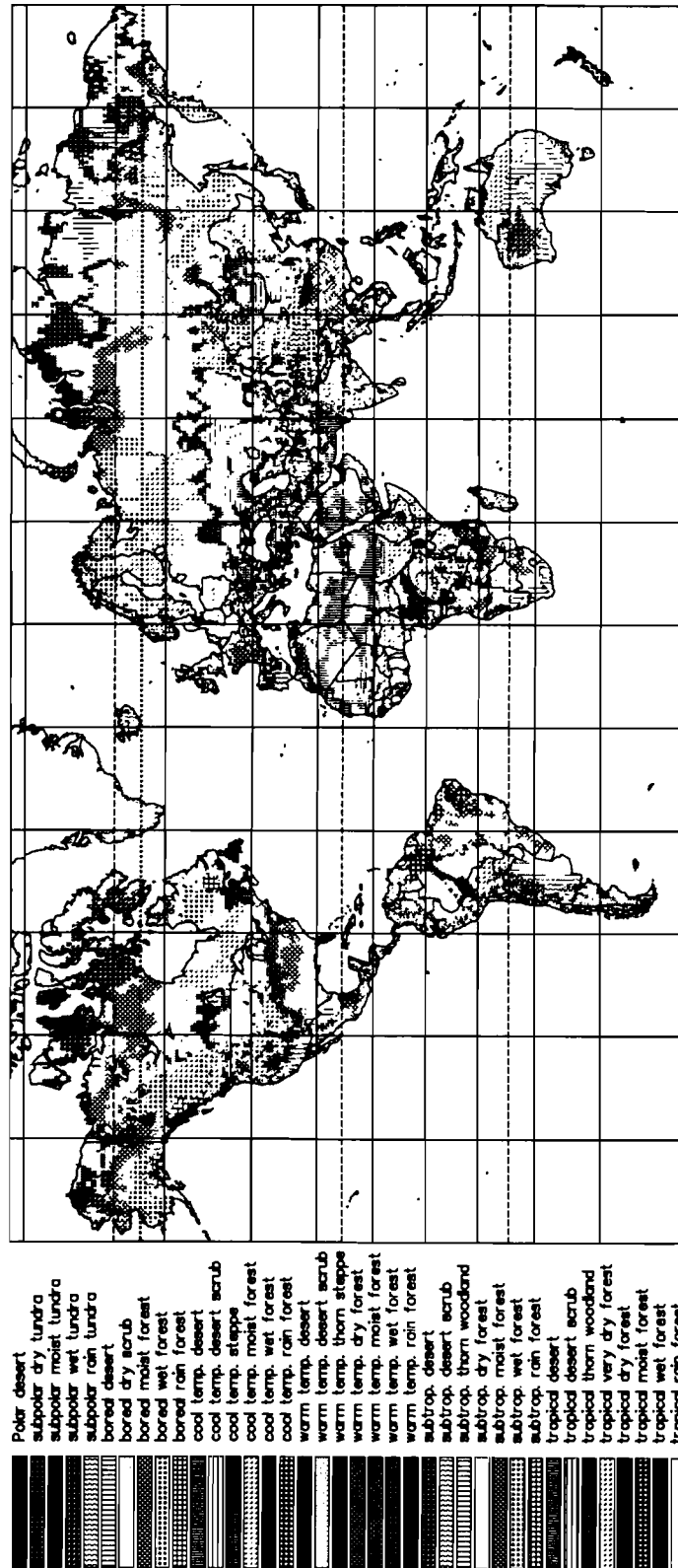


Figure 3. A Holdridge life zone world map with the differences between present climate and a double CO₂ future climate. The marked areas are the original life zones, determined on the basis of present climate.

