The Potential Effects of Climate Change on the Native Vascular Flora of North America

A Preliminary Climate Envelopes Analysis
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REPORT SUMMARY

A Preliminary Climate Envelopes Analysis

This EPRI study is a first attempt to identify the vascular plant species of North America north of Mexico that– because of their geographical distributions and biological or ecological characteristics–might be especially vulnerable to climate change and resulting reorganization of plant communities. Findings in this study provide an initial estimate of the magnitude of the threat imposed by climate change and a means of identifying endangered species to facilitate proactive conservation efforts.

Background

Large-scale climatic changes, such as increases in mean annual temperature often referred to as "global warming," could potentially cause a major reorganization of biomes, habitats, and plant distributions; local destruction of many plant populations; and, perhaps, significant numbers of species extinctions. Further, rapid rates of warming coupled with the highly disturbed nature of much of the North American landscape raise concerns that plant distributions could not adjust as successfully as during past periods of climate change. Such events would clearly have broad ecological and economic impacts and present major challenges to the conservation of biodiversity.

Objectives

To develop a database and general method for predicting the effects of climate change; to estimate the number of vulnerable species using this method, describe patterns of vulnerability, and rate vulnerable species in terms of their potential for northward migration; to define potential regional effects on plant diversity; to encourage proactive conservation efforts to preserve threatened species.

Approach

The project team matched the reported geographical distributions of 15,148 native North American vascular plant species with climate data for 194 geographical areas, enabling them to estimate the climate envelope for each species. They used three analytic methods to construct these envelopes, based on the upper and lower limits of temperature currently experienced by each species within its present range. Finally, they recalculated each area's climate given the projected increase in mean temperature.

Results

Published models of future climates predict a possible increase in mean annual temperatures of 3°C within the next century. Assuming a species might be eliminated from an area where the new climate falls outside the present climate envelope, then 7-11% of North America's native plant species would be out of their envelopes in a climate 3°C greater than present. Rare species would be disproportionately affected, with 10-18% entirely out of their climate envelopes. In addition, 17-33% of the 354 species that are protected or are candidates for protection under the U.S. Endangered Species Act would be out of their climate envelopes in a +3°C climate. Some species, however, might be able to persist at their present sites due to the availability of suitable microhabitats or genetic variation in climate tolerances.

The local effects of climate change on plant species would vary considerably if species withdraw from the southern or low-elevation portions of their ranges in states such as California, Texas, Arizona, Florida, Louisiana, and Alabama. Species may expand their ranges northward as new areas become climatically suitable, producing significant changes in local floras. However, species vary in their ability to migrate, depending on limitations imposed by dispersal ability and/or specialized habitat requirements.

An estimate of dispersibility suggests that species with narrow climate envelopes tend to lack characteristics promoting mobility. This report briefly discusses the implications of these results for future conservation and land management activities.

EPRI Perspective

Rapid climate Change could pose a threat to plant species diversity in North America, presenting biological and ethical challenges to species conservation efforts. Management of species threatened by climate change could involve restoration and transplantation of species among preserves or into new northern locations and/or ex situ propagation of critical species. This project will help conservationists identify vulnerable species that require specialized conservation actions. EPRI is planning to perform additional climate change scenarios under this project.

TR-103330

Interest Category

Global climate

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ABSTRACT

To assess the potential effects of global warming on the North American flora, the reported geographical distributions of the 15,148 native North American vascular plant species were matched with climate data for 194 geographical areas to estimate the current "climate envelope" for each species. Three methods of analysis were used to construct these envelopes, all based on the limits of mean annual temperatures currently experienced by each species within its present range. Published models of future climates predict a possible increase in mean annual temperatures of 3°C (5.4°F) within the next century. Assuming that species might be eliminated from areas outside their present climate envelope, then about 7% to 11% of North America's native plant species would be entirely out of their envelopes in a +3°C climate. Rare species would be disproportionately affected–between 10% and 18% of these species would be entirely out of their climate envelopes. However, some rare species may be able to persist at their present sites due to the availability of suitable microhabitats or genetic variation in climate tolerances. Of the more common species, only about 1% to 2% would be vulnerable in a +3°C climate. The local effects of climate change on plant species would vary considerably if species withdraw from the southern or low-elevation portions of their ranges. Species may expand their ranges northwards as new areas become climatically suitable for them, producing significant changes in local floras. Species vary in their ability to make such migrations, depending upon limitations imposed by dispersal ability and/or specialized habitat requirements. An estimate of dispersibility suggests that species with narrow climate envelopes tend to lack characteristics promoting mobility. Additionally, the highly fragmented nature of today's human-dominated landscape and the rapid rates of warming suggested by many climate models make species migrations more problematic. The implications of these results for future conservation and land-management activities are briefly discussed.

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The authors participated in this work in diverse ways. The general research problem was defined by Chaplin, in consultation with Morse and Kartesz. Maddox subsequently assisted by refining the method of analysis and defining the data requirements. Kartesz, over the past two decades, developed the taxonomic classification used here, the list of native species, the basic phytogeographical data, and the initial draft of the species-biology data. The supplemental phytogeographical data was developed by Maddox and Morse, and the remainder of the species biology and habitats data by Maddox, Thurman, and Kutner, with programming assistance by Honey. Climatological data were obtained and processed by Maddox, Honey, Thurman, and Morse. Data analyses were performed primarily by Honey, Kutner, Maddox, and Morse. Interpretation of results was primarily by Kutner, Maddox, and Morse. Kutner and Morse wrote most of the text of the present report, in consultation with the various other authors, drawing on an earlier draft primarily by Maddox and Morse. Substantial assistance in preparing the report was provided by Virginia Crouch, Carol Annable, and Laura Pottmyer. Brandy Clymire provided invaluable assistance with creating maps and other figures, and formatting the text for publication.

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INTRODUCTION

The vegetation and plant species composition of any site is, on a broad scale, the product of the area's climate. Temperate deciduous forest, boreal forest, prairie grassland, desert, and tundra are examples of plant communities and ecosystems that occur in distinct climatic regimes and contain characteristic species, many of which are specifically adapted for life within their particular setting. These diverse communities and ecosystems constitute the broad phytogeographic patterns that have traditionally been called life-zones and biomes.

During past periods of climate change, particularly the alternations of cold and warm climates during the Pleistocene glacial and interglacial periods over the past two million years, plant species' distributions shifted many hundreds of kilometers during intervals of a few thousand years. Best documented are the changes in floristic composition of numerous sites over the past 20,000 years, since the last glacial maximum. The responsiveness of species' distributions to climate change provides further evidence for the critical role that climate plays in determining plant distribution patterns.

These strong associations between plant species distributions and climate alert human society that an altered global climate might have profound effects on biodiversity. Large-scale climatic changes, such as the increases in mean annual temperature often referred to as "global warming", could potentially cause a major reorganization of biomes, habitats, and plant distributions, local extirpations of many plant populations, and, perhaps, significant numbers of species extinctions. Such events would clearly have broad ecological and economic impacts, and present major challenges to biodiversity conservation. Furthermore, the possibly rapid rates of warming suggested in many predictions, coupled with the present highly fragmented and disturbed nature of much of the North American landscape, raise concerns that plant distributions could not adjust as successfully as they have during past periods of climate change.

This study is a first attempt to identify the kinds of vascular plant species of North America north of Mexico that, because of their geographical distributions and biological or ecological characteristics, might be especially vulnerable to climate change and resulting reorganization of plant communities. This identification may lead to further research or protection efforts for such species. Additionally, this work provides estimates of the potential effects of global climate change on regional patterns in plant species diversity.

This study has five major goals:

1. to develop a database and general methodology that is useful for estimating the effects of climate change and is independent of particular climate predictions or models,
2. to estimate the number of vulnerable species over the *entire* native flora using a consistent methodology,
3. to describe patterns of vulnerability in terms of species rarity, taxonomic affinity, species-biology characteristics, and general habitats,
4. to describe potential regional effects on phytodiversity, and
5. to attempt an initial rating of vulnerable species in terms of their potential for northward migration.

The present report is organized into eleven sections plus one appendix. After this introduction, the second section presents a brief history of climate and climate change in North America. Factors affecting plant distributions are then discussed in the third section, placing the role of climate in determining plant species' ranges in perspective in relation to geology, topography, and other critical influences. The fourth section reviews the ability of plants to persist through periods of climatic stress and to disperse and become established in novel, climatically more suitable areas. Special attention is here given to the problem of species migration into new areas appropriate both in terms of climate and other habitat factors, should global temperatures increase. The fifth section introduces the "climate envelopes" method for relating the present distribution of a species to climate parameters, and projecting possible floristic consequences of specified modifications to those parameters.

The botanical information used in the present analysis is described and its sources identified in the sixth section. The seventh section, on methods, describes the types of climate envelopes used in this analysis and the factors that were analyzed. Results of the analysis are presented in summary form in the eighth section. These results, their implications, and the limitations of data and analyses used here are discussed in section nine. The tenth section presents conclusions and recommendations, including some implications of climate change for plant species conservation. The final section provides the references cited. Specific details on the sources of the plant-distribution data are provided as an appendix.

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CLIMATES OF NORTH AMERICA: PAST, PRESENT, AND FUTURE

Climate is an integral and dynamic component of a plant's environment. Present weather patterns, while variable from season to season or year to year, exhibit certain trends over longer time scales that have significant effects on plant distributions. Over the past two million years, North America has experienced substantial variation in climate, from continental "Ice Age" glaciations to periods substantially warmer than the present. An understanding of the landscapes and climates in which the continent's plants have evolved and reached their present distributions is essential for predicting the possible effects of future climate changes on the vegetation of North America.

The North American Continent

The geographic area of the present study is North America north of Mexico, hereafter generally referred to as "North America". This region of about 21.5 million km^2 (8.3 million mi^2) includes the contiguous United States, Canada, Alaska, and Greenland:

Topographically, North America is characterized by a large, relatively low-lying central region surrounded by elongated mountain complexes to the west and east. The western mountains, such as the Rockies, Sierra Nevada, and Cascades, generally trend north-south, with the Rocky Mountains becoming east-west in Alaska. These western ranges often reach elevations over 4,200 meters (14,000 feet), and are substantially higher in Alaska and the Yukon. The Appalachians of the eastern U.S. and Canada, which reach 2,000 meters (6,500 feet), generally trend northeast-southwest, while the lower, geologically related Ozarks and Ouachitas in Arkansas, Missouri, and Oklahoma trend nearly east-west. In northeastern Canada, mountains exceeding 2,000 meters (6,500 feet) extend from coastal Labrador northwestward into the Arctic islands.

Past and Present Climates of North America

It is widely recognized that the Earth's climate has varied substantially in the past. These variations, ranging in time scales from millions of years to hundreds of years, include a general cooling trend over the past several hundred million years. Over the past two million years, a series of about twenty cycles of continental glacial and interglacial periods has been superimposed on this cooling trend. On a still shorter time scale, fluctuations in global climate of a few degrees Celsius, such as the 'Little Ice Age' a few centuries ago, have occurred as well.

Climates of the Past

E.C. Pielou, in her 1991 book *After the Ice Age,* says of the present time, "we are now living in an unusual interval in an unusual age." Her "unusual age" is the Pleistocene, which for the past two million years has been dominated by continental glaciations, unlike most earlier times in the Earth's history. The past ten thousand years, what geologists have called the Holocene or Recent, is Pielou's "unusual interval." Originally considered to be the geologic period since the end of the Pleistocene, it is now regarded merely as an interval between cycles of glaciation.

The Past 2,000,000 Years.

The predominant condition of the North American landscape over most of the past two million years has been continental glaciation, with globally cool temperatures, low sea levels, and immense continental ice sheets extending southward to about the fortieth parallel. Plant distributions were generally shifted southward (and down-slope) compared to the present, and broad, windswept treeless zones adjoined the ice. Alpine tundra was present in the southern Appalachians, and large, shallow lakes were common in the Southwest. Mountain glaciers were extensive in western North America, including Alaska.

Midglacial vegetation, during the time of maximum glaciation, is now known to have included unique species assemblages nowhere extant today. For example, the periglacial (glacial-edge) vegetation of southern New Jersey was a mosaic of forest and tundra, unlike any modem vegetation type (Watts 1979). The plant communities recognized today did not merely shift south and north collectively as units. In response to the changing environment, each species adapted and/or migrated independently to more suitable habitats.

While two million years has been ample time for evolution of new species to occur in many genera, it is believed that many (or most) of the more abundant North American plant species have persisted relatively unchanged since the previous interglacial period, if not longer (cf. Stebbins and Major 1965, Stebbins 1980, Wilson 1992).

The Past 20,000 Years.

The most recent (Wisconsinian) glaciation reached its maximum about 18,000 years ago. The glaciers have subsequently melted almost everywhere except Greenland and Antarctica. The current interglacial landscape, like those before it, is characterized by relatively warm temperatures, high sea levels due to melted glacial ice, and the northward (and up-slope) shifting of many plant species' ranges. The typical midglacial vegetation has been disrupted and replaced by novel vegetation types. Many of the Southwest's pluvial lakes have evaporated into salt flats, and most of those still extant are shallow and highly saline. Lakes and peat bogs are abundant in the regions previously glaciated. Mountain glaciers are now small or completely gone.

Global temperatures reached an interglacial maximum about 10,000 years ago (Pielou 1991). This warm period was followed by a cooling trend which has been predicted to result in another continental glaciation perhaps 10,000 years into the future. The period of maximum interglacial temperatures is now often called the Altithermal, but sometimes termed the Hypsithermal or the Xerothermic. Temperatures during this warm period were above the present-day averages and the regional precipitation patterns were different from those today.

As discussed by Pielou (1991), Ritchie (1987), and others, the timing of this thermal maximum did not occur simultaneously across the continent. During that period, for example, prairies were more abundant in Ohio, Indiana, and Illinois, and oaks and hickories dominated forests in places where beeches and maples now occur (Braun 1950).

The Past 2,000 Years.
A cooling trend, with minor fluctuations, has followed the Altithermal (Pielou 1991). These fluctuations include a centuries-long warm stage called the "Little Climatic Optimum", which reached its peak approximately 1,800 years ago, with a climate that was somewhat warmer than the present, and the "Medieval Warm Period" (which allowed colonization of Greenland) lasting from 800 to 1100 A.D. The latter warm period was followed by a cooler period termed the "Little Ice Age", which lasted from about 1350 to 1870 A.D. The Little Ice Age is an unique example of short-term climate fluctuations because it has been well documented not only in paleontological records but also in historical accounts such as records of changes in agricultural patterns in northern Europe (Bryson and Murray 1977, Pielou 1991).

The Past 200 Years.
Although the global climate also varies over relatively short time spans, these changes have occurred at magnitudes much smaller than between glacial and interglacial periods (Webb 1992). The climate over the past two hundred years has been dominated by the warming trend following the Little Ice Age. Since this warming began before widespread industrial development, it is assumed to be a natural fluctuation in the longer-term cooling leading to the next glaciation (Pielou 1991).

Present Climate Trends: Global Warming?

Of more immediate interest, on a scale of decades and centuries, is the possibility that anthropogenic influences could exaggerate the current natural warming trend. This could lead to Altithermal-like temperatures within a geologically short time. The possibility of rapid temperature increase is often referred to as "global warming"; Schneider (1989) provides a history of the phrase.

Anthropogenic Factors

Human activities, most notably the emission of carbon dioxide (CO_2) from the burning of fossil fuels, are placing new stresses on the climate system by altering the amounts of radiatively active gases in the atmosphere. Global fossil fuel emissions in 1989 and 1990 resulted in the release of 6.0 ± 0.5 billion tons of carbon per year. Another major source of CO_2 emissions is land use changes, primarily deforestation, resulting in approximately 1.6 billion tons of carbon released per year (IPCC 1992). These figures are expected to rise as population growth and industrialization of developing countries lead to an increased consumption of fossil fuel resources and continuing changes in land use patterns.

With projected increases in the emission of $CO_{2,}$ methane, nitrous oxide, chloroflorocarbons, and other greenhouse gases, the equivalent concentration of carbon dioxide in the atmosphere is expected to double early in the next century. Even if carbon emissions are stabilized at present levels, the total amount of CO_2 in the atmosphere will continue to increase for some time.

Natural Trends

The earth's climate is influenced by many natural phenomena. Glacial periods are thought to be caused by complex long-term cyclic variations in the tilt of the earth's axis and its orbit around the sun, as well as the relative distribution of continents and ocean. In addition, there are numerous natural events which are known to affect global climate, especially on time scales of a few years.

Cyclic events include periodic fluctuations in the intensity of solar radiation and the El Niño-Southern Oscillation. Solar cycles occur on a variety of time scales; the most commonly known and best understood is the eleven-year sunspot cycle. It is thought that the recent period of decreased solar radiation may have partially offset anthropogenic global warming. In the next century, anticipated increases in solar activity could result in a maximum warming of 0.8°C and may intensify the effects of predicted global warming (Damon 1992). During E1 Nino events, which occur every four to seven years, the changes in oceanic and atmospheric circulation patterns result in warming of the eastern Pacific and have widespread effects on precipitation and temperature in North and South America (cf. Glynn 1988).

Large volcanic eruptions, such as the June 1991 eruption of Mt. Pinatubo in the Philippines, release sufficient quantities of aerosols, particulates, and other compounds to alter the radiative balance of the atmosphere and certain atmospheric chemical reactions. The sulfur compounds released by volcanoes lead to slight global cooling, but the volcanic materials settle out of the atmosphere within a few years and do not have any long-term impacts on climate (Gore 1992, AGU 1992).

These natural climate variations create additional challenges in detecting the impacts of anthropogenic stresses and developing accurate global climate models. In the past decade, global mean temperatures have been higher than expected from natural trends. The time interval and magnitude of warming, however, are insufficient to distinguish anthropogenic global warming from natural climate variations. Nevertheless, the late 1980s, 1990, and 1991 were some of the warmest years recorded by climate stations (IPCC 1992). In late 1991 and early 1992, however, average global surface temperatures were slightly cooler, possibly due to the 1991 eruption of Mount Pinatubo in the Philippines (AGU 1992).

Evidence for Global Warming

Evidence for global warming–natural or otherwise–during the past few decades has come from a variety of sources. Temperature records indicate a global average temperature increase on the order of 0.5° ± 0.1°C since the end of the Little Ice Age, at a maximum rate of about 0.5°C per century (Webb 1992). While widely accepted, the accuracy of these data has sometimes been questioned due to the lower precision of early measuring instruments, the relatively short time span of these records (which have only been available since about the 1860s), data gaps, and the possible effects of urban heat islands on the temperature record (since many of the measurements were taken in formerly rural areas now heavily populated). Karl et al. (1988) provide further discussion of these concerns.

Other lines of evidence also show that global warming has clearly occurred over the past two centuries. Tree ring records covering the past 1,000 years demonstrate a high level of correlation between tree growth patterns around the world and the temperature record. Increases in tree growth rates from the past century are anomalous, exceeding any growth rates in the last thousand years (Jacobi and D'Arrigo 1992). Cores from high-elevation, low-latitude glaciers have also been used to examine the recent and long term temperature record preserved in the ice, and the rapid retreat of various glaciers is another indication of global warming (Thompson 1992). In addition, there seems to be a subsurface geothermal record of past terrestrial surface temperatures which researchers are working to interpret (Pollack and Chapman 1993).

Rates of Past and Future Climate Change

The earth has experienced many transitions between cooler and warmer climates as ice ages began and ended during the past two million years. These changes have taken place at a variety of rates. While the onset of glacial periods has tended to occur gradually, over several thousand years or more, the transitions from glacial to interglacial periods have taken place somewhat more abruptly. Evidence from deep-sea sediment cores and polar ice caps indicates that there have been numerous temperature fluctuations of smaller amplitude and frequency during both glacial and interglacial periods (Pease et al. 1989). Recent studies of Greenland ice cores have revealed several abrupt regional climate changes, including large variations in climate during the last warm interglacial period, a time when the mean temperature was about 2°C warmer than today (GRIP 1993, Dansgaard et al. 1993). While the climate changes that occurred over several thousand years at the end of the last major glacial period were rapid on a geological time scale, they hardly compare to the estimated rates of future anthropogenic climate change, in which an increase in global temperatures of perhaps 3°C could occur within 100 years (IPCC 1992).