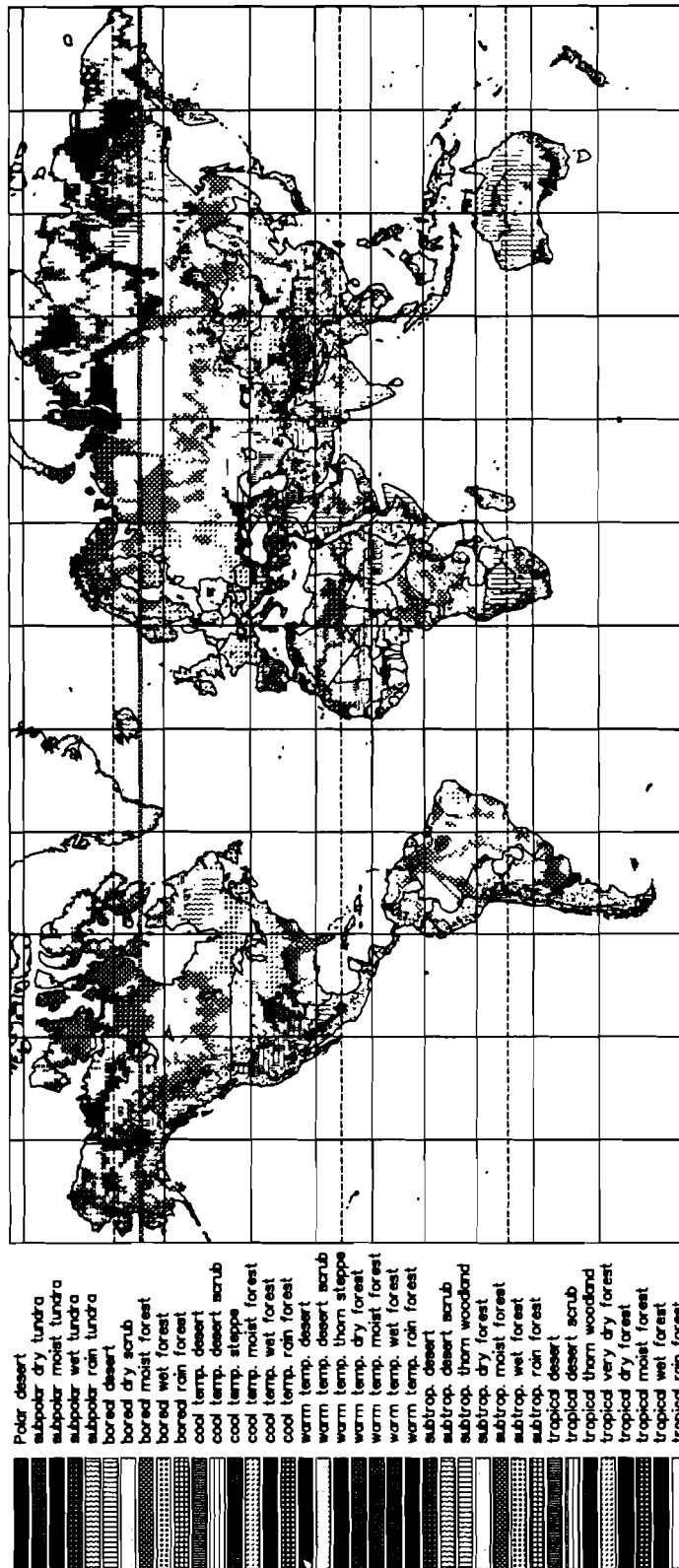


Figure 4. A Holdridge life zone world map with the differences between present climate and double CO₂ future climate. The marked areas are the future life zones determined on the basis of simulated climate.

Table 1. Areas (in 10^6 km^2) occupied by the different Holdridge life zones for present climate and a probable future climate under a doubling of CO_2 .

Latitudinal Region	Life Zone	Current Climate	Future Climate	Difference
Polar	Desert	8.3	4.6	- 3.6
	Dry Tundra	0.9	1.0	+ 0.1
	Moist Tundra	3.3	2.4	- 0.9
	Wet Tundra	3.5	2.4	- 1.1
	Rain Tundra	2.1	1.6	- 0.5
Boreal	Desert	0.4	0.4	+ 0.0
	Dry Bush	1.8	1.9	+ 0.1
	Moist Forest	10.9	8.3	- 2.5
	Wet Forest	4.6	6.0	+ 1.3
	Rain Forest	0.9	1.0	+ 0.2
Cool Temperate	Desert	1.1	0.8	- 0.1
	Desert Bush	2.0	1.8	+ 0.2
	Steppe	7.5	7.7	+ 0.2
	Moist Forest	8.9	10.4	+ 1.6
	Wet Forest	1.3	1.9	+ 0.6
	Rain Forest	0.2	0.4	+ 0.2
Warm Temperate	Desert	0.9	1.0	+ 0.2
	Desert Bush	1.6	1.2	- 0.5
	Thorn Steppe	2.2	1.7	- 0.4
	Dry Forest	3.7	2.7	- 1.0
	Moist Forest	3.0	2.6	- 0.3
	Wet Forest	0.2	0.3	+ 0.1
	Rain Forest	0.0	0.1	- 0.0
Subtropical	Desert	7.2	6.3	- 0.8
	Desert Bush	5.1	2.8	- 2.2
	Thorn Steppe	4.8	4.3	- 0.5
	Dry Forest	8.9	8.0	- 0.8
	Moist Forest	15.1	11.7	- 3.3
	Wet Forest	2.1	1.3	- 0.8
	Rain Forest	0.1	0.1	+ 0.0
Tropical	Desert	4.2	8.6	+ 4.4
	Desert Bush	1.1	0.9	- 0.2
	Thorn Steppe	1.8	1.6	- 0.2
	Very Dry Forest	3.1	5.6	+ 2.4
	Dry Forest	7.6	13.1	+ 5.5
	Moist Forest	4.8	7.6	+ 2.9
	Wet Forest	0.2	0.7	+ 0.6
	Rain Forest	0.0	0.0	+ 0.0
Total:		135.2	135.2	

Table 2. Summary of percentage change in areal extent of the different Holdridge life zones for present climate and a probable future climate under a doubling of CO₂. "STABILITY" indicates the area with similar life zones under both climates. "CHANGE" indicates those which change from the current life zone into another. "EXPANSION" indicates those which change from another life zone into the current life zone. (All values are relative to the area occupied under present climate.)

Latitudinal Region	Life Zone	Change	Stability	Expansion
Polar	Desert	56.0	44.0	0.0
	Dry Tundra	45.9	54.1	63.8
	Moist Tundra	36.9	63.1	35.6
	Wet Tundra	25.3	74.7	44.2
	Rain Tundra	27.6	72.4	48.7
Boreal	Desert	19.6	80.4	87.8
	Dry Bush	41.7	58.3	64.3
	Moist Forest	52.2	47.8	24.2
	Wet Forest	54.6	45.4	73.9
	Rain Forest	43.1	56.9	74.6
Cool Temperate	Desert	47.3	52.7	27.4
	Desert Bush	37.1	62.9	57.3
	Steppe	58.7	41.3	44.6
	Moist Forest	64.3	35.7	53.4
	Wet Forest	64.0	36.0	89.7
	Rain Forest	61.3	38.7	111.3
Warm Temperate	Desert	51.1	48.9	66.6
	Desert Bush	22.2	77.8	48.5
	Thorn Steppe	16.9	83.1	62.7
	Dry Forest	26.5	73.5	47.4
	Moist Forest	35.5	64.5	52.9
	Wet Forest	56.5	43.5	82.3
	Rain Forest	36.8	63.2	18.9
Subtropical	Desert	50.6	49.4	38.3
	Desert Bush	23.2	76.8	33.1
	Thorn Steppe	26.0	74.0	63.6
	Dry Forest	40.4	59.6	50.4
	Moist Forest	54.6	45.4	23.3
	Wet Forest	52.2	47.8	10.4
	Rain Forest	65.9	34.1	34.8
Tropical	Desert	94.7	5.3	100.2
	Desert Bush	18.5	81.5	62.7
	Thorn Steppe	38.4	61.6	49.9
	Very Dry Forest	63.4	36.6	112.3
	Dry Forest	85.1	14.9	86.2
	Moist Forest	95.4	4.6	61.9
	Wet Forest	100.0	0.0	245.4
	Rain Forest	-	-	-

plantings would be required to sustain its distribution northwards.