While even moderately rapid global warming or cooling has been rare, paleontological records show evidence of rapid regional cooling or warming during the last glacial retreat, particularly in various high-latitude areas. The most widely studied of these temperature changes is the Younger Dryas oscillation to near-glacial temperatures (Walker et al. 1991) between approximately 11,000 and 10,000 years ago, which has been linked to evidence of changes in the surface and deep-ocean circulation patterns of the North Atlantic (Jansen and Veum 1990). Paleontological evidence indicates that the end of the Younger Dryas episode was a period of rapid local warming in the North Atlantic region. The rates of local climate change may have been as high as 2°C or more per century (Webb 1992). Dansgaard et al. (1989) and Lehman and Keigwin (1992) report an apparent 7°C (12°F) local warming within 50 years in south Greenland.

Possible Future Climates

Assuming the climatic cycles of the past two million years continue in their general form, the next continental glaciation should be well under way several thousand years from now. However, if anthropogenic global warming becomes substantial, the onset of this next glaciation could be delayed, and its extent reduced.

Models and Predictions of Future Climate

The increasing concentration of greenhouse gases may cause significant warming in the global average temperature by increasing the opacity of the atmosphere to outgoing radiation and trapping heat that would otherwise have dissipated into space. General circulation models (GCMs) are used to estimate the effect of increased atmospheric carbon dioxide on global climate. The GCMs endeavor to mathematically represent knowledge about the interaction between the atmosphere, oceans, ice, biota, and the land as an integrated system.

Uncertainties in Predictions.
GCM predictions of possible climate change are not exact, being limited both by our incomplete understanding of natural phenomena and the limited capabilities of even the largest and fastest computers. Among the major uncertainties in current models are the roles of clouds, and the nature of the interaction between the atmosphere and the oceans.

The GCMs are also not yet capable of consistently predicting the manifestations of climate change on regional or local levels. If ocean and atmospheric circulation patterns change, the local effects on climate may include altered amounts and timing of rainfall or snowfall, evaporation rates, and temperature ranges. These local differences in precipitation and temperature could have a significant impact on the growth and reproduction of many plants.

The IPCC Scenario.

The Intergovernmental Panel on Climate Change (IPCC) was established in 1988 by the World Meteorological Organization (WMO) and the United Nations Environment Programme (UNEP) to advise world leaders on the extent of potential global warming and its impacts. As summarized in the IPCC assessment, current modelling studies predict a possible 1.5 to 4.5°C (2.7 to 8.1°F) increase in mean global temperature in the next 50 years at an average global rate of 0.3°C (0.5°F) per decade (IPCC 1990 and 1992). The regional and local effects of climate change could vary significantly; it is unlikely that all parts of North America would experience the same degree of warming. The timing and quantity of regional precipitation would be similarly altered. General circulation models cannot yet reliably predict changes on this scale, so a uniform temperature change scenario is useful in preliminary attempts to evaluate the potential impacts of climate change. Most models suggest that an expected doubled atmospheric CO_2 is likely to cause a 3°C (5.4°F) mean increase in global temperature (WMO 1982, NRC 1983, Schneider et al. 1992); this estimate is used as the principal scenario examined in the present study.

3

CLIMATE AND PLANT DISTRIBUTIONS

On a broad scale, light, temperature, and precipitation, and their seasonal patterns, are the most important physical factors affecting distribution–the phytogeography–of individual plant species, as well as major types of vegetation. Other factors, such as topography, geology, soils, microclimate, and the nature and frequency of natural disturbances and biotic interactions are more important in determining local distributions of species and vegetation.

Several classic plant geography texts provide an introduction to the subject; among the major descriptive works pertinent to North America are those by Good (1964), Gleason and Cronquist (1964), Polunin (1960), Cain (1971), and Takhtajan (1986). Recent theoretical concepts are emphasized by such authors as MacArthur and Wilson (1967), MacArthur (1972), Harper (1977), Grime (1979), Pielou (1979), and Woodward (1987).

Major Factors in Plant Species Distributions

No plant species grows everywhere on earth; even widespread weeds have geographic limitations. It is commonly recognized that climate is a factor second only to the distribution of land, water, and daylight in determining where a plant species is physiologically capable of growing and reproducing. At any site, plant species composition and character of the vegetation are determined, in general, by the area's climate. Horticultural and agricultural experience, as well as numerous floristic and ecological studies, support this view.

Most species do not grow everywhere that they could survive. Where a species *does* grow depends on many other factors, both geographic and historic. A brief survey of the principal limitations to the distributions of plant species demonstrates the importance of factors such as geology and topography that are functions of the landscape itself and do not shift appreciably with climate changes. Other factors, such as hydrology, fire patterns, and soils, are more closely related to regional climates and are significantly affected by changes in the magnitude and patterns of temperature and precipitation.

Some range limits are better understood from the more subtle perspectives of climate history or landscape history; plant longevity, seed-banking, or clonal persistence; or chance factors in dispersal, establishment, and extirpation. Competition from other, locally more successful species is yet another constraint on most species' ranges.

Continental Patterns

Within a continent, the number of plant species and the composition of the flora differ for each region. Floristic factors often considered include total species numbers in an area as well as numbers of endemics, peripherals, and disjuncts. Endemics are those species found only in a specified area, such as a state or province. Species are referred to as peripherals in regions that are at the outermost limits of their general distributional range and only barely enter the area of interest. (The northern or southern range limits of species in specified areas are of particular interest in climate-change studies.) Disjuncts are species that occur in locations that are significantly separated from the rest of the species' range.

In North America, for example, the floras of California, Texas, Arizona, Oregon, and Florida are high in both native species numbers (Kartesz 1992) and in their proportion of endemic species. The floras of boreal regions such as Alaska are relatively species-poor, as are the floras of non-mountainous inland states such as North Dakota or Nebraska. Size alone does not determine a state's floristic richness. More important are the presence of certain ecological factors such as mountains and/or a seacoast. Some small states, such as Maryland or New Jersey, have many more native vascular plant species than the much larger Great Plains states, since coastal areas provide such diverse habitats as salt marshes, dunes, and freshwater intertidal (estuarine) shores. On the other hand, few of the states east of the Mississippi have as many native species of vascular plants as any of the Western mountain states.

Regional landscape factors such as elevation, topography, and bedrock geology further constrain species' distributions within a continent. These factors are important to the natural landscape on a local scale (cf. Radford et al. 1981). For widespread species, landscape factors determine the distribution of local populations on a fine scale. These local factors, however, may control the entire distribution of rare species that occur only within a small area.

Latitudinal Patterns.

It has long been recognized that regional species diversity tends to increase toward the equator, correlating strongly with such climatic factors as higher mean annual temperatures, increased insolation, decreased seasonality, and longer frost-free seasons (MacArthur 1972, Stevens 1989). It is commonly assumed that individual species are limited toward the pole by physical stresses, and toward the equator by biotic stresses such as competition, disease, or predation (cf. Pielou 1979). This theory is easy to support empirically but difficult to validate in any comprehensive way (Colwell and Fuentes 1975).

Although latitudinal changes in a continental flora are actually continuous, biogeographers commonly recognize two apparent discontinuities. First, the poleward limit of the "tropical" flora tends to occur, with notable exceptions, near sea level in the vicinity of the Tropic of Cancer. This latitude tends to be the limit of killing frosts, a stress to which horticultural experience has shown many (but not all) tropical species to be sensitive.

Second, the higher latitudes (and higher elevations) have a "tree line" or limit of tree growth, beyond which no tree species reach full size except under peculiar local circumstances. Useful reviews of arctic and alpine vegetation include those by Bliss (1971), Billings (1973), Bonan and Shugart (1989), Larsen (1989), Smith and Knapp (1990), and Stevens and Fox (1991). The arctic tree line is determined by the cold temperatures, the short growing season (in both light and temperature), and the low angle of direct solar radiation of this region. These climatic conditions affect plant growth by limiting water absorption, translocation, and photosynthesis. While these physiological limits vary from species to species, there are several widespread boreal conifers that have approximately the same northern limits.

Longitudinal Patterns.

East-west patterns of species distribution within a continent are correlated with temperature extremes (continentality) that tend to increase towards the interior of continents, and with regional patterns of precipitation, which in turn are often related to the presence of mountains. Near ocean shores, the climate is buffered by large expanses of seawater, resulting in milder winters and cooler summers than areas further inland. The contrasts between maritime and continental climates are important to the overall climate pattern of large continents.

Mountains.

In mountainous regions, species occur in elevation zones determined by the cooler air temperatures that characterize higher elevations (cf. Billings 1990). This cooling, called the dry adiabatic lapse rate, is caused by the decrease in atmospheric pressure with increased elevation (cf. Watts 1971, Peters 1992), and results in about 0.6°C to 1.0°C temperature change per 100m of elevation (or 3.5° to 5.9°F per 1000 feet). Some species occur only at high elevations in a given mountain range, others at mid-elevations, and others only at low elevations, with the species richness of mountaintops generally less than that of lower elevations (Stevens 1992). Few if any plant species occur from base to summit on any large mountain.

As noted earlier, high mountains have a timberline similar to that of the arctic regions, beyond which no trees can survive. Alpine tundra, above the tree line, looks superficially similar to arctic tundra but differs substantially. The thin air of high-elevation tropical mountains allows rapid night-time cooling and even freezing temperatures, but the intense year-round insolation in the montane tropical paramo contrasts strongly with the dim light, intense cold, and lengthy winter darkness of the polar tundra (cf. Smith and Young 1987). Alpine summits of temperate mountains are intermediate in these respects between those of tropical and arctic regions.

Mountain ranges in humid climates produce regional precipitation variations called "rain shadows," in which uplift of the prevailing winds causes increased precipitation on the upwind slope (the west slope in most of North America), and a "shadow" of decreased precipitation downwind. In North America, the most intense rain shadows are formed by the Sierra Nevada, the Cascades, and the Rockies. The strong effect of mountain ranges on precipitation patterns is a major factor in determining species and vegetation distribution patterns.

Bedrock Geology and Soils

Climate is one of the five major factors determining the formation and distribution of soils since temperature and precipitation are known to affect soil processes both directly and indirectly. In regions that are hot and rainy, chemical reactions occur more rapidly and soluble compounds are more swiftly leached from the upper portion of the soil. Soil development is also indirectly related to climate through its controls on vegetation, which in turn influence soil type. Global climate, vegetation, and soil maps tend to have a high degree of correlation. The factors that affect soil formation are discussed in greater depth by Gibson and Batten (1970) and Buol et al. (1973).

The bedrock geology, and the overlying soils, however, can exert a substantial influence on local floras when strongly contrasting substrates are present. For example, in Appalachia, a contact between sandstone and limestone strata can show a dramatic shift in the composition of the herbaceous flora on a scale of meters. Locally distinctive rock outcrops often support plant species otherwise unknown in their region. Kruckeberg (1969) provides an introduction to the topic, with an emphasis on limestone and serpentine.

Since most soils are climatically determined, soil characteristics could be significantly affected by changes in the magnitude and patterns of temperature and precipitation. Many soils, however, take decades, centuries, or millennia to develop. With rapid climate change, plants may face pressures to migrate before suitable soils are available. Species adapted to both a specific substrate, such as serpentine or limestone soils, and a limited climate range may encounter additional problems because the particular soil type may not exist or be too distant where the climate becomes suitable.

Limestone.
Calcareous rocks such as limestone and dolomite produce alkaline soils, which are preferred by some plants, and intolerable to others. The regional distribution of limestone (and related rocks) thus contributes substantially to the pattern of plant species' distributions. In North America, some regions have substantial areas of limestone, such as the Central Lowlands, the Edwards Plateau of Texas, and the Great Valley of the Appalachians. On the other hand, in some areas such as southern California, limestone outcrops are few, and limestone-dependent plant species such as *Erigeron parishii* (Parish's daisy) or *Astragalus albens* (Cushenbury milk-vetch) have limited ranges (USFWS 1992a).

The plant species diversity of an outcrop of limestone (or any other kind of bedrock) is increased considerably by local topographic relief. For example, the floras of north-facing and south-facing limestone cliffs in the Appalachians differ dramatically (Morse 1983*a*, Riefner and Hill 1984). Unusual bedrock at high elevations can be very significant floristically. The alpine limestone areas in the Steens Mountains of southeastern Oregon, for example, support many disjuncts and several endemic species (Peck 1961, Meinke 1983). The Guadelupe Mountains of western Texas and adjacent New Mexico are another floristically important range of limestone mountains (NMNPPAC 1984).

Serpentine.

There are several soil and rock types upon which relatively few plant species can grow. These substrates are particularly important to plant distributions, and hence to rare plant conservation. Serpentine is by far the most important of these. Most species do not tolerate the heavy metals and unusual ion ratios of serpentine and related rocks, while numerous serpentine-tolerant but poorly competitive species are unable to succeed in the surrounding vegetation. They are confined to these outcrops where competition from invading species is reduced (cf. Grime 1979). The peculiar floras and high endemism on serpentine are reviewed by Kruckeberg (1969) and Brooks (1987). Kruckeberg (1984) provides further information for California serpentines, and Reed (1986) and Dann (1988) for serpentines in eastern North America. The dozens of endemics and the many disjuncts found on serpentine make a substantial contribution to the overall species richness of the areas in which these peculiar rocks occur.

Sand Deposits.

Dune systems, and other deposits of deep sand, also contribute substantially to unique plant species' distributions. In North America, drifting dunes are characteristic of the Atlantic and Gulf coasts, and are also present along the Pacific Coast and the Great Lakes, as well as some desert areas. Areas of "pine barrens" or "sandhills" occur irregularly throughout the Atlantic Coastal Plain. Similar habitats are found in much of the glaciated and periglacial portion of the continent, and occasionally elsewhere.

Many rare plant species are confined to these sandy places, for example in the New Jersey Pine Barrens (Forman 1979), the Carolina Sandhills (Barry 1980, Christensen 1988), or the Lake Wales Ridge of south-central Florida (Myers 1990). Eroding sandstone ledges also provide similar loose-sand habitats on a more localized basis (Core 1966, Morse 1979, Harmon 1981), often with disjunct occurrences of such characteristic deep-sand species as *Hudsonia* (sand heather). *Swallenia alexandrae* (Eureka Dunes grass) of the Mojave Desert (cf. Munz and Keck 1968) is one of the many examples of desert species that occur only on drifting sand.

Microclimates

Factors such as ground-level air temperatures, relative humidity, dew concentrations, exposure to winds, persistence of snow, length of frost-free growing season, and duration and intensity of sunlight vary considerably in any but the most monotonous landscape. The local *microclimate* variations in almost any small area due to these factors are often greater than the differences in regional climate of places hundreds of kilometers apart, as shown, for example, in the detailed microclimates study by Wolfe et al. (1949) of a small valley in south-central Ohio. Since individual plants experience these local conditions, and not merely the regional climate, microclimates have considerable influence on local plant distributions, and hence on species' overall ranges.

Microclimates and Local Topography.

On a small scale, topographic features such as slope aspect commonly contribute to the maintenance of microclimates that may be warmer (and drier) or cooler (and moister) than the regional climate in which they occur. In the Northern Hemisphere, south-facing slopes tend to be warmer and drier than those that face north. Cool-dry microclimates also regularly occur, for example on windswept mountain saddles. Warm-wet microclimates are rarer, but can occur, for example, near large water bodies.

The contrast in species composition on nearby north-facing and south-facing slopes in temperate or boreal areas is often dramatic. In the mid-Appalachians, for example, the sparsely vegetated "shale barrens" (Platt 1951, Keener 1983, Morse 1983b) are found on steep south-facing slopes of shale talus. Adjacent north-facing slopes on the same bedrock are cooler and more humid, supporting rich forests. Platt (1951) reports that the shale barrens can have midsummer surface temperatures of 63°C (145°F), among the warmest recorded anywhere worldwide (cf. Brock 1970). Characteristic rare or endemic species of the Appalachian shale barrens include *Trifolium virginicum* (Kate's Mountain clover), *Oenothera argillicola* (shale-barren evening primrose), and *Clematis albicoma* (white-haired leather-flower).

The cool, wet cliffs near waterfalls or in steep, shaded gorges can also provide habitats for localized endemic or disjunct species otherwise absent from the local flora. Two of the many examples of this phenomenon are the regional endemics *SuIlivantia oregana* in sheltered habitats in the Columbia River Gorge (Meinke 1983) and the fern *Vittaria appalachiana* (the Appalachian gametophyte) in the southern Appalachians (Farrar and Mickel 1991).

Relation of Microclimates to Regional Climate Change.

Some microclimates, such as those associated with hot springs or permafrost, are caused by phenomena nearly independent of the current regional climate, and are resilient to climate change. For example, cold-air (algific) talus slopes in Iowa (Frest 1984) and West Virginia (Hayden 1843, Core 1968) produce moist chilled air (ca. 4°C or 39°F) throughout the summer, due to persisting underground ice deposits of unknown but apparently late-glacial age. These microclimatic conditions maintain disjunct populations of otherwise boreal or high-elevation species presumably relict from late-Wisconsinian times.

Other microclimates, such as those of south-facing or north-facing slopes, provide local variations on the regional climate. In temperature at least, these microclimates would change in the same direction as any change in the regional climate, but not necessarily by the same amounts. The data used in the present study are not precise enough to analyze any of these smaller-scale patterns, although these patterns are clearly important for fine-scale assessments of vulnerability to climate change and potential management alternatives for locally vulnerable species.

The extent to which cool microclimates would be affected by climate change is unclear. Numerous ensembles of disjunct populations of otherwise more boreal species exist on north-facing cliffs or in steep gorges. This suggests that they have persisted there since late-glacial time, and survived the Altithermal in place, since the likelihood of post-Altithermal establishment of such multi-species assemblages is remote.

If areas with relatively cool microclimates were to warm significantly, then species endemic to these areas may be particularly vulnerable to climate change. There may be no adjacent habitat to which they can readily move as the regional climate becomes warmer. For example, *Erythronium propullans* (Minnesota trout lily) is found only on cool north-facing slopes in southern Minnesota (Coffin and Pfannmuller 1988). Long-distance dispersal would be required for this species to move to another area of similar microclimate. As another example, the cool ravine slopes along the Apalachicola River in Florida, where *Torreya taxifolia* (Florida torreya), *Taxus floridana* (Florida yew), and other endemics occur (cf. Stalter and Dial 1984), would presumably get warmer if the regional climate warmed, but they might not experience as much warming as the adjacent uplands.

Interactions of Climate and Landscape

Since the landscape is a product of its underlying geology and its climate history (cf. Garner 1974), it is often difficult to separate climate from substrate and topography as factors influencing plant species' distributions. For example, many widespread soil types are more indicative of climate history than substrates. Several landscape processes are strongly influenced by the local or regional climate. Hydrology is affected not only by precipitation amounts and patterns but also by evaporation rates, which depend on temperature and relative humidity. The frequency and intensity of fire is similarly affected by a complex interaction of climate and vegetation.

Hydrology.
The geographic and seasonal distribution of surface and near-surface water controls the distribution of the substantial portion of the flora that depends on aquatic or wetland habitats. Lakes, ponds, swamps, marshes, and floodplains require a consistent presence of water from one source or another, and have distinctive species assemblages. Carpenter et al. (1992) review possible effects of climate change on freshwater hydrological systems.

Many rare plant species are associated with vernal pools and other intermittent wetlands, formed by seasonally rising and falling water tables. The vernal pools of California are well known for their distinctive floras (Barbour and Major 1988), as are the vernal ponds of New Jersey (cf. Cavileer and Gallegos 1982). Water-table fluctuations in New England and southern Nova Scotia produce comparable pond-shore zones with distinctive floras (Keddy and Wisheu 1989).

Fire.

Natural fire is a significant factor in many vegetation types, such as prairies, chaparral, pine barrens, and heathland, as well as many forest habitats. Gleason and Cronquist (1964), among others, provide an overview of such fire-dependent communities. Plants in these ecosystems have developed several strategies to survive fire, including regrowth from underground parts or seed-banking. Some large trees, such as *Sequoiadendron giganteum* (giant sequoia), are protected by a thick, fire-resistant bark. The seeds of some species require fire to break dormancy, and some conifers, such as *Pinus anneuata* (knobcone pine) and dwarf forms of *Pinus rigida* (pitch pine), require fire for the cones to open and disperse seeds. Many rare plant species are tolerant of fire, but are overtopped and crowded out by other, fire-intolerant species if the intervals between fires are too long or natural fire cycles are altered (cf. Forman and Boerner 1981).