As plant distributions are an outcome of competition between individuals and new, better adapted species are not yet available, the species present could remain due to lower competitive pressure. If individuals are surviving in an unappropriated environment, higher mortality rates will be observed as a result of an increased environmental stress at a species environmental limit. The world could then be faced with a vegetation decline on a large spatial scale (up to 50% according to the above analysis). This change, occurring during a short time-scale (up to one century), has no equivalent in history and as a result, many species may become extinct. Such a decrease in biodiversity is irreversible. For example, after the sudden crash in species number at the end of the Permian period (some 240 years ago), it took more than 5 million years to recover (Erwin 1989). After this crash the evolutionary path had changed in a direction leading to the dominance of mammals.

Improvements of Static Equilibrium Models

The above-described example of a static equilibrium model has some severe disadvantages, like many other models of this type. These models do not include rates of changes, only amplitudes of change, and present only the possible distributions of potential vegetation types under a specified climate. Transient responses cannot be studied with such models. As global climatic warming spreads northwards (locally several hundreds of kilometers), the time-scale will be important. Single plant species often lack migration potential fast enough to keep up with expected climate changes. Models, which do not take into account competition and possibly migration rates, cannot predict the actual vegetation transients under a climatic change.

Dynamic models for vegetation succession have been developed. The most successful group has been developed for forests and is based on the gap-models developed by Botkin et al. (1972), Shugart (1984), and Prentice and Leemans (1990). At IIASA, we have combined one of these models (FORSKA, Leemans and Prentice 1989) with specific environmental driver routines (Bonan 1989) to simulate the global dynamics of boreal forests, because they are one of the ecosystems where the largest changes will occur (see above). The boreal forest is also a relatively simple system, with few well known species, located in a few countries (Canada, Alaska, Norway, Sweden, Finland, and the USSR), which makes the collection of data, impact monitoring networks, and exchange of knowledge much easier.

The boreal model incorporates the growth of single trees, not in an empirical, but in a mechanistic way, and incorporates competition between these trees, resulting in a realistic forest structure. The environmental driver includes permafrost dynamics, moisture and temperature effects, fire and other ecological disturbances, which all have their specific effect on the growth of trees. The model soon will be used to simulate the impacts of climatic change on the boreal forest and along its borders.

The boreal forest covers ca. 10% of the world's land surface. By modeling this part only, we can examine no impacts elsewhere. The development of a dynamic global vegetation model, including all ecosystems and species, becomes necessary. In cooperation with the International Geosphere-Biosphere Program (IGBP), we have started to develop such a model. Difficulties which arise here are the different characteristics of terrestrial ecosystems, like grasslands, forests and their transients. The present approach taken at IIASA is illustrated in Figure 5 (Prentice et al. 1989). This approach can include a wide range of environment-vegetation interactions and plant-plant interactions. Single species will not be represented; they will be classified into "functional groups" according to their ecological functions. The first, initial results of this model may be ready in mid-1990.

Environmental Data Bases

All these model exercises need huge amounts of data. At IIASA we are compiling a set of environmental data bases of geographical information, such as vegetation, soil, topography and climate. All our data bases are linked to a gridded map of the world on a 5° resolution,

and are model independent. The Holdridge life zone classification was one of the first applications to use these data bases. The data bases are updated and improved continuously, and new subjects are added.