Fires occur mainly in vegetation with a high dead-to-live biomass ratio, most frequently in areas with seasonal or periodic droughts and occasional strong winds. Some vegetation types appear to promote fire by maintaining a high density of dead biomass, often coupled with flammable oils or resins in the dominant plant species. While fire-dependent vegetation is widespread in North America, it is rare in desert regions, due to the sparseness of vegetation, and uncommon in humid areas except on unusual substrates (such as deep sand). Climate changes affecting regional temperatures, precipitation patterns, or soil moisture could have substantial effects on the frequency and intensity of natural fires, and hence on the suitability of an area for fire-dependent but competition-intolerant species. Effects on the distribution of plant species and vegetation type due to changes in fire frequency could be far greater than those due to the direct effects of the climate change on the plants.

Variation in Climate Tolerance Within Species

As horticultural experience shows (cf. White 1926), many species of plants can tolerate a broader climate range than is represented by their present geographic distributions. While the species is the fundamental unit of taxonomy, species are often made up of infraspecific taxa such as varieties and subspecies. In other cases, substantial clinal variation within a species is known, but it does not fall into distinct infraspecific taxa. Recognizable ecotypes occur in many species, and forms and other single-gene expressions are also widely known. Considerable genetic variation for tolerance to heat and moisture stress may occur between populations or among individuals in a given population.

Techniques such as the present "climate-envelope" analysis treat species as typological entities, with the assumption that each individual population of a species has the full climate tolerance shown collectively by the species throughout its geographical range. While useful as a first approximation, this assumption presumably leads to the categorization of many species as apparently secure, due to a broad geographic range, when none of their local populations would be able to adapt readily to substantial climate change. The assumption is particularly questionable in cases in which a widespread species is composed of several much more restricted subspecies, as in *Trillium pusillum* (dwarf trillium) (cf. Roe 1978), or of substantially differentiated ecotypes regardless of taxonomic classification, as in *Pinus ponderosa* (ponderosa pine) (cf. Millar and Libby 1991). For these and many other species, there also may be within-species genetic variation for climate tolerance that makes these estimates of climate envelopes too large.

As another example, *Ptilimnium nodosum* (harperella) is a rare semi-aquatic plant known from 14 sites from the mountains of West Virginia and Maryland to the coastal plain of Georgia (Maddox and Bartgis 1991). Thus, it has a wide climate envelope, if considered a single species, despite its rarity. However, early accounts of these plants divided them into three geographically separate species, one each from Maryland and West Virginia, from South Carolina and Georgia, and from Alabama. Kartesz (1993), however, includes all these populations in a single, more widespread species, without any infraspecific taxa. Recent study of allozyme variation in the *Ptilimnium nodosum* complex shows that there are significant electrophoretic differences among the three groups, which perhaps warrant the subspecies designation (Kress et al. in press). These three population groups presumably have different climate tolerances, and would each be more vulnerable to climate change than suggested by the large geographic range of the collective species.

Kartesz (1993) recognizes thousands of varieties and subspecies among the native U.S. and Canadian plant species. The infraspecific taxa of a particular species generally occur in distinct or moderately overlapping portions of the species' entire range. Therefore, subspecies and varieties generally have narrower climate envelopes, and would likely be more vulnerable to a smaller amount of climate change individually than the corresponding full species would appear to tolerate. Examining species collectively, with their infraspecific taxa combined into a single unit, allows for a broader, more conservative, interpretation of the data, with focus on vulnerability of entire species rather than infraspecific units within them.

4

DISPERSAL AND PERSISTENCE OF PLANT SPECIES

The ability of various plant species to adjust to a changing climate depends significantly on their dispersal and persistence capabilities. The species most likely to survive projected rapid temperature changes will be those that are able to migrate to areas where the climate is becoming more appropriate to their requirements, and/or to continue growing in areas where the climate is becoming less appropriate.

The time requirements for both dispersal and persistence vary considerably from one species to another, preventing whole communities from moving as units in response to regional climate changes. Species persistence as climate changes may be limited more by occasional extremes of temperature and changes in the frequency and severity of local disturbances (such as drought, storms; and fires) than by small shifts in the average climate. On the other hand, stress-tolerant species may benefit from extreme climates if competitors are locally depleted or eliminated.

Unusually rapid climate change, on local, regional, or global scales, would thus have differing effects on species, depending on either their susceptibility to stress or their mobility. Furthermore, fragmentation of the natural landscape brought about by European colonization and development may substantially restrict the ability of many plant species to migrate in response to future climate change.

Dispersal Potential of Species

Plants, unlike many animals, are greatly limited in their abilities to migrate quickly to new areas in response to changing conditions. Plant dispersal depends largely upon outside forces such as wind, water, and animals; seeds otherwise tend to fall to the ground immediately beneath the parental plant. Ridley (1930) and van der Pijl (1972) provide the classic reviews of plant dispersal. Carlquist (1974) and Tryon (1971) provide further observations on long-distance dispersal to islands.

Even if a species is vulnerable to extirpation in its present range, it may survive (or even increase) during climate change if it can disperse rapidly enough to novel areas of more suitable climate and establish, compete, and persist there. To quantify the likelihood of dispersal, species can be categorized by their apparent dispersal abilities as indicated by various characteristics of their life-history strategies, such as breeding system and dispersal mechanism.

Incremental Local Dispersal

Even for highly dispersible species, most seeds land within short distances, perhaps tens of meters, of the parental plant. A smaller proportion of a plant's seeds travel somewhat further, perhaps some hundreds of meters. Incremental expansion of a species' range occurs as successive generations each disperse a short distance. A population can thus become more abundant in a local area, and, over centuries and millennia, move moderate distances as long as the habitat is sufficiently continuous. Plants with longer generation times tend to have slower rates of range expansion. Even habitat-generalist species, however, may confront virtually uncrossable barriers to incremental range expansion, such as high mountains, wide rivers, deserts, or the absence of critical but unusual substrates. Landscape fragmentation due to human activities creates additional barriers to local dispersal.

Long-Distance Dispersal

Of far more biogeographic interest is the distance that one spore or seed in a billion may travel. Once caught in a storm wind, eaten by a bird, stuck in an animal's fur or feathers, or washed downstream in a flood, a seed can potentially travel hundreds of kilometers. Such *long-distance dispersal,* while vanishingly rare in any individual case, becomes a near-certainty for common, abundantly fruiting species, viewed over centuries (Ridley 1930, Love 1963, Carlquist 1966 and 1974).

Birds and the wind are the major agents of long-distance dispersal. In North America, the migratory patterns of birds tend to follow north-south paths, while they may fly locally in any direction. In addition, individuals of some bird species regularly (e.g. daily) travel over distances of many kilometers and so may serve as an intermediate distance dispersal agent for some plants. Prevailing winds from west to east in temperate zones facilitate the spread of wind-dispersed species in that direction. East-to-west winds are common in the high Arctic and in tropical regions, including southern Florida. Spores and small seeds lifted into the upper air currents by tornadoes or other violent storms can travel for thousands of kilometers. Hurricanes, prevalent in the Southeast, disperse small seeds hundreds of kilometers in all directions, and can move any fruit shorter distances.

The ability of species to disperse occasionally over relatively long distances greatly facilitates rapid range expansion. This process permits establishment of new centers of dispersal which are disjunct from the species' original range. For species of insular habitats or fragmented landscapes, long-distance dispersal is essential since such species cannot expand incrementally from one site to another.

The establishment of species after arriving in a new place is as important as their ability to travel to new locations. The probability of successful long distance colonization involves both the probability of propagules reaching a distant place and the likelihood of the plant becoming established there once its propagules arrive.

Historic Rates of Species Dispersal

Long-distance dispersal is rarely observed directly. It is more productive to examine the historical and paleontological record for evidence on rates and patterns of species dispersal, both under relatively constant conditions and during periods of climate change. The many detailed studies of post-glacial floras in North America offer numerous examples of rates of species dispersal in continental landscapes during changing climates. Ruddiman and Wright (1987) provide a thorough introduction to this extensive literature.

During the warming that began about 15,000 years ago near the end of last glacial period, various tree species responded to the change in climate by migrating north at a rate of 10 to 45 km per century, depending on the species and local conditions. In the fossil record, the range of American beech trees *(Fagus)*, for example, expanded by - approximately 20 km per century (Davis 1981). One of the maximum recorded rates of tree migration took place approximately 9,000 years ago in northwest Canada, when the range for spruce *(Picea)* was expanding northward at about 200 km per century (Ritchie 1987).

Gear and Huntley (1991) describe the rapid regional climate changes between 4,400 and 3,800 years ago in Scotland, caused by changes in large-scale atmospheric circulation patterns. These climate fluctuations resulted in a northward range expansion of *Pinus sylvestris* (Scotch pine) of about 80 km with an estimated rate of range boundary movement of 375 to 800 meters per year for this wind-dispersed conifer. This rate is thought to represent the maximum possible for the species.

Limited Dispersibility of Rare Species

Many rare species have limited chances of dispersing over large distances. For plants with a given size and type of fruit, rare species are less likely than comparable widespread ones to disperse into a particular remote site, since rare species typically have fewer source plants within any given dispersal distance than do more abundant species. More common species that have low seed production are also relatively limited in dispersibility.

Many rare species also have reduced dispersal capabilities. Loss of dispersibility is well documented for island endemics (Carlquist 1974), and is also expected to occur in species of habitat islands within a continent. Ferren and Schuyler (1980), for example, note the loss of dispersibility in several species of freshwater-intertidal (estuarine) plants, such as *Bidens bidentoides* (Maryland bur-marigold). Another example, *Hudsonia montana* (mountain sand-heather), found only on a few tiny bedrock outcrops in the

North Carolina mountains, lacks the mechanisms for animal or wind dispersal found in the other two species of *Hudsonia* (Morse 1979).

Dispersibility can also be restricted if a species' dispersal agent is lost. For example, a number of plant species of the Chihuahuan Desert appear to have depended on now-extinct large mammals for their dispersal (Janzen 1986).

Predicting Species' Dispersibility

Chance events figure prominently in determining which seeds actually reach a location and become established as new occurrences of a species (cf. Gleason 1926). Accordingly, predictions based on a species' characteristic dispersal mode and distance are merely indicators of its capabilities. Since surviving climate change may depend upon a species' ability to migrate to areas with a more favorable temperature, it is important to predict which species have a greater *chance* of successful migration.

The overall capability of a species to disperse and establish in new localities is of interest to many biologists, including weed scientists and biogeographers. Baker (1974) provides a general review, and Leston (1957) and Tryon (1971) consider the topic with regard to relative ability of various kinds of species to reach oceanic islands. Peters (1992) addresses the dispersal and colonization ability of plants during a shifting climate.

Species with high potential to spread tend to be abundant, prolifically fruiting, and capable of substantial long distance dispersal by birds, wind, or other means. Hermaphroditic self-compatibility or apomixis increases a species' ability to colonize, since only one propagule need arrive to start a new population. Pollination by wind, by generalist insects, or by self-pollination also increases potential expansion, since specific pollinators are not necessary at a new location. Longevity, especially in woody plants, detracts from range expansion potential by lengthening the generation time.

Since parasitic or hemiparasitic species depend upon the presence of another species, they are likely to have more difficulty in dispersing than do autotrophs. For many species, the mature plant is autotrophic, but the seedlings require associates (cf. Harper et al. 1970). Orchids, for example, produce large quantities of minuscule seeds per fruiting individual. These wind-dispersed seeds lack food reserves, and require the presence of an appropriate mycorrhizal fungus in order to germinate (Luer 1975). Most orchid species depend on parasitic or symbiotic relationships with mycorrhizal fungi for the early survival of their seedlings, a particularly significant consideration in orchid conservation (cf. von Oettingen 1992).

Successful migration for both short- and long-distance dispersers also depends upon the availability of suitable habitat for an arriving seed, as well as lack of significant competitors or threats at the site of germination (cf. Stebbins 1971, Bazzaz 1979). Unlike animals, seeds cannot select optimal places to settle and grow. Therefore, the chance of an arriving seed landing in suitable habitat may be quite low, particularly for patchily distributed habitats controlled by topography, hydrology, or geologic substrate.

For obligate outcrossers, establishment of breeding populations requires the arrival and establishment of a nearby second individual within the lifespan of the first plant that arrives in an area. Otherwise, the isolated individual might persist, and perhaps spread clonally, but would be incapable of producing seed or spores within the newly colonized site for further dispersal. Many outcrossing species are further limited by the need for a specific pollinator.

Persistence of Species

The capability of plant populations to persist during unfavorable conditions is one of the fundamental questions of phytogeography, a view well expressed by Fernald (1926). Persistence is of critical importance to the study of the potential effects of possible rapid climate change on plant species' distributions for two reasons. First, some but not all species may be able to survive within their present habitats in spite of significant climate change. Second, the ability of different species to tolerate changing and increasingly unfavorable conditions will determine the degree of "ecological inertia" in the regional flora.

Means of Species Persistence

The generalized life cycle of a typical plant (cf. Harper 1977, Whitson and Massey 1981) offers several means for persistence on scales of decades and centuries. Most trees can live many hundreds of years, and many tree species respond to trunk damage by resprouting from their roots. Clone-forming perennials can often maintain themselves by local vegetative propagation almost indefinitely, thus not requiring sexual reproduction and seedling establishment. Many kinds of seeds are now known to remain viable in soil seed banks after dormancies of decades. These various strategies allow plant genotypes to maintain themselves at a site through periods when the usual processes of reproduction, dispersal, and establishment cannot occur.

Individual trees of such species as *Sequoiadendron giganteum* (giant sequoia) and *Pinus longaeva* (Great Basin bristlecone pine) are known to live up to several thousand years, suggesting they may have germinated under climate conditions substantially different from the present. Isolated stands of certain self-incompatible clone-forming shrubs appear to have spread vegetatively over thousands of years, tolerating climate change but not reproducing, as in *Gaylussacia brachycera* (box huckleberry) (Coville 1919, Wherry 1972). Large clonal stands of the tree *Populus tremuloides* (quaking aspen) may be similarly old (Cheliak and Dancik 1982). Braun (1961) considers individual stands of another clone-forming shrub, *Paxistima canbyi* (Canby's mountain-lover), to be Tertiary (pre-Pleistocene) relicts in southern Ohio. No sites for either the *Gaylussacia* or the

Paxistima are known anywhere north of the Wisconsinian glacial boundary, although both occur not far south of that line.

Vegetative fragmentation is another mechanism that can maintain a genotype in a local area, and occasionally spread it more distantly. This process is particularly common among pteridophytes, as well as many aquatic species. Establishment of a rooted fragment, however, requires conditions similar to those necessary for seedling establishment. Vegetative fragmentation, therefore, would not contribute as significantly as clonal expansion to persistence of a plant occurrence through climatic bottlenecks. On the other hand, fragmentation can help plants increase their numbers rapidly during favorable conditions, ultimately increasing their chances for survival when conditions are poor.

Asexual spore or seed production (agamospermy, apomixis, etc.) and self-compatibility can help isolated individuals increase in numbers under adverse or varying conditions by providing means for replicating and dispersing locally successful genotypes (cf. Loveless and Hamrick 1984, Asker and Jerling 1992). Many facultatively apomictic species appear to alter their reproductive strategy in response to environmental stimuli. The ability of a species to reproduce both sexually and asexually would seem to contribute significantly to its persistence through climatic bottlenecks.

Adaptation, Evolution, and Speciation

Brock (1970) notes that species of warm climates usually have temperature optima similar to their environmental temperatures, while species of cold climates tolerate cold well, but grow better in warmer temperatures. Over periods of gradual climate change lasting hundreds to thousands of years, genetic adaptation (evolution) may occur within populations of a species, populations may diverge evolutionarily from the others, and new species may appear.

Speciation in plants occurs through two principal means (cf. Levin 1971, Barton and Chattlesworth 1984, Wilson 1992). Gradual divergence of disjunct populations is generally assumed to take many millennia unless the populations are so small that genetic drift is significant. The observation that endemism is low in glaciated and periglacial areas (cf. Argus and Pryer 1990) adds strength to the view that speciation generally occurs over intervals longer than 10,000 years. Exceptionally rapid speciation is documented primarily in facultatively apomictic groups such as *Rubus* (blackberries and other brambles), in which many North American species appear to have developed since European settlement of the Midwest (cf. Braun 1961). On the other hand, judging from comparisons with fossils, some species appear unchanged since pre-Pleistocene times, for example *Sequoia sempervirens* (coast redwood) and *Cupressus macrocarpa* (Monterey cypress) in California (Stebbins and Major 1965), as well as *Torreya floridana* (Florida torreya) and other species discussed by Takhtajan (1986).

Polyploidy and other sudden but rare events occasionally initiate new species within a single plant generation. For example, genetic evidence shows that recent polyploidy produced two glacial-region endemics, *Betula murrayarna* (Murray's birch) in Michigan (Barnes and Dancik 1985) and *Adiantum viridimontanum* (Vermont maidenhair fern) in New England (Paris 1991). Although reproductively isolated from their parental populations, such species initially share most of the characteristics, including climate tolerances, of the plants from which they are derived, as shown by Gottlieb (1979) for Oregon's recently evolved *Stephanomeria malheurensis.* On the other hand, older hybrid-derived polyploid species have ranges and habitats different from their presumed parental species, as in *Vaccinium angustifolium* (a lowbush blueberry) (Vander Kloet 1988) or *Gymnocarpium dryopteris* (boreal oak fern) (Pryer and Haufler 1993).

In general, for the anthropogenic climate change anticipated from the expected doubling of atmospheric CO_2 in the next 50 to 100 years, adaptation and speciation are not likely to occur fast enough to alter the general trends and patterns of plants' responses to global warming (Peters 1992). In particular, species with long generation times, such as trees, would not be able accomplish evolutionary adaptation (Davis and Zabinski 1992). This conservatism of thermal tolerance adaptations in plants is indeed the fundamental assumption that allows paleoecologists to infer past climates from fossil pollen and other records.

Many species that currently have narrow distributions may actually be adapted to much broader climate tolerances. A species that once inhabited a sizable range with a large climate envelope may now have a significantly reduced distribution, but still retain its previous climate adaptations. Substrate-limited species such as those of serpentine soils or the shale barrens and sandstone ledges of the Appalachians are restricted by their habitat requirements to small ranges (past and present) and presumably persisted in place during episodes of climate change, thereby becoming adapted to a changing climate.

Localized endemics or refugial disjuncts presumably have also persisted in place for the past 10,000 years or more, from cold late-glacial times to the present climate. Since most evolution-rate studies suggest that some of these species could be older than 20,000 years, local populations presumably survived not only the glacial maximum but also the Altithermal, with climates substantially warmer than the present. For example, Bartgis (1991) suggests that some, but not all, of the hundreds of Appalachian shale barrens served as midglacial refugia for the various shale-barren endemics, which are not known from regions further south. To have remained at particular sites over this time, these populations must either have very broad climate tolerances or else have adapted and re-adapted as the temperature and precipitation changed substantially. In either case, such populations may be pre-adapted to future climate changes of similar magnitude.

Similar considerations regarding climate-change tolerance may apply to some disjunct occurrences of species common elsewhere. For example, *Thuja occidentalis* (northern white cedar) occurs in two quite different habitats in Appalachia. The stands on cool, shaded north-facing limestone cliffs are presumably glacial relicts persisting in a suitable microclimate (cf. Morse 1983a). However, a few *Thuja* stands in West Virginia occur instead on warm, sunny south-facing limestone outcrops in a peculiar savanna-like vegetation unknown elsewhere (Bartgis 1993). If these populations are descendants of the midglacial (or earlier) vegetation, they have tremendous tolerance to local climate change.

Ecological Inertia

Vegetation types, and individual plant species, do not instantly respond to a changing climate. Instead, there is considerable "ecological inertia" (Davis 1984, Pielou 1991) as populations slowly decline but still persist in areas that have become less appropriate for them. If climate change is accompanied by an increased frequency of catastrophic events such as drought, fires, or hurricanes, the vegetation could undergo rapid alterations.

Dynamic Nature of the Current Flora.
While there is general consensus that a time lag exists between changes in the climate and the vegetation's response due to slow dispersal rates, persistence of and competition with the existing plants, there are various theories about the extent to which the current flora is in equilibrium with the climate. Davis (1984) concludes that plant communities are "in disequilibrium, continually adjusting to climate and continually lagging behind and failing to achieve equilibrium before the onset of a new climatic trend." Braun (1950) and Pielou (1991) similarly conclude that vegetation is slow to respond to climate change and has an astonishing ability to persist in unfavorable habitats, and Ritchie (1987) and Payette et al. (1989) also express similar conclusions. However, an opposing perspective was suggested by Wright (1984), who considers the current vegetation and climate to be in harmony, with past associations composed of mismatched mixtures of species.

An intermediate position is developed by Webb and Bartlein (1992). Called dynamic equilibrium, this theory addresses the importance of rates and time scales for both climate change and vegetation response. The degree to which the flora is in equilibrium or disequilibrium depends primarily on a comparison between the rate of climate change and the time lag of plants' response. As long as the vegetation response lag is less than the rate of climate change, the system is in a state of dynamic equilibrium. However, the rate of climate change in the next century may be much faster than the rate at which plants can respond by migrating or adapting, resulting in ecological disequilibrium.

The time necessary for the development and maturation of suitable soils can affect a species' invasion of climatically suitable areas. In southern Ohio, for example, many species such as *Aesculus octandra* (yellow buckeye) can be found on mature soils a few kilometers south of the historic extent of Wisconsinian glaciers, but not on the young soils of nearby glaciated portions of the same bedrock formations (Braun 1961).

Evidence for different speeds of colonization has come from discrepancies between paleoecological insect and pollen records (cf. Walker et al. 1991). While insects may migrate rapidly, trees and shrubs may take hundreds of years to become established after a climate shift. On the other hand, these woody plants may persist for centuries after further changes in the climate, while some insects may decline immediately with adverse climate change.

Many species appear to be still adjusting to the climate changes since the last glacial maximum. Several tree species that had relatively small native ranges in North America at the time of European settlement were readily cultivated in a much larger area. These species soon escaped and naturalized, suggesting that they had not yet dispersed to these areas before pioneer settlement. In western Ohio, *Catalpa speciosa* (northern catalpa), *Maclura pomifera* (Osage orange), and *Robinia pseudoacacia* (black locust) were planted by early settlers, as Werthner's (1935) accounts show, and are now thoroughly naturalized there (cf. Braun 1961), yet these conspicuous trees were absent in the pre-settlement vegetation.

Refugia

Sites with unusually sheltered or exposed habitats, and corresponding cooler or warmer microclimates, may serve as *refugia,* the "places from the past" (Morse 1982) in which species once locally more common can still persist. These refugia are places where the microclimates are significantly different from the regional climate. Some refugia depend additionally upon differences in hydrology or soil type.

Any topographically diverse landscape abounds with minor refugia. Floristically notable refugia occur when regionally rare conditions preserve a large number of disjunct or relict endemic species. Among the most significant small refugia in eastern North America is the ravine system along the east bank of the Appalachicola River in the Florida Panhandle and adjacent Georgia. Best known for its now fungus-blighted stands of *Torreya taxifolia* (Florida torreya), dozens of other species there are either endemic or significantly disjunct (cf. Stalter and Dial 1984, Clewell 1985).

In times of a warming climate, cool mountain summits can become significant refugia. The high mountains of the Southern Appalachians, for example, have long been recognized as a major center of endemism and disjuncts, providing a relatively cool, moist climate in a region of moderate latitude and generally warmer climate (Brooks 1965). Many mountaintops in the Great Basin are also important refugia (cf. Wharton et al. 1990).

When the climate cools, refugia can form in places that remain warm and dry compared to the regional landscape. During the past ice age, coastal areas and high mountains that were never covered by glaciers were the two main types of refugia for many species of both plants and animals (Pielou 1991). The thin, well-drained soils atop cliffs or bluffs are an important refugium of prairie species in, for example, southern Ohio (cf. Braun 1969). Similarly, sheltered valleys on Alaska's North Slope protect relict stands of trees that were able to cross the Brooks Range during the Altithermal (Hultén 1968).

During episodes of climate fluctuations, both warm and cold microclimatic refugia become floristically important in complex landscapes. For example, Braun (1969) describes sites in southwestern Ohio having Altithermal prairie relicts on blufftops over gorges supporting stands of late-glacial relicts such as *Thuja occidentalis* (northern white cedar).

Concerns for Possible Floristic Effects of Climate Change

As noted earlier, a 3°C (5.4°F) mean increase in global temperature within the next century is suggested as a likely outcome under a scenario of an equivalent doubling of atmospheric carbon dioxide due to human activities (IPCC 1992, Schneider et al. 1992). The rate of climate change in the next several hundred years may therefore be five times greater (or more) than the maximum rate of global climate change in the past 18,000 years, including the period of most rapid deglaciation from 13,000 to 9,000 years ago (Overpeck et al. 1991).

The strong association between plant species distributions and climate suggests that an altered global climate could have profound effects on biodiversity. Large-scale climatic changes potentially could cause a major reorganization of species within present biomes, changes in habitats and plant distributions, extirpations of many plant populations and, perhaps, significant species extinctions. Further discussion of these concerns is provided by many recent authors, including Peters and Darling (1985), Bolin et al. (1986), Houghton and Woodwell (1989), Maddox and Morse (1990), Neilson and King (1991), Gore (1992), Stoltzenberg (1992), and Wilson (1992). -The recent book *Global Warming and Biological Diversity* (Peters and Lovejoy 1992) provides a current review of the subject.

Rapid Range Shifts Required

Various authors have suggested that such an amount of rapid climate change would require northward shifts of plant ranges of up to 500 km within the next century, a period that exceeds the potential rates of many plant species' migratory ability (Davis 1984, Davis and Zabinski 1992). For example, Davis and Zabinski (1992) estimate that the habitat suitable for *Fagus* (beech) may shift northwards 700 to 900 km, but these nut-producing trees would have to migrate 40 times faster than they did in the past to keep up with anticipated rates of climate change. Rates of migration for various taxa, as calculated from the fossil pollen record, are presented by Shugart et al. (1986). The migration rates for these trees range from about 0.05 to 1.5 km per year (5 to 150 km per century).

Thus, the amount of change in eastern North American vegetation in the next several hundred years might be greater than the total amount of change that occurred in the past 10,000 years. Even the relatively rapid migration rates recorded for pine trees in Scotland about 4,000 years ago (Gear and Huntley 1991) would not be adequate to respond to anthropogenic climate change that may occur at rates more than five times faster than any changes since the last glacial maximum.

The correlation of seasonal patterns and daylengths with increasing latitude may place further constraints on the ability of many species to successfully respond to a rapidly changing climate. Both daylength and temperature are used by plants as phenological signals; daylength is determined primarily by latitude, while temperatures depend on the regional climate. Many plant populations have localized phenological adaptations, and do not reproduce as effectively under significantly different conditions. If the regional climate changes, species dependent primarily on daylength as a phenological signal would need to adapt to the new climate to remain in the same latitudinally determined daylength conditions, or adapt to other daylength conditions if they disperse northwards (cf. Daubenmire 1978). On the other hand, species dependent on temperature as a phenological signal would need to adapt with climate change, or disperse to novel areas with more suitable temperatures.

Landscape Limitations to Species Migration

Natural landscape barriers and discontinuities place significant limits on migration of species affected by climate change, even without the substantial human-caused disruption of intervening habitats. For example, the many species found in Gulf Coast savannas on deep sand could not become established on Piedmont bedrock to the north. Differences between east-west mountains (such as the Ozarks/Ouachitas, Uintas, and the Brooks Range) and north-trending ones (Appalachians, Rockies, and Sierra/Cascades) may have comparable effects. Great Lakes rarities found mainly on sandy shores of lakes Michigan and Huron could be limited by the scarcity of sandy habitats on the rocky shores of Lake Superior to the north. Species of the limestone formations of the Edwards Plateau of Texas, especially those confined to canyon environments, are another group without sufficiently similar habitats directly northward for even the more readily dispersible species. Habitat limitations such as these would prevent species from expanding their ranges northwards, regardless of human activities.

The orientation and location of mountain ranges in Eurasia and North America played a significant role during Pleistocene glaciations, affecting the type and number of plant species lost from each continent (Polunin 1960, Daubenmire 1978). In Europe, the east-west trending Pyrenees, Alps, and Caucasus mountain ranges (and bodies of water) formed substantial barriers that prevented southward migration of species during glacial maxima to areas with a warmer climate. Paleoecological studies have shown that many genera of temperate zone trees became extinct in Europe at this time. In North America, however, the largest mountain chains trend north-south and did not form a substantial geographic barrier. Many plants were able to migrate southward either along these mountain ranges or in the lowlands, and then return slowly northward as the ice melted.

Possible Changes in Sea Level

Reid and Trexler (1991) review possible effects on biodiversity of sea-level changes that would result from melting of polar ice in a warmer climate. While coastal landforms such as marshes and barrier dunes have shifted with past climate changes, a substantial rise in sea level within a century would provide little time for landforms and vegetation to adjust. Particular concern is expressed for various rare species that occur only in estuaries or along coastal shores, such as *Amaranthus pumilus* (seabeach amaranth) and *Aeschynomene virginica* (sensitive joint-vetch).

Far greater changes in sea level than expected with anthropogenic climate change occurred during glacial cycles, accompanied by regional isostatic adjustments to the weight of the continental glaciers (cf. Pielou 1991), leaving coastal plant species as far inland as Ottawa (Porsild 1941). Similar changes occurred in lake levels and drainage patterns in and near the glaciated regions (cf. Ritchie 1987). As with the direct effects of possible rapid temperature increases, the concerns for effects on biodiversity of sea-level changes focus more on the possible rate of change than the ultimate magnitude.

Anthropogenic Landscape Changes

The present interglacial in North America differs significantly from all previous glacial cycles. The ability of plant species to respond to climate change may therefore be quite different now than in past times. First, the presence of dense human populations is an unique aspect of the present interglacial in North America. Humans have changed the landscape and have introduced many species of plants, animals, and diseases from other continents. Another, and perhaps related, distinction between this interglacial and earlier ones is the unexplained and unprecedented loss of dozens of species of large mammals in a wave of extinctions between 12,000 and 9,000 years ago.

The year 1492, when Europeans began extensive exploration and colonization of the New World, marks the beginning of the greatest change in the North American landscape since *the first* Pleistocene glaciation two million years ago (cf. Pielou 1991, Peters 1992, Shetler 1992, Wilson 1992). Initial contact was followed by increasingly widespread agricultural, urban, and industrial development. South of central Canada, only small areas of apparently unaltered landscape remain. On close inspection, these areas show many influences of the post-Columbian European invasion. The massive scale and irreversible nature of these changes dwarf those caused by the late-glacial Asiatic invaders and their Native American descendants, or by the transient settlements of Scandinavian Vikings in the northeastern portion of the continent about a millennium ago.

Landscape modifications include fragmentation of natural habitats, farming of prairies, clearing of forests, draining of wetlands, alterations in fire and flood frequencies, changes in pollination and dispersal agents, loss of native herbivores, and introduction of exotic plant species and herbivores, parasites, and diseases. Silver (1990), Cronon (1983), and Crosby (1986) provide further background on the history of these changes, and Cooper and Brush (1991) consider effects of post-Columbian settlement on aquatic systems. Most native plant species now live in a highly fragmented landscape which further separates appropriate habitat patches and increases dispersal distances. Many of the continent's remaining natural and semi-natural areas are being used more intensely by humans, due to population growth and increased accessibility, creating additional pressures on many rare plant populations. If most plants naturally disperse only 10-150 m per year, then human-altered landscape patches can constitute potentially unsurmountable barriers to dispersal.

Climate Change and Conservation Planning

The possibility of anthropogenic climate change received little attention, if any, during selection and design of present national and state parks, wilderness areas, wildlife refuges, and privately managed nature preserves such as those of The Nature Conservancy. Many such preserves were established to maintain particular ensembles of plant or animal species or particular vegetation types, on the unstated assumption that the appropriate habitat conditions could be maintained locally (cf. Hoose 1981, Morse 1987).

While much has been written about the potential effects of climate change on biodiversity (e.g., Peters and Lovejoy 1992), less is available on potential responses by conservation and land management organizations that could mitigate these effects. Both the public and private sectors of the United States have invested many billions of dollars over the past several decades in protection and management of lands important to biodiversity conservation.

While identifying specific conservation strategies which address the potential effects of climate change is beyond the scope of this report, some examples may be informative. When comparing otherwise similar sites for conservation, those with high topographic relief are possibly more resilient to climate change than are relatively fiat sites, since they offer more opportunities for upslope and southern-to-northern aspect shifts in species' populations. The relative lack of weedy exotics would also be important. Weedy exotics, when present, may be expected to outcompete many of the natives that would need to disperse and colonize within different portions of a site. Preserves with diverse habitats and sites providing topographically unusual or geologically rare locations would also be critical areas to which vulnerable plants might disperse, or be introduced through human intervention. Maintaining a variety of such areas as potential *future habitats* for species associated with those geologic features may be necessary, even if the species for which a preserve was first established become extirpated there.

Transplantation of plant populations into new areas may be required if endemic species or unique occurrences are threatened with loss in their present sites and are not likely to migrate to other suitable habitat. Maunder (1992) provides an overview of this still-controversial topic. An increasing role for *ex situ* propagation of species of high interest may also be required (cf. Falk and Holsinger 1991).

5

PREDICTING FLORISTIC CONSEQUENCES OF CLIMATE CHANGE

Many studies of possible effects of climate change on plant distributions have focused on several well-studied species of either agricultural crops or forest trees. In these investigations, reasonably specific predictions can be made since local distributions are known and readily related to climate data, and habitat requirements and dispersal capabilities are well-known. Furthermore, these studies have generally involved widespread, common species of typical landscapes, for which elevation and microclimate are not as significant. The various predictive studies by Margaret Davis and her colleagues on forest tree species (e.g., Davis and Zabinski 1992) are exemplary of this approach. Easterling et al. (1992) consider possible effects of climate change on crop yields for wheat, corn, and soybeans in the Midwest. McDonald and Brown (1992) consider vulnerability of mammal species in the Great Basin region.

At the other extreme, there have been several studies of the potential impacts of climate change on major global vegetation zones. The Life Zone Classification developed by Holdridge (1947, 1964) as a method of predicting potential vegetation based on temperature and precipitation data has been utilized frequently in these studies. Emanuel et al. (1985) use the Holdridge classification system to compare a map of global vegetation zones developed from climate station data with a vegetation map based on a general circulation model simulation of average temperature with increased atmospheric CO_2 concentration. This study demonstrates that ecosystem level vegetation patterns appear to have a high degree of sensitivity to changes in the average temperature. Similar results are presented by Leemans and Halpin (1992). The results of several regional and site specific analyses are presented in Peters and Lovejoy (1992). Romme and Turner (1991), considering possible vegetation changes in the Greater Yellowstone ecosystem, note that changes in precipitation could have even greater effects than changes in temperature for the mixture of vegetation types in that complex region.

Experimental data on temperature tolerances have been used to determine the climate ranges over which certain species are capable of growing (cf. Brock 1970). Such work is most valuable in studies of agricultural crops, commercial timber trees, and horticultural taxa, for which management techniques minimize disease, competition, and predation. The results of these laboratory climate tolerance studies are less pertinent to investigations of species growing in the natural landscape.

Predictions about the effects of climate change on select numbers of species or on major vegetation zones do not provide much information about the patterns of species vulnerability for entire floras. Even rough estimates of species vulnerability among the 15,148 vascular plant species native to North America north of Mexico require multiple approximations and simplifying assumptions regarding the distribution of species and climates. Over-simplification, however, could result in an unrealistic representation of actual conditions. The climate envelopes method used here is suitable for analyzing the available data.

The Concept of Climate Envelopes

The climate envelope of a particular species is defined by the range of climate the species experiences in its current geographical distribution. Self-evident from ecological niche theory, the concept is used, for example, by Andrewartha and Birch (1954) in comparing the "preferred temperatures" of various animal species or Lindsay (1953) in estimating expected distributions of weeds. A quantitative presentation is provided by Hutchinson (1957, 1978); Levins (1968), Vandermeer (1972), and Futuyma and Moreno (1988) provide further background on niche theory. Overpeck et al. (1991) compare present distributions of several groups of plants with distributions predicted by climate parameters.

The climate-envelope concept is similar to the work of Nielson et al. (1989) on the limits of ecoregions, as well as various studies of realized niche. Holdridge (1947, 1964) used the climate parameters mean annual biotemperature and average annual precipitation to develop his Life Zone Classification System based on these two factors and the potential evapotranspiration ratio, a measure of effective humidity. The hardiness zone maps widely used in horticulture (e.g., Cathey 1990) also reflect this concept, as applied to the climatologically similar regions in which various cultivated plants can be expected to survive. Drawing on horticultural experience, Wyman (1965) concludes that plant hardiness depends primarily on temperatures, secondly on rainfall, and thirdly on soil type.

Assumptions of Climate-Envelope Analysis

While there are many factors that could be used in a climate envelope analysis, as discussed below, there are five major assumptions implicit in the method developed for this study:

1. Climate determines the range of plant species.

2. Mean annual temperature is an adequate approximation of a plant's climatic range.

3. Species distribution is at equilibrium with present climate.

4. A species' current climate envelope is equivalent to its physiological tolerance of climate variation.

5. The envelopes incorporate all the temperature variations within the region(s) inhabited by the species.

Together, these assumptions state that the current distribution of each species is the product of climate and that temperature is a sufficient representation of climate.

While acceptable as working approximations, each of these assumptions is incorrect to some degree in a substantial number of cases, making predictions for individual species risky using only the analysis employed here. Nevertheless, these assumptions provide a consistent frame of reference for identifying broad patterns of species vulnerability to climate change among the many thousands of species in a continental flora. The climate-envelope analysis can also be useful in suggesting particular species meriting further, more detailed examination.

Relating Climate to Plant Distributions

The climate envelope of a species can be estimated by determining the range of climates recorded in the set of geographic areas in which the species is reported to occur. If a species' range is divided into units (states, counties, within-state zones, etc.), and one or more climate stations are associated with each of these units, then an overall climate envelope for the species can be estimated. An important consideration is that the intent of the envelopes is to provide estimates of the *magnitude* of the climate range of a species' distribution, not an overall average value for this climate.

Climate data are developed from weather stations that represent scattered points on the landscape, while plant distributions are more nearly continuous. Therefore, a systematic method for associating particular climate records with portions of plant species' distributions must be selected to facilitate production of climate envelopes for large numbers of species.

Climate Data.
The distribution of climate stations on the landscape is not random, with most observations from urban or agricultural areas. In particular, climate stations are generally located in open, level settings, so the full range of topographically induced microclimates in an area is not expressed in standard climate data, better thought of as macroclimate data. Wolfe et al. (1949) provide further discussion of these limitations.

Plant Distribution Data.
A further limitation to climate-envelope analysis is the poor level of resolution in available data on the ranges of most plant species (cf. Morse et al. 1981, Wessman 1992). In many cases, it is difficult to ascertain from standard references even the major portions of large states in which a particular species grows, much less the proximity of

a given species to particular climate stations. On the other hand, there is now detailed distribution information for most of the rarest plant species in the U.S. and Canada, often to the level of every known occurrence.

Use of Regionalized Data.

Ideally, climate envelopes for each species would be developed by determining the exact, microclimatically adjusted ranges of climate for each particular species. However, even if species distributions were known well enough to do this, the available climate data are not sufficiently precise. In practice, regional climate data (as obtained from weather stations) must be used in any broad-scale study, rather than specific microclimate data, despite the often substantial differences involved. Use of regional climate data may thus incorrectly estimate actual climate tolerances. By retaining relatively wide edges to species distribution maps, and thus to climate envelopes, a climate-envelope analysis is conservative and moderates the significance of the assumption that climate envelopes match climate tolerances.

State-Level Data.

The geographic boundaries of the U.S. states and Canadian provinces provide a first approximation of areas for which both plant distributions and climate data can be easily obtained. Plant distributions to the state level are generally well known, and have recently been consolidated by John Kartesz into an unpublished data file made available for use in this study. Similarly, all climate stations are readily associated with the state or province in which they are located.

Climate Envelope Examples

As an example of actual climate envelopes and how they differ, the North American distribution of two tree species in the same genus is presented for consideration. While *Abies balsamea* (balsam fir) is widespread in boreal regions, *Abies fraseri* (Fraser fir) is endemic to the southern Appalachians (Little 1971). Each species experiences a range of temperature, precipitation, and other climate parameters within its geographic range. Mapping the climates they experience onto hypothetical niche space (Hutchinson 1957) yields the climate envelope. A temperature axis of such a map would show a large range for balsam fir, with northern Canada being the coldest region where it occurs, and West Virginia the warmest. (However, in West Virginia, the species occurs only at high elevations which are not represented well in climate data.) On the other hand, Fraser fir occurs only at higher elevations in small portions of the Southern Appalachian states, and experiences a much narrower range of climate. Additional climate parameters could be mapped along other axes of this multi-dimensional envelope.