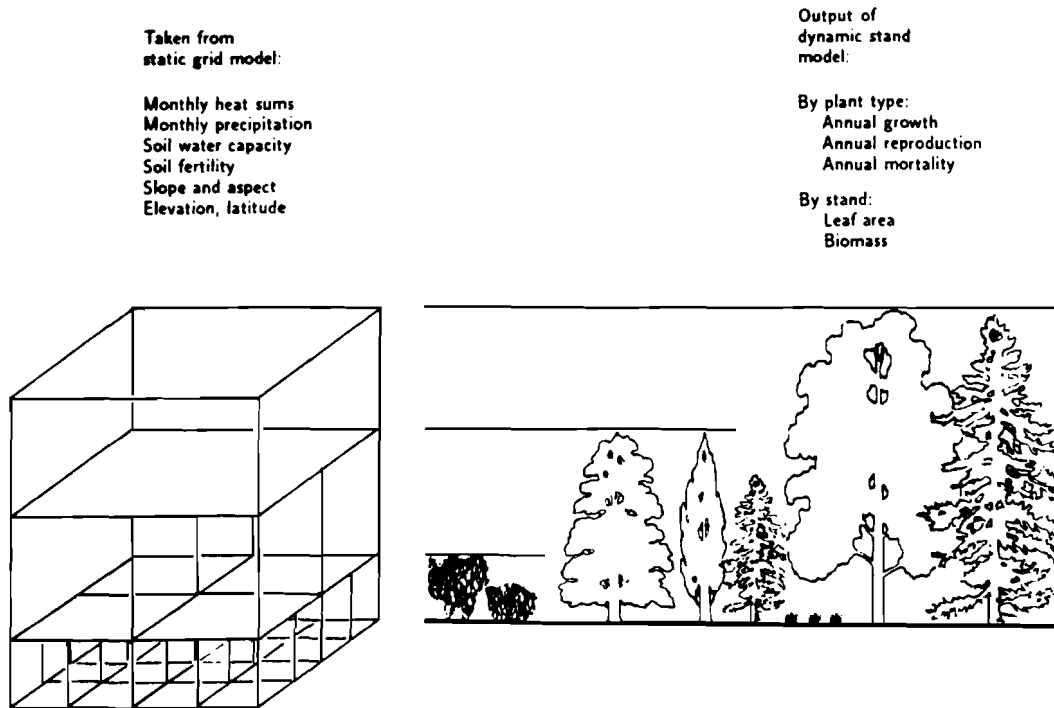


Figure 5. A conceptual form of a dynamic vegetation model. The tallest plants shade out shorter ones; the number of simulations required for smaller-stature plants is greater than for tall plants. Each vertical layer of vegetation is subdivided into separate layers in which different sized individuals of one species can grow (Prentice et al. 1989).

CONCLUSIONS

Climate and vegetation are closely related. Although we have much knowledge about the spatial distribution of vegetation patterns, we hardly know how the different spatial and temporal patterns of vegetation are generated in a mechanistic way. The understanding of such dynamics are of increasing importance for accessing the possible impacts of any climate change.

I perceive the near future as a composite of many exciting scientific challenges in which scientists from different fields, traditions, approaches and countries collaborate seriously to unravel the dynamic links within the biosphere. This will be the only way to make available the information necessary for policy-makers and the public to decide about a sustainable development of mankind within the biosphere.