Climate Parameters of Interest

Many climate parameters have been suggested as limiting factors for species distributions. Generally, these include temperature, precipitation, and seasonal patterns in these factors. Besides averages, the frequency and intensity of weather extremes (such as hard freezes or dry summers) can also be major factors in limiting species' ranges. Also, the interaction of temperature and precipitation suggest the importance of evapotranspiration values to plant geography (cf. Field et al. 1992).

Temperature as Approximation of Climate

Complex models could consider many of these climate factors, but a simpler and more practical model characterizing the climate for thousands of plant species must focus on just a few of these interacting values. The mean annual temperature can be used as a single parameter to characterize a region's climate.

A factor analysis of four characteristics of climate data from 3,233 U.S. and Canadian climate stations was conducted to identify the parameters by which the climate stations differed most. In addition to mean annual temperature, the mean total precipitation, the difference between mean July and mean January temperature (indicating seasonality of temperature), and the difference between mean total July and mean total January precipitation (indicating seasonality of precipitation) were considered. Using the Statistical Analysis System (SAS), two factors were extracted using a maximum likelihood estimation procedure with a Harris-Kaiser rotation.

The first factor, explaining 94% of the variance in the climate data, is primarily an axis of annual mean temperature and seasonality of temperature. The second factor is predominantly a precipitation factor. The linear equations for the two axes are:

$$\text{Factor 1} = 0.945 + (0.104 \text{x} \text{Annual Temperature}) + (0.0001 \text{x} \text{Annual Precipitation}) - (0.0628 \text{x} \text{Seasonality of Temperature}) + (0.0035 \text{x} \text{Seasonality of Precipitation}) \quad (1)$$

$$\text{Factor 2} = -0.088 + (0.013 \text{x} \text{Annual Temperature}) - (0.00002 \text{x} \text{Annual Precipitation}) - (0.0017 \text{x} \text{Seasonality of Temperature}) + (0.015 \text{x} \text{Seasonality of Precipitation}) \quad (2)$$

The strong correlation between Axis I and mean annual temperature indicates that mean annual temperature is the best *single* approximation of these climate data.

Other Climate Factors

The climate envelopes used in this preliminary analysis are based only on mean annual temperatures. Other temperature factors, such as presence of frost-free areas and lengths of growing seasons, are also significant considerations in plant distributions. Precipitation is also a highly important factor in species distribution, as are seasonal variation in temperature and precipitation. Infrequent events, such as harsh winters, hot summers, or severe storms, all contribute significantly to limitations of a species' range. Any increase (or decrease) in the frequency and intensity of such events would affect species' distributions, but in ways different from a uniform change in mean annual temperatures.

Choice of Geographic Units

A crucial aspect of applying the climate-envelopes technique to a large number of species is the selection of a set of geographic units for which both climate data and species-distribution data can be obtained. Broad geographic units typically have wide ranges of climate and many species of plants,. some of them occurring only in small portions of the area. Units that are too narrow typically have relatively few (or no) climate-observation stations, and may not have adequately detailed information on the presence of plant species.

Many kinds of climate data are available. In the United States, weather records for the past century from hundreds of observing stations have been summarized as the Historical Climatology Network data file (Karl et al. 1990), and data for many additional U.S. climate stations through 1988 is presented by NOAA as "Comparative Climatic Data," extracted from the Local Climatological Data Annual Summaries published for each station (NOAA 1988). For Canada, similar data are available, including the 30-year temperature records for 2,250 observing stations published in the Canadian Climate Normals series (Canadian Climate Program 1982). The *Climatic Atlas of North and Central America* (Steinhauser 1979) is another important reference, including isotherms of mean annual temperatures at intervals of 2.5°C on 1: 10,000,000 scale maps of North America.

States and Provinces

Climate data and species-distribution data can both be readily related to the U.S. states and Canadian provinces. However, state-level sspecies presence/absence data are often inadequate for the construction of meaningful climate envelopes that approximate species' geographical ranges, especially for large or topographically diverse states which can have great climate ranges. Plant distribution data developed only to the level of state or province fail to reflect possible impacts of climate change on narrowly endemic species or those which occur in small parts of climatically diverse states or provinces. The reported occurrence of a species at even one site in that area means that the entire climate range of the state or province is attributed to the species in the climate envelopes analysis. If the climate envelope of a state or province exceeds 3°C, for example, any species occurring anywhere in that area would be considered by a climate-envelopes study to be resilient to climate change of that magnitude.

The poor correlation between plant distributions and state boundaries affects both wide-ranging and narrowly endemic species. The range of almost any widespread species includes at the peripheries states or provinces which it barely enters (cf. Kartesz and Kartesz 1977). The range limits of many widely ranging species are in only the warmest or the coolest portion of the limiting state or province, as shown, for example, by Crow and Storks (1980) for New Hampshire, Crovello and Keller (1981) for Indiana, and Argus (1992) for Ontario. Many large states, particularly California (Stebbins and Major 1965) and Texas (Hatch et al. 1990), also contain many narrowly endemic species confined to small areas with relatively small climatic ranges. Consequently, creation of climate envelopes that are more consonant with actual species distributions is preferable.

Counties or Grid Cells

Counties, grid cells, or other small geographic units would give much more neatly fitting climate envelopes, but are impractical in a broad-scale study because relatively few plant species are mapped range-wide to this degree of resolution. Also, long-term climate observations are not available for many such places, particularly in remote areas. Finally, even if the data were available, the quantity of information to be recorded, standardized, and analyzed at this scale would be enormous.

Within-State Regions

Within-state regional units provide a middle ground, exchanging great precision for moderate practicality. Plant distribution data can usually be associated with broad regions of a state, particularly if these follow the physiographic provinces and other natural regions customarily used in the botanical literature. Even distinguishing lowlands from mountainous areas in a state provides a substantial data refinement from a climatological perspective. If the regions are not overly small, they are likely to have at least a few climate stations, minimally adequate for developing statistically useful climate estimates. (Areas lacking climate data need to have climates estimated from nearby stations at similar elevations.)

Estimating Effects of Climate Change

The general technique used here was developed by Whittaker (1967) in assessments of the possible impacts of weather modification. He identifies the positions of various species' populations on an environmental gradient, postulates modification of the gradient by a discrete amount, then determines which species would have positions that are within the boundaries of the modified conditions.

Uniform Temperature Increase

The principal climate-change scenario analyzed here addresses a possible uniform increase of mean annual temperatures throughout the study area. Predictions from climate models, as well as paleoclimate data since the last glacial maximum, show that the nature and intensity of past or future climate change varies considerably from region to region. Changes would, for example, be greater in the Arctic than the tropics in some situations, or perhaps more intense inland than near coasts. However, the various current models differ substantially in their predictions for specific areas, and do not yet provide sufficient resolution to specify particular predictions for the distribution units considered here. Therefore, a uniform climate increase was used as an acceptable simplification for an initial analysis, allowing the development and application of a climate envelope technique for large numbers of individual species. Later, the same distribution data could be used to test possible effects of any specific climate-change prediction that could be mapped to the geographic units used here.

In comparison to climate change scenarios involving regional differences but with the same overall magnitude (e.g., +3°C globally), this uniform-increase analysis assumes too much warming in some areas, and too little in others. With the use of a different climate-change scenario, some species here considered vulnerable might be considered secure, while other species here considered secure might be considered vulnerable. The particular effects of regional variation in predicted climate would depend on the model chosen, but the overall proportion of vulnerable species would depend primarily on the extent of climate change in areas with the largest numbers of narrowly distributed species. For example, there are far more rare species in subtropical latitudes than in the Arctic, so a model predicting warming mainly in the northern latitudes would show effects on fewer species than the uniform-change model used here. On the other hand, a model predicting greater local warming in the Southwestern states would show effects on a very large number of species, due to the high degree of endemism in that region.

More Complex Scenarios

Data on many additional climate parameters are available, and can be easily associated with the geographic zones used in this climate-envelopes analysis. These other climate variables were not addressed in the present study primarily because models of possible global climate change do not yet consistently predict such factors as future precipitation and seasonality.

Mountainous Areas

Substantial elevational variation in climate is present in mountainous regions. The elevation range in an area suggests the magnitude of the minimal climate envelope, even if all other factors are constant. For each 100 meters of elevation, the envelope needs to have at least 0.6° to 1.0°C of variation to accommodate the temperature change due to elevation alone. (This equates to 3.5° to 5.9°F per 1,000 feet of elevation.) However, relatively few mountaintop climate stations are represented in the standard climatological data sets, and mountaintop data are missing from many states. in addition, climate stations were not necessarily present at the lowest elevations in each state, particularly from canyon floors in plateau regions.

A more refined climate-envelope analysis could employ elevation-adjusted zones to include a minimum envelope size that relates to the actual elevation range of the plant habitats in that zone. Such an adjustment was not made in the present study. The net effect of this limitation is that many of the climate envelopes used here for zones in mountainous terrain are too narrow, and might contribute to considering a species to be vulnerable to climate change when it actually is more resilient. Another alternative would be the use of regionalized climate maps, which take elevation into account, rather than use data from individual climate stations.

6

SOURCES OF BOTANICAL DATA

The information assembled and analyzed in this study was obtained from many sources, including the scientific literature, several substantial botanical and climatological databases, and species reference files maintained by The Nature Conservancy. Data developed by the Natural Heritage Network were also consulted for some species.

The study area, North America north of Mexico, is the large, continuous region including the 48 contiguous United States, Canada, and Alaska. Also considered were all immediately adjacent offshore islands under U.S. or Canadian jurisdiction, as well as Greenland. Since the study area is restricted to continental North America north of Mexico, not all parts of the United States are addressed. Hawaii, Puerto Rico, the U.S. Virgin Islands, Guam, and the various other outlying U.S. territories or possessions are excluded.

The accumulated knowledge of the taxonomic classification and geographical distribution of the plant species of North America is fundamental to this study. These data, represented in many thousands of botanical publications, are summarized in two databases developed over the past two decades by John T. Kartesz of the North Carolina Botanical Garden, in cooperation with hundreds of taxonomic and floristic specialists throughout North America and internationally. These state-level geographical distribution data were thoroughly researched and widely reviewed, yet contain a modest percentage of errors of both commission and omission that are still being detected and corrected.

A greater number of inaccuracies, particularly omissions, presumably occur in the species distributions data for the within-state geographic zones developed here. This level of detail was not developed for all states or provinces. Also, the proportion of species for which within-state distribution data were readily available varied among the states and provinces that were geographically subdivided. Finally, the data on species with southern ranges extending into tropical climates in Mexico or the Caribbean are significantly incomplete.

Taxonomic Classification

This study considers full species of vascular plants native to North America north of Mexico. The vascular plants include the angiosperms (flowering plants), the gymnosperms (conifers and their relatives), and the pteridophytes (ferns and fern allies). The angiosperms consist of two major groups, monocots and dicots.

Nonvascular plants, such as algae, fungi, lichens, or mosses, were not considered.

Subspecies and varieties were not separately addressed in this study, but instead considered parts of their respective full species. Nonreproducing hybrids were excluded, since these in general do not represent unique components of genetic diversity. Also excluded were the 94 North American vascular plant species considered by The Nature Conservancy to be extinct or possibly extinct (Russell and Morse 1992), and the one such species *(Franklinia alatamaha)* believed extinct in the wild, yet extant in cultivation.

All decisions regarding taxonomic classification and botanical nomenclature in this study follow a data file, provided by John Kartesz, of the galley proof of the revised edition (Kartesz 1993) of his *Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland* (Kartesz and Kartesz 1980). This checklist summarizes the best available knowledge of the taxonomy and nomenclature of the vascular plant taxa (species, subspecies, varieties, hybrids, etc.) occurring in the noncultivated landscape of North America north of Mexico or in the outlying U.S. areas of Hawaii, Puerto Rico, or the U.S. Virgin Islands. It furthermore attempts to account, through synonymy, for every additional name in significant current or recent usage for any taxon within its geographic scope. All information in the two-volume *National List of Scientific Plant Names* by the U.S. Soil Conservation Service (1982) was considered by Kartesz, as were the data in the only other recent North American checklist, the *Flora North America* list by Shetler and Skog (1978).

Taxonomic Concepts

The species and infraspecific taxa recognized by Kartesz are intended to reflect the conclusions of the most recent generally accepted taxonomic works on each group, brought up to current generic concepts in each family. New nomenclatural combinations were made as needed to correct past errors or to place accepted taxa into their appropriate genera or species, in a series of publications in the journal *Phytologia* (Kartesz and Gandhi 1992, and references cited therein).

The generic classification closely resembles that of the genus list by Gunn et al. (1992), with notable exceptions, but was developed independently. With minor exceptions, the family classification follows Cronquist (1981).

Taxonomically Difficult Groups

For most genera, the number of species recognized varies only moderately from one taxonomic treatment to another, even from decade to decade, except as additional species are discovered. However, in certain taxonomically difficult genera, there is still considerable debate about even the order of magnitude of the number of species which ought to be recognized.

Many of these problem groups involve facultatively apomictic hybrid polyploid complexes (cf. Asker and Jerling 1992), for which it is difficult to apply the customary species concepts. Some North American genera having large numbers of taxonomically ambiguous apomicts are *Amelanchier*, *Crataegus,* and *Rubus* in the family Rosaceae, and *Antennaria* and *Hieracium* in the Asteraceae (Compositae), as well as such genera as *Bouteloua, Eragrostis, Panicum, Poa,* and *Setaria* in the taxonomically controversial grass family (Poacaeae).

The treatment of pteridophytes (ferns and their relatives) in the Kartesz checklist deserves special mention, since it includes many species recently detected through modern techniques such as isozyme analysis. In addition, many new species of *Botrychium* recently discovered by W. H. Wagner and his colleagues (cf. Wagner and Wagner 1990) are also included by Kartesz.

Infraspecific Taxa Not Addressed

Infraspecific taxa are not individually considered in this study because doing so would have substantially increased the amount of information needed and delayed the preliminary results presented here. In addition, information on the geographical distribution of subspecies and varieties is only marginally complete at the state or province level, and very difficult to assemble for the within-state geographical zones used here. Furthermore, the use of infraspecific taxa is not uniform between genera and families, which would have led to an inconsistent standard of analysis. Finally, taxonomic knowledge of subspecies and varieties is often weaker than for full species.

Nonstandard Species Not Considered

The Nature Conservancy continues to track data on a taxonomically questionable species so long as any Heritage Program or other Conservancy cooperator continues to recognize it (Morse in press). However, for the present work, data were developed and analyzed on only the native North American species recognized by Kartesz (1993). The taxonomic synonymies provided by Kartesz were used as needed to incorporate Conservancy data on nonstandard species into the data set used for this analysis.

Status of Plants as Native

Species are considered native in this analysis if they occur in an area and maintain themselves naturally there, without direct or indirect past or present human intervention (cf. Morse 1988). Distinguishing native plant species from exotics is not always easy, largely because historical data on species' ranges at the time of first

European exploration or settlement are seldom available. The effects of the activities of Native Americans on species' distributions are even less well known (cf. Nabhan 1992). The dynamic nature of species' natural ranges creates additional complications. It is often difficult to distinguish whether newly established occurrences of a plant are due to natural dispersal or due to intentional or accidental human intervention.

The status of species as native or introduced in the study area (North America north of Mexico) was determined by Kartesz, primarily from floristic and monographic sources. In the present analysis, the small number of ambiguous cases were assumed to be exotics, rather than natives. These are primarily widespread tropical species whose status in southernmost Florida or the Southwest is unclear.

A small number of native American species are considered exotics in much of their present ranges. As mentioned earlier, *Catalpa speciosa* (northern Catalpa) and *Maclura pomifera* (Osage orange) occurred at the time of European settlement only in small regions of the south-central United States. They were widely planted, and are now thoroughly naturalized in much of the eastern and central portion of the continent, such as Ohio (cf. Braun 1961). This state-by-state distinction is not yet fully recorded in the available data. Such species were treated in the study as if they were native in their entire current North American range, thus crediting them larger and climatically more diverse distribution ranges than' they actually had in their presettlement distributions.

Data on Species Distributions

The basic phytogeographical data on distributions of species by states, provinces, and similar areas has been developed by Kartesz over the past two decades, and was provided by him for use in this analysis. These data were supplemented by additional data on within-state (or within-province) distributions for selected areas, as well as data on tropical distributions of southern species.

Basic Phytogeographic Data

There has been a resurgence of interest over the past decade in documenting the vascular-plant floras of the various U.S. states. Of the 64 basic North American geographical units considered by Kartesz, only the District of Columbia now lacks at least a working checklist of its vascular plants. About three-quarters of the states and provinces have checklists, distribution atlases, or floristic manuals that were published or revised within recent years. Altogether, about 300 standard publications present perhaps 90% of the state-by-state distribution records for the North American vascular flora.

Kartesz provided a substantial revision in November 1991, of his unpublished data set on state-level species distributions, which he had provided in working-draft form to the

Conservancy in 1986. Records in this file correspond taxonomically to his revised checklist.

Sources of Distribution Information.
The basic geographical data set developed by Kartesz provides distributions of the taxa recognized in the revised Kartesz (1993) checklist to states and provinces. The unpublished geographical distribution data used here were compiled by Kartesz from such sources as regional and local floras, rare plant lists, and taxonomic monographs, as well as consultations with hundreds of local botanists, taxonomic specialists, and plant conservationists. Many thousands of herbarium specimens were also checked. The many comments received on state-specific review drafts circulated over the past several years were particularly helpful. Each entry in the Kartesz data file is documented by a literature reference, specimen voucher record, or other source citation in his project records, maintained at the North Carolina Botanical Garden.

This data file provides information on the reported presence (and, implicitly, presumed absence) of each recognized species and infraspecific taxon in each of the 49 continental U.S. states, the 12 Canadian provinces and territories, and Greenland. Kartesz also recorded distributions for vascular plants reported in Hawaii, Puerto Rico, the U.S. Virgin Islands, and St. Pierre & Miquelon, areas outside the geographic scope of the present study.

Geographic Units.
As is customary in Canadian botanical work (cf. Rouleau 1978, Argus and Pryer 1990), Kartesz recognizes a few additional sub-provincial areas in his Canadian distribution data. The Northwest Territories are divided into their three administrative districts (Franklin, Keewatin, and Mackenzie), and mainland Labrador is distinguished from insular Newfoundland within the province of Newfoundland and Labrador.

In the present analysis, 64 state- or province-level North American geographic areas are recognized. Four floristically minor geographical units within North America were not addressed: the District of Columbia; the District of Franklin and the Hudson Bay islands within the Northwest Territories; and St. Pierre & Miquelon, a group of French islands offshore of Newfoundland. Also, it should be noted that the preliminary species distribution data sets used for Utah and Wyoming were substantially less accurate than those for other areas, due to inclusion of species records from sources later found to be unreliable.

Limitations to the Geographic Data.
The consolidation of published distribution records results, on average, in a slight over-estimate of the flora of each area, since several kinds of erroneous records can be unintentionally incorporated. First, misidentifications reported in older literature are not always addressed in more recent works, leaving it ambiguous whether a recent author even knew of an older report. Second, plants thought to be native may have actually occurred in an area only in cultivation. Third, records near state or province

boundaries may be incorrectly attributed to the wrong geographical unit. Fourth, plants reported in older literature under a particular name may now be classified in some other, more recently recognized species, leaving the state or province with no representatives of the original, more broadly construed species.

Supplementary Phytogeographic Data

Two kinds of species distribution data supplement the state-level floristic information developed by Kartesz. First, fourteen U.S. states and four Canadian provinces were divided into smaller geographic units to create more accurate species distributions and climate envelopes. Second, data were added on tropical distributions of many species.

Basis for Subdivided Areas.
Subdivisions of states or provinces were principally made for areas with large climate ranges or areas which contain significant numbers of species with current southernmost range limits. However, due to lack of species-distribution data in appropriate forms, not all states or provinces which meet the above criteria were subdivided. The subdivisions generally follow physiographic provinces and other natural regions commonly used in North American floristic work. Selection of the zones for each subdivided area either followed published works or were developed by project staff in consultation with botanists familiar with each region's landscapes, vegetation, and flora. The divisions also took into account the nature of available within-state plant distribution data.

Figure 6-1 shows the pattern over North America of the 194 vegetation zones used in the study. For example, Texas is divided into the ten zones used by Hatch et al. (1990), and California is divided into twelve zones based largely on the treatment by Munz and Keck (1968). Appendix I provides further explanation of the selection of sub-state and sub-province zones and the sources of the species-distribution data for them.

Tropical Distributions.
To estimate more accurately the warm end of climate envelopes for species that occur at the southern edge of the study area, an incomplete list was developed of species occurring in the study area as well as in Mexico, Panama, Jamaica, or the U.S. Caribbean. For Mexico, three floras were consulted: Shreve and Wiggins (1964) for Sonora, Wiggins (1980) for Baja California, and the Veracruz series edited by Gómez-Pompa. Other data on tropical distributions came from databases–a database version of D'Arcy's (1987) checklist for Panama; the Conservancy's data for Jamaica, primarily from Adams (1972); and unpublished data files developed by Kartesz for Puerto Rico and the U.S. Virgin Islands.

While these data are still incomplete, 3,111 native North American species were identified as also occurring in one or more of the above tropical regions. Data missing from tropical regions can result in narrower climate envelopes, based only on a species' U.S. distribution. This can suggest that a species is vulnerable to climate change when in reality it actually has a broad and secure envelope. This limitation is most significant for the plants of the southernmost states–California, Arizona, New Mexico, Texas, and Florida.

Figure 6-1
Distribution Zones

Map of North America depicting the geographic units ('zones') used in the plant distribution database. There are a total of 194 zones.

Eurasian Species.
Particularly in the boreal and arctic regions, many North American species also occur as native species in Europe, Asia, or both. For the vast majority of these, such as *Linnaea borealis* (twin flower), the species' climate range in North America is similar to that elsewhere in its range. However, particularly in Greenland and Alaska, a small number of species with large Eurasian ranges have only limited North American distributions. For example, *Salix sphenophylla* is a widespread willow in Siberia, but is found in North America only at a single site in Alaska (Hultén 1968). The Eurasian ranges of such species were not considered in the present analysis, resulting in an underestimation of their climate ranges. On the other hand, a few Alaskan species, such as *Primula tschuktschorum* (Chukchi primrose), are Beringean, occurring only in small areas of similar climate on each side of the Bering Sea (cf. Hultén 1968).

Other Botanical Data

Several additional types of botanical data were obtained for estimating dispersal potentials of species, considering species rarity, and differentiating upland from wetland species. Much of that information was assembled by project staff or obtained from unpublished files previously developed by The Nature Conservancy in cooperation with the Natural Heritage Network.

Species Biology Data

Information about the growth forms (tree, shrub, etc.), durations (annual, perennial, etc.), and trophic types (autotroph, parasite, etc.) recognized in this study was developed by Kartesz from the taxonomic and floristic literature. Data on several additional aspects of species biology were assembled by Conservancy staff. This information included breeding system (dioecious, monoecious, hermaphroditic, etc.); occurrence of apomixis or agamospermy; outcrossing rate (primarily selfing, mixed selfing and outcrossing, primarily outcrossing, etc.); occurrence of self-compatibility; pollination vector; and seed-dispersal vector.

Use of Broad Taxonomic Patterns.
Since the number of plants in this study is large (over 15,000 species), it was impractical to fill in data fields individually for each characteristic for each species. Such detail also proved unnecessary, since the consistency of many characteristics at various higher taxonomic levels is not only the basis of the taxonomic hierarchy itself, but also a powerful means for recording descriptive data through hierarchically related data files (cf. Morse et al. 1971, Morse *1974a,b).* Taxonomic patterns at the family and genus levels were often used here to fill in these data fields for individual species. Information was obtained from monographs and review papers and entered into three hierarchically

related data files (for family, genus, and species). Information was added automatically to the species-level data fields when family- or genus-level data were entered.

The predominant trait for each biological characteristic was recorded in the family or genus files along with a code for the source of the information. Some family or genus groups apparently have no exceptions for certain characteristics. For example, all species in the family Pinaceae (the pines) are wind-pollinated, and all species in the genus *Salix* (willows) are dioecious. Therefore all species within these groups were recorded as presumed to exhibit that character. Other characteristics are more variable. As an example, the seeds of most of the 2,000 North American species of the Asteraceae (Compositae) are dispersed by wind (Cronquist 1981). However, the genus *Bidens* (the beggar-ticks) is generally animal-dispersed (Ridley 1930), with the rare estuarine species *Bidens bidentoides* being water-dispersed (Ferren and Schuyler 1980). In the databases developed for this project, the family Asteraceae was coded as generally wind-dispersed, the genus *Bidens* as generally animal-dispersed, and the species *B. bidentoides* as water-dispersed.

The existence of exceptions or suspected exceptions are noted in these data records, using a code system coupled with text fields for comments. A data-quality field in each species file reflects the existence of these exceptions and the taxonomic level (family, genus, or species) of the source of the data. If families or genera exhibited a mixture of character states, entries were made on a species-by-species basis, and no generalizations were made for that character at the family or genus level.

Sources of Species-Biology Information.
The following major sources were used to develop species-biology data at the family and genus levels:

Data field	Principal Sources
Breeding Systems	Richards (1986), Cronquist (1981), East (1940), Fryxell (1957), and Connor (1979).
Agamospermy including Apomixis	Asker and Jerling (1992), Fryxell (1957), and Richards (1986).
Outcrossing Rates	Fryxell (1957), East (1940), and Richards (1986).
Self-compatibility	Fryxell (1957) and East (1940).
Pollination Vectors	Proctor and Yeo (1973) and Meeuse (1961).
Seed Dispersal Vectors	Ridley (1930) and van der Pijl (1972).

Additional data at the species level were obtained from numerous published floras, monographs, and other publications, as well as the rare-plant literature and substantial unpublished information in the Conservancy's files and computerized databases.

Species Habitat Data

A detailed data file on habitats of wetland plants was provided by Porter B. Reed from the U.S. Fish and Wildlife Service's National Wetlands Inventory (NWI) database. These data include the degree of association with wetlands (e.g., obligate or facultative) for all North American wetland plant species, as summarized in the "National List of Plant Species that Occur in Wetlands" (Reed 1988). The NWI habitat classification system is based on the proportion of occurrences that are in wetlands. Obligate wetland species, for example, are those with at least 95% of occurrences in wetlands while facultative wetland species are those that occur in wetlands 66-95% of the time. Species that do not have a clear association with wetlands are assumed to be upland species.

Species Rarity Data

As noted by Smith (1976), Grime (1979), Drury (1980), Stebbins (1980), Rabinowitz (1981), Reveal (1981), Kruckeberg and Rabinowitz (1985), and others, there are several substantially different kinds of rarity of plant species. For many plants, the most important factors in rarity are the number of places the species occurs, its overall numerical abundance, and the size of its entire geographical range.

Two sets of species rarity data were considered here, those from the Natural Heritage Network's element ranking system and those from the *Federal Register* statuses developed by the U.S. Fish and Wildlife Service in implementing the requirements of the Endangered Species Act of 1973. A third widely cited method of designating rarity is the set of statuses used by the International Union for the Conservation of Nature and Natural Resources (IUCN), not yet widely applied to North American plants (cf. Lucas and Synge 1978).

Conservancy/Heritage Ranks.
To identify species sufficiently rare to need site-by-site attention in conservation planning, land management, and environmental review, The Nature Conservancy, in cooperation with the Natural Heritage Network, has developed a conservation priority ranking system for species and plant communities (Jenkins 1985). In this system of element conservation priority ranks, a range-wide (global) "element rank" is determined for each species. In simple form, it is a five-level scale from G1, for the rarest and most vulnerable species, to G5, for species that are demonstrably widespread, abundant, and secure. Several additional ranks are used in other circumstances not pertinent to the present study, such as suspected extinction. Similar ranks are also used at the national and subnational (state or province) levels. The

Conservancy/Heritage global ranking system is described in greater detail by Morse (1987), Argus and Pryer (1990), and Master (1991).

G1 = Critically imperiled globally because of extreme rarity (5 or fewer occurrences or very few remaining individuals or acres) or because of some factor(s) making it especially vulnerable to extinction.

G2 = Imperiled globally because of rarity (6 to 20 occurrences or few remaining individuals or acres) or because of some factor(s) making it very vulnerable to extinction throughout its range.

G3 = Either very rare and local throughout its range or found locally (even abundantly at some of its locations) in a restricted range *(e.g.,* a single western state, a physiographic region in the East) or because of other factors making it vulnerable to extinction throughout its range; in terms of occurrences, in the range of 21 to 100.

G4 = Apparently secure globally, though it may be quite rare in parts of its range, especially at the periphery.

G5 = Demonstrably secure globally, though it may be quite rare in parts of its range, especially at the periphery.

Ranks for individual species are assigned and reviewed by Conservancy and heritage program staff, as well as other cooperators, and are based primarily on (a) the number of populations and individuals, (b) the intrinsic biological vulnerability of a species (such as small geographic ranges, narrow habitat requirements, or constraining life-history strategies), and (c) the difficulty in mitigating known threats to the species.

The Conservancy's and Natural Heritage Network's element-ranking work for North American vascular plants is still incomplete, with a few thousand species not yet addressed. While most of the globally rare species received early attention in ranking due to their inclusion in existing state or federal lists, there are a number of locally abundant, or seemingly stable, rarities that have not yet appeared on rare plant lists. These species are being detected as comprehensive U.S. and Canadian element ranking continues. Other inadequately ranked species occur in Mexico or the Caribbean as well as the United States, and cannot be ranked globally until further data from those areas is obtained. Nevertheless, the set of species already ranked is representative of patterns of rarity in the North American vascular plant flora.

Global ranks for use in the present analysis were copied in December 1991, from the Conservancy's central scientific databases. These ranks were then rounded to the major ranks (G1, G2, G3, G4, G5, and Unranked) used here, ignoring the precision ranges and indications of taxonomic uncertainty contained in the original data. Since additional element ranks developed or revised during 1992 were not addressed here, and some taxonomic differences between these databases were not readily resolved, approximately 23% of the species analyzed here were unranked.

USFWS Federal Register Statuses.
In implementing the Endangered Species Act of 1973, the U.S. Fish and Wildlife Service drew upon a 1975 report by the Smithsonian Institution to identify species for which official listing was needed and justified. Thousands of species, subspecies, and varieties have been subsequently considered. About 250 plant taxa are now officially listed as endangered or threatened (USFWS 1992b), a few dozen are currently formally proposed for such listing, and around 2,000 are currently considered candidates for listing (USFWS 1990).

The statuses of candidates and former candidates are announced in periodical comprehensive notices of review in the *Federal Register*, with the most recent notice for plants from February 21, 1990. Candidates are divided into *Category 1*, for which "the Service has on file enough substantial information on biological vulnerability and threats to support proposals to list them as endangered or threatened species", and *Category* 2, for which "there is some evidence of vulnerability, but for which there are not enough data to support listing proposals at this time" (USFWS 1990). *Category 3C* is used for former candidates now considered too abundant or secure to require listing. Several other categories are used in other cases not pertinent here.

Federal Register statuses used here are complete through 1990, and include many (but not all) 1991 listing actions. Since proposals for listing almost invariably result in listings within a short time, the 'proposed' and 'listed' statuses were here combined under the 'endangered' or 'threatened' category, as appropriate. The various miscellaneous statuses were combined into a category 'other' to facilitate analysis. A modest amount of taxonomic cross-matching was needed to intergrate the *Federal Register* information into the present data set. This matching was done using synonymy files provided by Kartesz, and species were not individually reviewed.

Information Limitations

Limitations to the data are inherent in the incomplete state of botanical knowledge about the vascular plant species of North America north of Mexico. The taxonomic classification of about 5% of these plants is still debatable, and significant new geographical records appear in virtually every issue of regional botanical journals. Habitat information and species biology data are rarely available in consistently presented forms across large numbers of species. The lack, in several states, of comprehensive within-state species distribution data in a readily useable form was a major limiting factor in this analysis: Decisions about which states to subdivide into distributional zones for more precise climate envelopes were often made on the basis of availability of these data. Nevertheless, the data set analyzed here is by far the best such information available.

7

METHODS OF ANALYSIS

For each species in this study, climate envelopes (as described earlier) were determined by three methods using mean annual temperatures to approximate the range of climates that each species experiences within its current geographical distribution. The resulting set of climate envelopes, coupled with data on taxonomic classification, habitats, species biology, and rarity, was then analyzed to determine the possible extent of species vulnerability under a scenario of potential climate change.

Many types of climate envelopes are possible. Any could be applied to the database of species distributions, as long as the descriptive variables (i.e., climate data) could be related to the geographic zones used here.

Three Models of Climate Envelopes

Three methods of determining climate envelopes were chosen to provide a range in the estimates of vulnerability to possible climate change. The first method of analysis, based on the full range of reported mean annual temperatures in the zones where a particular species is recorded, is the most conservative. In this "Full Range model," the climate envelopes are large and thus are the most likely to underestimate the number of species that would be vulnerable to potential climate change.

Envelopes were also created by a technique involving standard deviations. In this statistical method, the temperatures for each zone were calculated as the mean of the observed mean annual temperatures minus one standard deviation (minimum), through the mean plus one standard deviation (maximum). These envelopes are generally much narrower than the full ranges of observed temperatures; under statistically ideal circumstances, this method estimates the central 68% of the range of temperatures present in a region. However, if the climate stations are very few, or are not statistically well distributed on the landscape (as in Nevada), the "Standard deviation method" can incorrectly represent the true distribution of mean temperatures.

The final method trims 16% from both extremes of the full temperature range. This approach approximates the intent of the analysis by standard deviations by identifying the central 68% of the range, but accommodates data that have a non-random distribution. In tables and figures, results from this method are identified as the "68% trim model."

Relating Climate Data to Plant Distribution Zones

For the climate-envelopes analysis, the maximum and minimum mean annual temperatures were determined for each of the 194 geographical zones used here to map plant species distributions. The range of mean annual temperatures in a zone were calculated on data from climate stations within the zone. Quantitative determination of climate envelopes was possible for most of the distribution zones in the contiguous United States and Canada. Approximation and interpolation were required for Alaska, Greenland, and for a few small zones elsewhere due to inadequate climate station data.

Climatological Data

Climate data used to determine the mean annual temperatures for calculation of the 'climate envelopes' developed here were primarily obtained directly from standard government sources that summarize weather observations at climate stations throughout North America. The number of stations and the data available from these stations varied across the study area.

Contiguous U.S.

For the contiguous United States, data on the mean annual temperature, mean annual precipitation, and seasonality of temperature and precipitation were obtained from the 1,200 observing stations of the Historical Climatology Network (Karl et al. 1990). Each of these climate stations was assigned to one of the geographic zones in the present study. Climate stations are fairly well distributed throughout the area, and 83% (104 out of 125 zones) of the in-state distribution zones in the contiguous U.S. contain at least three (and usually more) climate stations. The average number of climate stations is approximately 13 per zone.

Two zones in the contiguous United States did not contain any weather stations in the HCN data set, and were assigned temperature values from other sources. The mountainous portion of South Carolina was assigned the climate data from the four observation stations in the southern zone of the North Carolina mountains. The mean annual temperature for Virginia's Eastern Shore was estimated by using data from NOAA (1988) for nearby Princess Anne, Maryland.

Alaska.

Climate data for 22 stations in Alaska were obtained from the Comparative Climatic Data for the United States through 1988 (NOAA 1988). Due to the sparseness of climate-station data for Alaska, the climate data for the various zones were approximated or interpolated by project staff. Zones in southern and southeastern Alaska have data from at least one climate station in the NOAA data.

Temperatures in the outer Aleutians, Nunivak, St. Matthew, and St. Lawrence Islands were based on climate station data from the Pribilof Islands. Temperatures for the eastern portion of the Brooks Range, the low hills between the Brooks Range and the

Arctic coastal plain, and the Anklin Mountains were extrapolated from appropriate adjacent zones.

Canada and Greenland.
Canadian data (Canadian Climate Program 1982) were obtained from 2,250 observing stations, with climate normals (monthly and annual mean temperature, monthly and annual total precipitation) calculated over the period 1953 to 1980. The southern, more populated areas of Canada are better represented by climate stations, but about 86% of the Canadian distribution zones used in this study include at least two climate stations.

Two zones in Canada (Anticosti Island and the Hudson Bay shore of Quebec) have climatological data from only one weather station. The tundra zone in Labrador lacked climate stations, and was assigned temperatures based on the weather station data from the adjacent tundra zone of northern Quebec. A climate atlas (Steinhauser 1979) was used to estimate the climate range for Greenland.

Areas with Limited Climate Data

Of the 194 distribution zones, 80% had more than one climate station, 15% had just a single climate station (mostly in Alaska, as noted above), and 5% had no stations and received climate data from other sources.

For zones with only one climate station, as well as zones for which climates were estimated, standard deviations could not be calculated, so the same number was used for the range of mean annual temperature in each of the three methods of analysis. This approximation was necessary for 13 zones in the contiguous U.S. states, two Canadian zones, and 23 Alaskan zones.

Calculation of Climate Envelopes for Each Species

For each species, the reported North American distribution was determined, based primarily on the data developed by Kartesz of the North Carolina Botanical Garden. The climate (temperature) envelope for each species was estimated by matching the reported geographical distribution of the species and the climate station data for the zones within that distribution. The *temperature envelope* of each species, based on the lowest and highest values of the minimum and maximum temperatures respectively among the zones in which the species occurs, was calculated for each of the three methods as indicated above. In this way, three different temperature envelopes were created for each of the 15,148 species.

For example, the rare aquatic umbel *Ptilimnium nodosum* (harperella), as previously discussed in the introduction to climate envelopes, occurs in Alabama, Arkansas, the Carolinas, Georgia, Maryland, and West Virginia. Each state has a minimum and maximum among its set of mean annual temperatures, whether that range is the actual observed range or is a calculated derivation of the observations. For each method, P. *nodosum's* temperature envelope is determined from the lowest value among the minimum temperatures and the highest value among the maximum temperatures. The envelopes formed by using the full range of mean annual temperatures, the standard deviations, and trimming 16% from both ends of the full range can have very different widths. The warmest and coldest zones for each of the three envelope model can also differ.

In the *Ptilimnium* case, the temperature envelopes formed by the three methods of analysis differ by as much as 2°C. The full range envelope, based on actual climate station data, is 11.6°C wide while the envelopes calculated by using the standard deviation and by determining the central 68% of the data are 9.6°C and 10.2°C, respectively. For this species, all three methods of analysis result in the same geographic unit for the warmest zone—the coastal plain of Georgia. The temperature envelopes differ, however, on the coldest unit. The minimum temperatures in the full range and 68% trim analyses are found in Maryland, but West Virginia is the coldest area in the standard deviation evaluation. These differences can lead to slight variations in the results for any species, depending on the model used.

Identification of Vulnerable Species

To consider possible species vulnerability to climate change, a uniform increase in mean annual temperature across the continental landscape was postulated in 1°C increments. The climate parameters of each area were recalculated on the basis of uniform temperature increases from +1°C through +20°C. No other changes in climate variables were included. Since the several general circulation models suggest that a 3°C (5.4°F) mean increase in global temperature is a likely outcome under a scenario of doubled atmospheric carbon dioxide (IPCC 1992), that estimate was used for all other analyses.

In this preliminary study, the mean annual temperature at each point in the landscape is assumed to be increased by a constant amount. Thus, in a +3°C scenario, the temperature range in each of the geographical zones has a postulated future temperature range 3°C degrees higher than the temperatures indicated for it by the current climate data.

Species are considered vulnerable to local extirpation in a particular zone if the postulated future temperature of the zone is outside of the present rangewide climate envelope for that species. A species is considered "vulnerable" to extinction from climate change if no zone within its current range has a postulated future temperature within the species' current climate envelope. Species not considered "vulnerable" are referred to as "resilient" to possible climate change.

Analysis of Dispersal Potential

A seven-level scale of dispersal ability was created to assess the potential different species may have for migrating into new areas. Although adapted to and constrained by the types of data available for the most species, this scale generally follows the conceptualization of "weediness" presented by Baker (1974), Harper (1977), and others.

The scale is based on the presence or absence of the following seven characteristics important to species mobility or spread potential:

1. Growth form herbaceous (including ferns and succulents),
2. Trophic type autotrophic,
3. Sexual system hermaphroditic (either the plants monoecious or the flowers perfect),apomictic, or sporophytic,
4. Breeding system with at least partial self-compatibility,
5. Pollination either self-pollinating or by wind or water,
6. Seed dispersal by wind or birds, and
7. Distribution with many populations (Conservancy/Heritage rank G4 or G5).