REFERENCES

- Akima, H. 1978. A method of bivariate interpolation and smooth surface fitting for irregularly distributed datapoints. *ACM Trans. Math. Software* 4:148-159.
- Bonan, G.B. 1989. A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forests. *Ecol. Model.* 45:275-306.
- Botkin, D.B., J.F. Janak, and J.R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *J. Ecol.* 60:849-873.
- Box, E.O. 1981. *Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography*. Dr. W. Junk Publishers, The Hague.
- Davis, M. 1981. Quaternary history and the stability of forest communities. Pages 132-153 in D.C. West, H.H. Shugart, and D.B. Botkin, eds. *Forest Succession: Concepts and Application*. Springer Verlag, New York.
- Emanuel, W.R., H.H. Shugart, and M.P. Stevenson. 1985a. Climatic change and the broad-scale distribution of terrestrial ecosystems complexes. *Climatic Change* 7:29-43.
- Emanuel, W.R., H.H. Shugart, and M.P. Stevenson. 1985b. Response to comment: Climatic change and the broad-scale distribution of terrestrial ecosystems complexes. *Climatic Change* 7:457-460.
- Erwin, D.H. 1989. The end-Permian mass extinction: What really happened and did it matter? *TREE* 4:225-229.
- Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. *Science* 105:367-368.
- Holdridge, L.R. 1967. *Life Zone Ecology*. Tropical Science Center, San José.
- Hämet-Ahti, L., T. Ahti, and T. Kopenen. 1974. A scheme of vegetation zones for Japan and adjacent regions. *Ann. Bot. Fenn.* 11:59-88.
- Köppen, W. 1936. Das geographische System der Klimate. In W. Köppen and R. Geiger, eds. *Handbuch der Klimatologie*. Berlin.
- Leemans, R. and I.C. Prentice. 1989. FORSKA, a general forest succession model. *Meddelanden från Växbiologiska Institutionen, Uppsala* 1989(2):1-60.
- Meteorological Office. 1972. *Tables of Temperature, Relative Humidity, Precipitation and Sunshine for the World. Part III. Europe and the Azores*. HMSO, London. 228 pp.
- Mitchell, J.F.B. 1983. The seasonal response of a general circulation model to changes in CO₂ and sea temperatures. *Quart. J. R. Met. Soc.* 109:113-152.
- Müller, M.J. 1982. *Selected Climatic Data for a Global Set of Standard Stations for Vegetation Science*. Dr. W. Junk Publishers, The Hague.
- National Geophysical Data Center. 1988. *10-Minute Topography Data Base*. U.S. Department of Commerce, Washington, D.C.
- Olson, J., J.A. Watts, and L.J. Allison. 1982. *Carbon in Live Vegetation of Major World Ecosystems*. Oak Ridge National Laboratory, Oak Ridge, TN, USA.
- Parry, M.L., T.R. Carter, and N.T. Konijn. 1988. *The Impact of Climatic Variations on Agriculture. Volume 1: Assessments in Cool Temperate and Cold Regions*. Kluwer Academic Publishers, Dordrecht.

- Prentice, I.C. and R. Leemans. 1990. Pattern and process and the dynamics of forest structure. *J. Ecol.* (in press).
- Prentice, I.C., R.S. Webb, M.T. Ter-Mikhaelian, A.M. Solomon, T.M. Smith, S.E. Pitovranov, N.T. Nikolov, A.A. Minin, R. Leemans, S. Lavorel, M.D. Korzukhin, H.O. Helmisaari, J.P. Hrabovszky, S.P. Harrison, W.R. Emanuel, and G.B. Bonan. 1989. Developing a global vegetation dynamics model: Results of an IIASA summer workshop. RR-89-7. International Institute for Applied System Analysis, Laxenburg, Austria.
- Shugart, H.H. 1984. *A Theory of Forest Dynamics*. Springer-Verlag, New York.
- Steila, D. 1966. An evaluation of the Thornthwaite and Holdridge classification as applied to the mediterranean borderland. *Prof. Geogr.* 18:358-364.
- Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. *Geogr. Rev.* 38:55-94.
- Tuhkanen, S. 1980. Climatic parameters and indices in plant geography. *Acta Phytogeogr. Suec.* 67:1-110.
- Walter, H. and H. Lieth. 1960-67. *Klimadiagramm-Weltatlas*. Gustav-Fisher-Verlag, Stuttgart.
- Weather Bureau. 1959. *World Weather Records 1941-1950*. U.S. Department of Commerce, Washington, D.C.