For each character, species are scored with a 1 if it possesses the mobility-related state of the character, and 0 if it does not. The seven scores were equally weighted, and summed for each species. Since all species examined had at least one of the selected characteristics, the "mobility" scores vary from 1 (least mobile) to 7 (most mobile). Scores for all seven of these characteristics were determined for 8,668 species. The remaining species did not have complete data on all of the above characters.

Software Employed

The data used in this study were developed as a set of related databases using the Advanced Revelation database-management system, a product of Revelation Technologies, Inc. To the extent possible, data structures used in this study were developed in parallel with the comparable units of the Conservancy's Biological and Conservation Data (BCD) System (Carr 1988), used by over 150 Conservancy offices, Heritage Programs, and other cooperators. While project data will be incorporated into the Conservancy's central BCD system, a self-contained set of related databases was used in this project. This approach was used to maintain taxonomic consistency, provide for additional resolution in the geographic data, provide for the three-tiered approach to the species biology data, and maintain design flexibility to respond to the evolving needs of the ongoing work.

Data from the Conservancy's central scientific databases (using the BCD system) were copied to the project databases in December 1991. This 'snapshot' copy of the data was kept constant during the data analyses; information in the BCD itself is revised continually. Most of the tabulations and calculations were produced using Advanced Revelation, Lotus 1-2-3, and the Statistical Analysis System (SAS). WordPerfect 5.1 and PageMaker 4.0 were used to produce the narrative report, and graphical output and maps were developed using Lotus, CorelDraw 3.0, and ARC/INFO.

8

RESULTS

The results presented here include an analysis of possible changes to the composition and distribution of the North American flora under several scenarios of uniform temperature increase, with emphasis on a possible +3°C (5.4°F) increase in mean annual temperatures. The three methods of calculating species' climate envelopes employed here provide a range of vulnerability estimates for each scenario of potential climate change. The analysis of the full range of mean annual temperatures within the zones of the North American distribution of each species is the most conservative. The envelopes created using the mean one standard deviation and the central 68% methods were smaller and gave similar results.

Effects of Uniform Temperature Increases

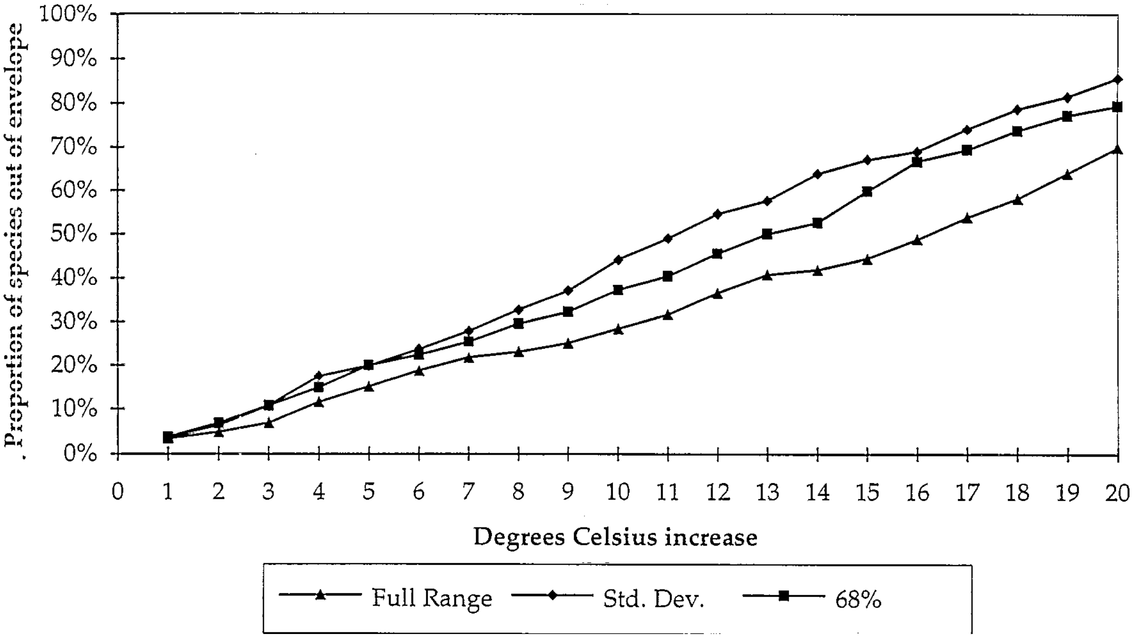

Figure 8-1 Increase above mean annual temperature

The proportion of species that were entirely out of their climate envelopes (all three models) as a function of the magnitude of temperature change.

Significant numbers of species would be entirely out of their temperature envelope in all scenarios of uniform temperature increase investigated, from +1°C to +20°C (Figure

8-1). About 7.0% to 10.8% (depending on the method employed to determine the climate envelope) of vascular plant species in the study area would be entirely out of their envelope in a +3°C climate; i.e., no part of the species' current range would have a climate within the species' estimated envelope. About 15.1% to 20.0% of species would be entirely out of their envelope in a +5°C climate. In the extreme case of a +20°C climate, considered primarily for reference purposes, 70% to 85% of all species would be vulnerable.

There are no clear temperature thresholds in the distribution of all temperature envelope widths at which significant numbers of species would be vulnerable to global warming. While the distribution of full-range temperature envelopes appears to be trimodal with peaks at 3-4°C, 11-12°C, and above 18-19°C, no clear pattern emerges in the distribution of climate envelopes calculated by the standard deviation or 68% trim methods.

Possible Effects of a Uniform 3°C Increase

An analysis of species vulnerability was performed for each of the three climate envelope models based on a temperature increase in +1° increments from +1° to +20°C. All other vulnerability analyses were completed using the three climate envelope models and a postulated +3° global increase in mean annual temperature. The characters analyzed included taxonomic group, species rarity, habitat, and several factors associated with dispersal and establishment ability.

Differences Among Taxonomic Groups

The 15,148 species in this study represent 233 families and 2,021 genera. Families, genera, and higher taxonomic groups differ dramatically in the proportion of their constituent North American species that are vulnerable. However, no large family or large genus has all its species determined to be vulnerable by the present analysis. While there is a significant correlation between the size of a family and the proportion of potentially vulnerable species ($r^2 = 0.78 - 0.85$), the genus size has little effect on the number of species out of their envelopes ($r^2 = 0.05 - 0.12$).

Higher Taxonomic Levels.

Of the 15,148 native North American vascular plant species, the vast majority (96.4%) are angiosperms (flowering plants). Of these, 77.8% of the total are dicots, and 18.6% are monocots. Much smaller numbers are gymnosperms (0.8%) and pteridophytes (ferns and fern allies) (2.7%) (Figure 8-2a). The pteridophytes are the most vulnerable of the major taxonomic groups, with 10.2% to 16.9% out of their climate envelopes while the monocots have a vulnerability of only 5.5% to 8.8% (Figure 8-2b)

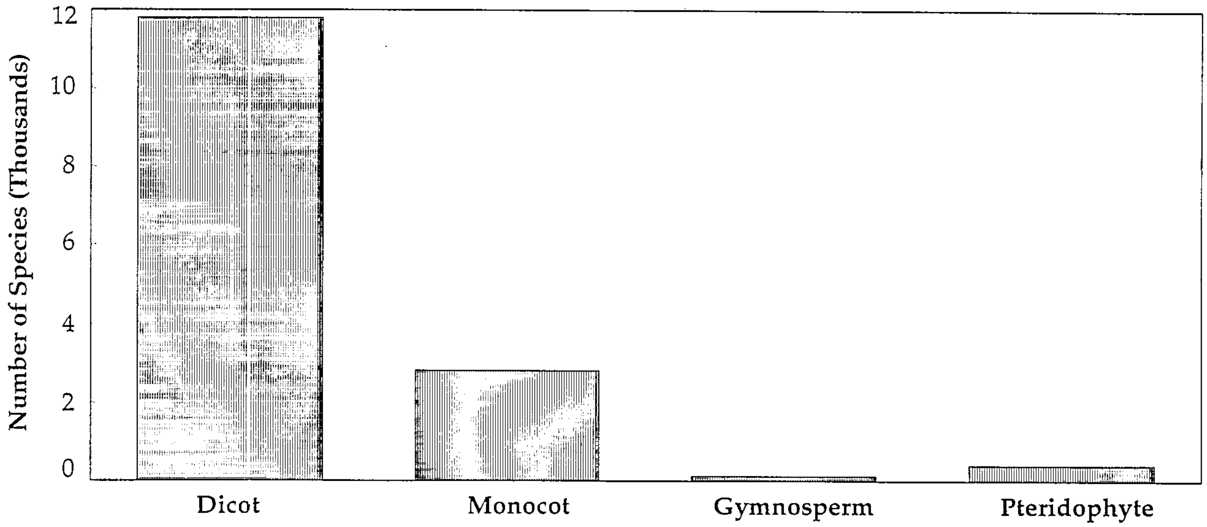

Figure 8-2a
Major Taxonomic Groups—Number of Species

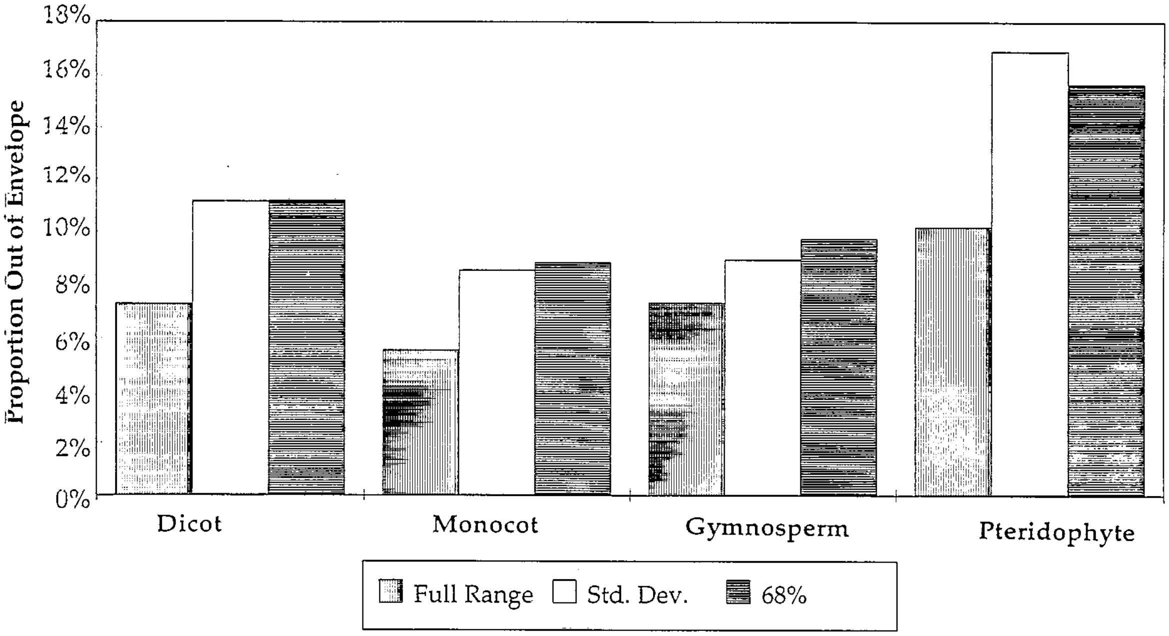

Figure 8-2b
Major Taxonomic Groups—Proportion Out of Envelopes

The proportion of species of different taxonomic groups out of their climate envelopes with +3°C temperature change. Data are incomplete for 23 species.

Large Families. The largest families in this flora (those with more than 50 native species) are shown in Table 8-1. The ten largest families together make up almost 36% of the native flora. The two largest families are the Asteraceae (sunflower family) and the Fabaceae (bean family), with 2,094 and 1,099 species respectively. Other notable large families are the Scrophulariaceae (figwort family), Rosaceae (rose family), and the Brassicaceae (mustard family).

Although there is a significant correlation between family size and the proportion of potentially vulnerable species, there are some considerable differences in numbers vulnerable species among families of comparable size (Table 8-1). Of the 68 species in the Acanthaceae (Acanthus family), 19.1% to 27.9% would be vulnerable in a +3°C scenario. The Primulaceae (primrose family) includes a similar number of species, but only 0.0% to 2.9% of these 70 species would be vulnerable under the same conditions. This varying response to climate change exists among the larger families as well. While 17.7% to 25.2% of the 254 species in the Euphorbiaceae (spurge family) would be vulnerable, only 3.1% to 5.7% of the 262 species in the Ranunculaceae (buttercup family) would be at risk. Of the 767 species in the Cyperaceae (sedge family), only 2.9% to 5.1% are vulnerable in a +3°C climate.

Large Genera.

The genera with the largest numbers of native North American species are shown in Table 8-2. The ten largest genera make up approximately 14% of the total native species of North America north of Mexico. Of these ten genera, *Carex* (sedges) is widespread continentally, particularly northward. The taxonomically controversial genera *Rubus* (blackberries and related brambles) and *Crataegus* (hawthorns), as treated here, are among the ten largest North American genera; they are primarily eastern and midwestern. The other seven largest genera, such as *Astragalus* (milk-vetches), *Penstemon* (beard-tongues), and *Lupinus* (lupines), are most species-rich in the western states.

There is little correlation between genus size and the proportion of species out of their envelopes. Substantial variety exists in numbers of species considered vulnerable in this analysis at the genus level (Table 8-2). *Oenothera* (evening primroses) has 53 species, of which 0.0% to 1.9% would be vulnerable in a +3°C world, while *Arctostaphylos* (manzanitas and bearberries) has 52 species, of which 36.5% to 40.4% would be vulnerable, including many that are endemic to small areas in California. Among the larger genera, 5.0% to 19.4% of the 146 species in *Crataegus* and 2.7% to 4.8% of the 146 species in *Erigeron* (fleabanes) would be vulnerable. In *Carex,* the largest North American genus, only 0.46 to 1.8% of the 439 species are vulnerable in a +3°C climate.

Table 8-1
Major Families

Family	Total Species	Full Rang	% Full Range	Std. Dev	% Std. Dev.	68 Trim	% 68 Trim
ASTERACEAE	2094	105	5.0%	192	9.2%	192	9.2%
FABACEAE	1099	72	6.6%	104	9.5%	120	10.9%
POACEAE	910	41	4.5%	73	8.0%	78	8.6%
CYPERACEAE	767	22	2.9%	39	5.1%	32	4.2%
SCROPHULARIACEAE	689	33	4.8%	51	7.4%	47	6.8%
ROSACEAE	618	30	4.9%	105	17.0%	61	9.9%
BRASSICACEAE	531	19	3.6%	45	8.5%	32	6.0%
LILIACEAE	412	17	4.1%	24	5.8%	30	7.3%
POLYGONACEAE	362	28	7.7%	32	8.8%	39	10.8%
APIACEAE	319	4	1.3%	11	3.4%	7	2.2%
BORAGINACEAE	311	23	7.4%	28	9.0%	34	10.9%
LAMIACEAE	281	16	5.7%	35	12.5%	45	16.0%
POLEMONIACEAE	272	7	2.6%	17	6.3%	15	5.5%
RANUNCULACEAE	262	8	3.1%	15	5.7%	12	4.6 %
EUPHORBIACEAE	254	45	17.7%	55	21.7%	64	25.2%
ONAGRACEAE	245	9	3.7%	12	4.9%	14	5.7%
HYDROPHYLLACEAE	224	11	4.9%	14	6.3%	14	6.3%
CARYOPHYLLACEAE	197	5	2.5%	15	7.6%	14	7.1%
ORCHIDACEAE	194	27	13.9%	37	19.1%	38	19.6%
MALVACEAE	178	29	16. 3%	35	19.7%	38	21.3%
ERICACEAE	170	21	12.4%	22	12.9%	25	14.7%
SAXIPRAGACEAE	161	3	3.1%	10	6.2%	7	4.3%
CACTACEAE	159	9	5.7%	12	7.5%	14	8.8%
RUBIACEAE	153	29	19.0%	33	21.6%	32	20.9%
CHENOPODIACEAE	128	3	2.3%	4	3.1%	4	3.1%
ASPLENIACEAE	125	9	7.2%	22	17.6%	19	15.2%
ASCLEPIADACEAE	120	9	7.5%	13	10.8%	16	13.3%
JUNCACEAE	120	2	1.7%	2	1.7%	2	1.7%
SOLANACEAE	108	10	9.3%	20	18.5%	22	20.4%
NYCTAGINACEAE	106	6	5.7%	10	9.4%	14	13.2%
GENTIANACEAE	98	5	5.1%	7	7.1%	5	5.1%
CONVOLVULACEAE	93	11	11.8%	15	16.1%	15	16.1%
ADIANTACEAE	91	13	14.3%	16	17.6%	16	17.6%
SALICACEAE	90	0	0.0%	1	1.1%	0	0.0%
VERBENACEAR	88	15	17.0%	19	21.6%	21	23.9%
CAMPANULACEAR	87	3	3.4%	8	9.2%	8	9.2%
FAGACEAE	84	3	3.6%	10	11.9%	10	11.9%
RHAMNACEAE	82	17	20.7%	18	22.0%	20	24.4%
PORTULACACEAE	81	0	0.0%	3	3.7%	3	3.7%
CRASSULACEAE	78	11	14.1%	15	19.2%	20	25.6%

Family	Total Species	Full Rang	% Full Range	Std. Dev	% Std. Dev.	68 Trim	% 68 Trim
VIOLACEAE	75	1	1.3%	3	4.0%	2	2.7%
AGAVACEAE	74	11	14.9%	19	25.7%	22	29.7%
LOASACEAE	73	2	2.7%	3	4.1%	3	4.1%
PRIMULACEAE	70	0	0.0%	2	2.9%	0	0.0%
ACANTHACEAE	68	13	19.1%	16	23.5%	19	27.9%
IRIDACEAE	67	2	3.0%	5	7.5%	4	6.0%
PINACEAE	64	1	1.6	1	1.6%	1	1.6%
AMARANTHACEAE	60	7	11.7%	13	21.7%	14	23.3%
CLUSIACEAE	57	5	8.8%	7	12.3%	7	12.3%
POLYGALACEAE	57	4	7.0%	8	14.0%	8	14.0%
CAPRIFOLIACEAE	52	0	0.0%	1	1.9%	1	1.9%
GROSSULARIACEAE	52	2	3.8%	2	3.8%	2	3.8%
PAPAVERACEAE	50	3	6.0%	4	8.0%	3	6.0%

The number of native North American species in families with at least 50 species and the proportion of species within each of these families that would be entirely out of their temperature envelopes in a +3°C climate for all three envelope analysis methods. These are listed in descending order of family size.

Table 8-2 Major Genera

Genus	Total Species	Full Rang	% Full Range	Std. Dev	% Std. Dev.	68 Trim	% 68 Trim
CAREX	439	2	0.5%	8	1.8%	5	1.1%
ASTRAGALUS	330	4	1.2%	7	2.1%	11	3.3%
PENSTEMON	224	3	1.3%	9	4.0%	6	2.7%
ERIOGONUM	212	13	6.1%	14	6.6%	16	7.5%
RUBUS	198	14	7.1%	58	29.3%	30	15.2%
PHACELIA	153	5	3.3%	8	5.2%	7	4.6%
ERIGERON	146	4	2.7%	7	4.8%	5	3.4%
CRATAEGUS	139	7	5.0%	27	19.4%	17	12.2%
LUPINUS	136	7	5.1%	10	7.4%	9	6.6%
CRYPTANTHA	114	1	0.9%	2	1.8%	4	3.5%
ASTER	107	1	0.9%	3	2.8%	1	0.9%
CASTILLEJA	106	8	7.5%	11	10.4%	12	11.3%
JUNCUS	101	2	2.0%	2	2.0%	2	2.0%
SENECIO	98	3	3.1%	4	4.1%	5	5.1%
DRABA	94	0	0.0%	3	3.2%	0	0.0%
SALIX	83	0	0.0%	1	1.2%	0	0.0%
CIRSIUM	82	4	4.9%	5	6.1%	4	4.9%
ALLIUM	81	2	2.5%	6	7.4%	2	2.5%
MIMULUS	78	2	2.6%	2	2.6%	3	3.8%
QUERCUS	78	3	3.8%	10	12.8%	10	12.8%
CYPERUS	77	5	6.5%	8	10.4%	8	10.4%

Genus	Total Species	Full Rang	% Full Range	Std. Dev	% Std. Dev.	68 Trim	% 68 Trim
ASCLEPIAS	75	2	2.7%	4	5.3%	5	6.7%
LOMATIUM	75	1	1.3%	5	6.7%	1	1.3%
ARABIS	71	2	2.8%	3	4.2%	2	2.8%
RHYNCHOSPORA	71	8	11.3%	12	16.9%	9	12.7%
VIOLA	71	0	0.0%	2	2.8%	1	1.4%
SOLIDAGO	70	1	1.4%	3	4.3%	1	1.4%
RANUNCULUS	69	0	0.0%	1	1.4%	1	1.4%
LESQUERELLA	67	3	4.5%	9	13.4%	7	10.4%
GALIUM	66	6	9.1%	6	9.1%	6	9.1%
MUHLENBERGIA	66	0	0.0%	0	0.0%	0	0.0%
CHAMAESYCE	65	6	9.2%	9	13.8%	9	13.8%
MENTZELIA	65	2	3.1%	3	4.6%	3	4.6%
PHLOX	65	0	0.0%	3	4.6%	1	1.5%
ATRIPLEX	62	2	3.2%	3	4.8%	3	4.8%
DELPHINIUM	62	4	6.5%	9	14.5%	5	8.1%
GILIA	62	2	3.2%	3	4.8%	3	4.8%
SAXIFRAGA	61	1	1.6%	5	8.2%	1	1.6%
DALEA	58	2	3.4%	4	6.9%	7	12.1%
POA	58	2	3.4%	4	6.9%	3	5.2%
ELEOCHARIS	57	2	3.5%	5	8.8%	4	7.0%
POTENTILLA	57	1	1.8%	3	5.3%	1	1.8%
OPUNTIA	55	2	3.6%	2	3.6%	3	5.5%
TRIFOLIUM	55	1	1.8%	2	3.6%	1	1.8%
CAMISSONIA	54	2	3.7%	2	3.7%	2	3.7%
POLYGALA	54	2	3.7%	6	11.1%	6	11.1%
OENOTHERA	53	0	0.0%	1	1.9%	1	1.9%
ARCTOSTAPHYLOS	52	19	36.5%	19	36.5%	21	40.4%
CALOCHORTUS	52	4	7.7%	4	7.7%	6	11.5%
RIBES	51	2	3.9%	2	3.9%	2	3.9%
HYPERICUM	50	4	8.0%	6	12.0%	6	12.0%
POLYGONUM	50	1	2.0%	1	2.0%	1	2.0%
SILENE	50	0	0.0%	2	4.0%	2	4.0%

The number of native North American species in genera with at least 50 species and the proportion of species within each of these genera that would be entirely out of their temperature envelopes in a +3°C climate for all three envelope analysis methods. These are listed in descending order of genus size.

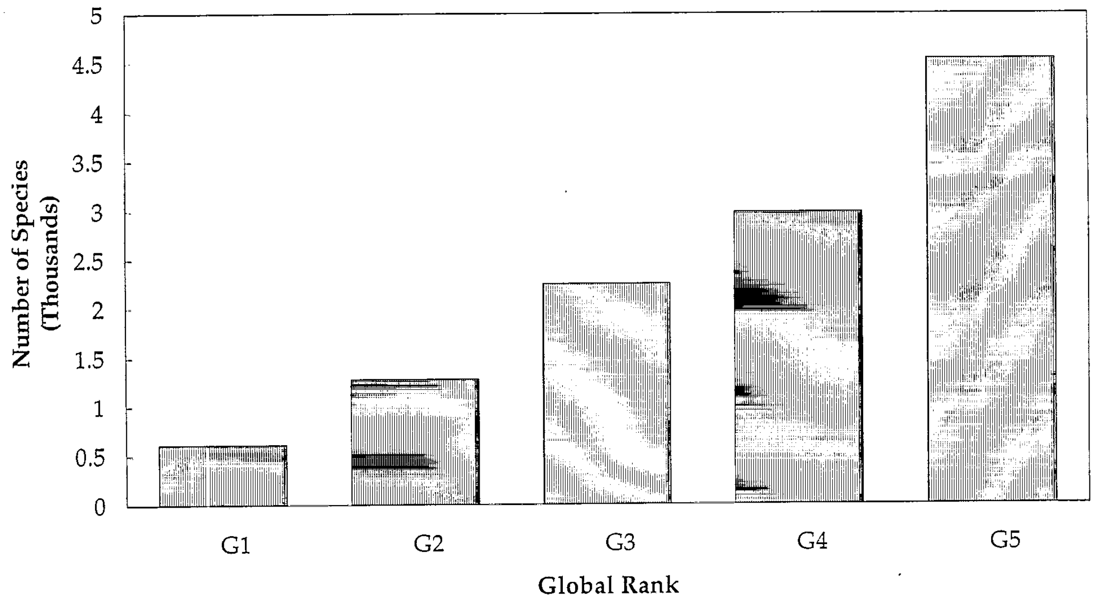

Figure 8-3a
Global Ranks—Number of Species

The total number of species in each Conservancy/Heritage Global Rank category. (Based on the 1991 dataset used in this analysis.)

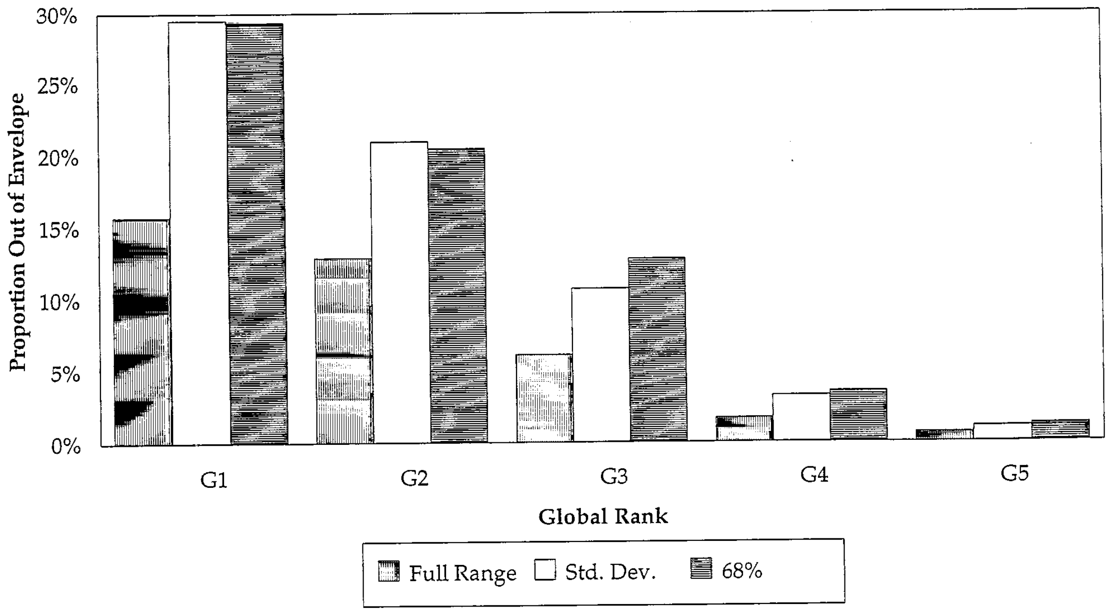

Figure 8-3b
Global Ranks—Proportion Out of Envelopes

The proportion of species in different Conservancy/Heritage Global Rank categories that were entirely out of their climate envelopes with a +3°C temperature change.

Effects on Rare Species

The possible effects of climate change on rare vs. common species were analyzed using the element ranks developed by The Nature Conservancy and the Natural Heritage Network, and the U.S. Fish and Wildlife Service's *Federal Register* statuses.

Conservancy/Heritage Ranks.
In the data set analyzed here, approximately 4,100 of the native North American vascular plant species are considered "rare" by The Nature Conservancy and Natural Heritage Network (i.e., ranked G1, G2, or G3; indicating they occur at fewer than 100 sites or are comparably vulnerable) (Figure 8-3a). These rare plants constitute about 27.3% of the present flora, but would be disproportionately affected by any amount of climate change considered here.

In a +3°C climate, the proportion of the rare species that would be entirely out of their climate envelopes is significantly higher than that for the entire flora. Approximately 9.6% to 17.6% of the rare species. (ranked G1, G2, or G3) would be vulnerable to a mean 3°C temperature increase. Of the common species (ranked G4 or G5), only 1.1% to 2.1% would be vulnerable under these conditions (Figure 8-3b). With the same amount of average climatic warming, 37.8% to 44.6% of the potentially vulnerable species are currently rare (ranked G1, G2, or G3). Only 7.5% to 9.8% of the vulnerable species are considered "common" (ranked G4 and G5).

In the data set used for this analysis, 23% of the species considered lack Conservancy/ Heritage element ranks. Approximately 16.5% to 22.6% of the unranked species would be vulnerable to a 3°C increase in mean annual temperature.

USFWS Federal Register Statuses.
Currently, about 354 full species of North American plants are protected or top candidates for protection (i.e., listed or proposed as Endangered or Threatened, or Category 1 candidates) under the U.S. Endangered Species Act (Figure 8-4a). In a +3°C climate, approximately 16.1% to 37.1% of the endangered and 5.6% to 18.5% of the threatened plant species would be out of their climate envelopes. About 21.6% to 36.4% of the Category 1 candidates for listing would be vulnerable under the same conditions (Figure 8-4b).

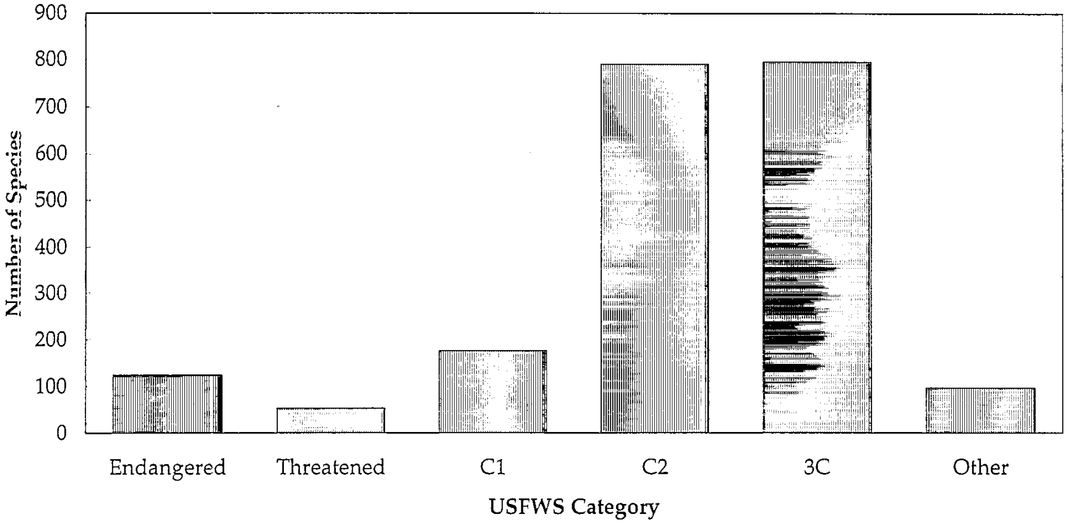

Figure 8-4a
USFWS Federal Register Status—Number of Species

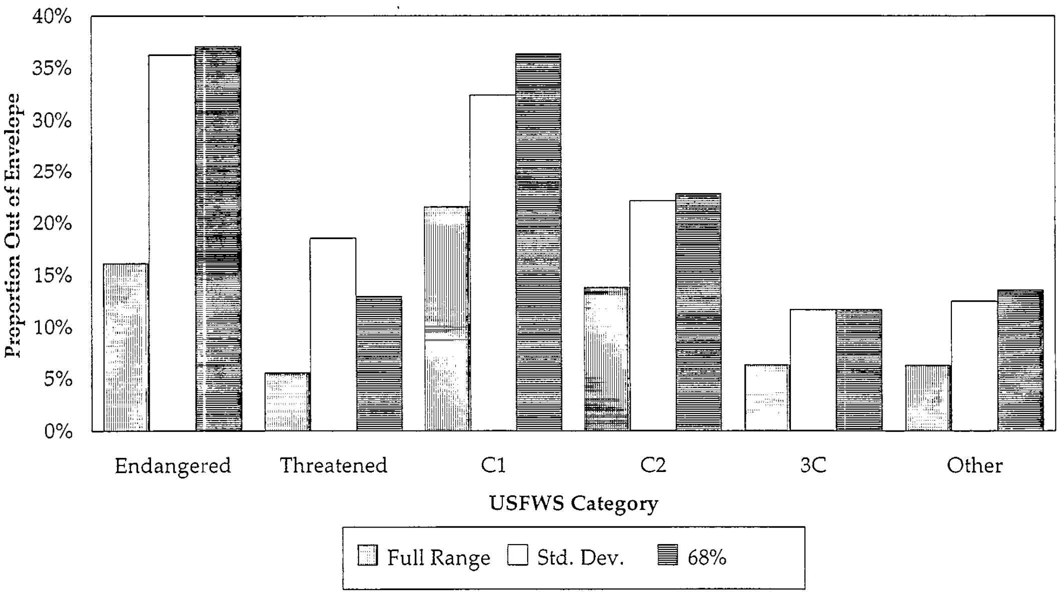

Figure 8-4b
USFWS Federal Register Status—Proportion Out of Envelopes

The proportion of species in different U.S. Fish & Wildlife Service Endangered Species Act categories that were entirely out of their climate envelopes with +3°C temperature change.

E = Listed and Proposed Endangered; T = Listed and Proposed Threatened; C1 = Category 1 candidate; C2 = Category 2 candidate; 3C = species formerly considered for listing, but which are no longer candidates; Other = all other categories

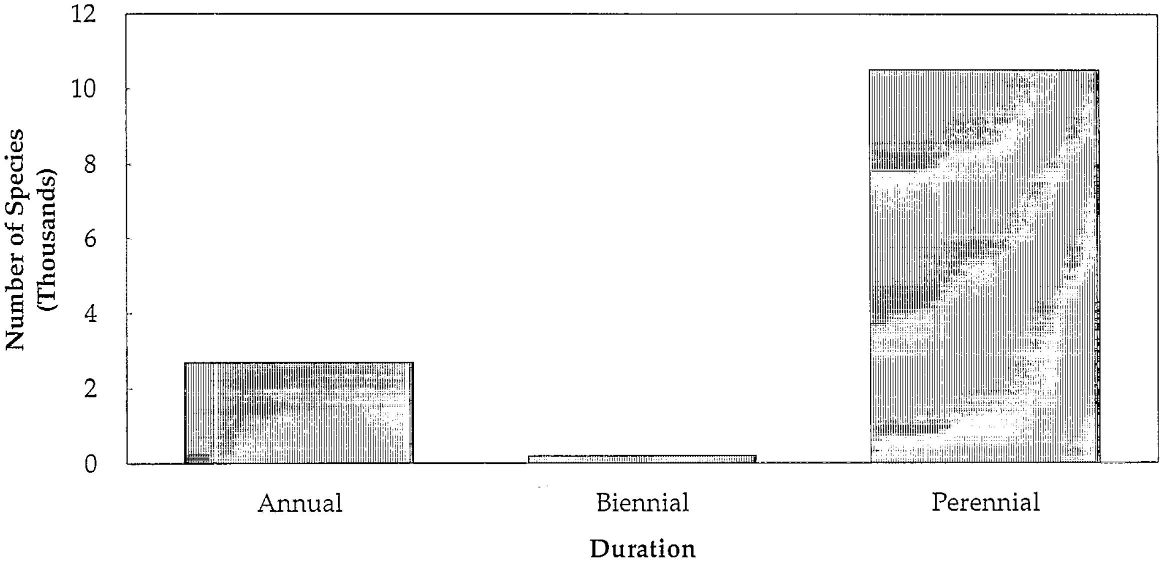

Figure 8-5a
Duration—Number of Species

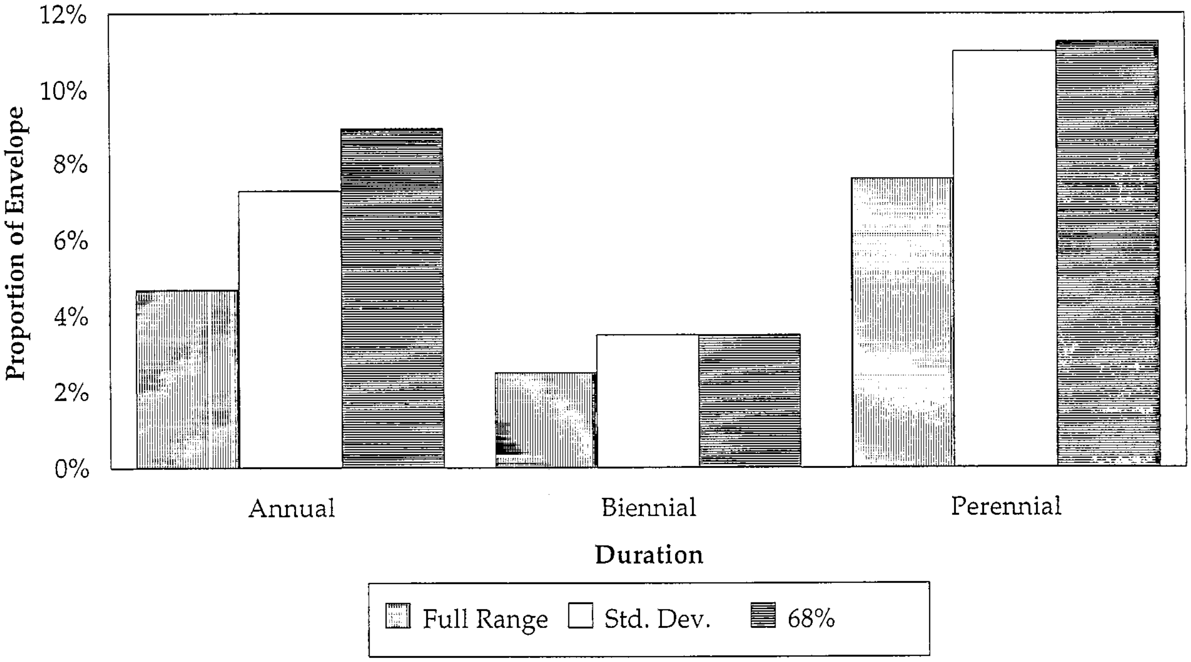

Figure 8-5b
Duration—Proportion Out of Envelopes

The proportion of annual, biennial, and perennial species out of their climate envelopes with a +3°C temperature change. Duration data are incomplete for 1,685 species.

Durations, Growth Forms, and Trophic Types

Species differ in their apparent vulnerability to climate change according to their durations and growth forms. The highest levels of vulnerability are found among woody species and other long-lived perennials. Differences among trophic types are slight.

Duration.
As a group, perennial species are more vulnerable than non-perennials (Figures *8-5a,b).* Approximately 7.6% to 11.3% of the perennial species would be entirely out of their envelopes in a +3°C climate. Only 9.0% of the annuals and only 2.5% to 3.5% of the biennials would be vulnerable under the same conditions. Data on duration (annual, biennial, perennial) were available for 13,463 species. Among these, the overall proportion of species out of their climate envelope in a +3°C world is 7.0% to 10.7%, roughly equivalent to the 7.0% to 10.8% observed for the entire flora of 15,148 species.

Growth Form.
Woodiness is correlated with greater vulnerability, as is increased size among the woody plants (Figures 8-6a,b). Herbaceous species are significantly less likely to be vulnerable to climate change than woody species. For example, 11.7% to 18.7% of the 1,424 shrub species and 24.3% to 27.3% of the 954 tree species would be entirely out of their envelopes in a +3°C climate. In contrast, only 4.4% to 7.5% of the 10,048 herbaceous species appear vulnerable to this amount of climate change (Figure 8-6b). Data on growth form were available for 13,134 of the species considered in this study.

Trophic Types.
The differences in vulnerability among species of different trophic types were very slight. Of the 36 species that are also insectivorous, 8.3% to 11.1% would be out of their climate envelopes, while 7.2% to 11.0% of the autotrophs and 6.6% to 10.3% of the parasitic species would be similarly affected (Table 8-3).

Table 8-3
Tropic Types

	Total Species Count	**% of Total**	**Full Range Out +3**	**Full Range % out**	**Std Dev Out +3**	**Std Dev. %out**	**68% Trim Out +3**	**68% Trim % out**
Autotroph	14288	94.3%	1024	7.1%	1550	10.8%	1570	10.9%
Insectivore	36	0.2%	3	8.3%	4	11.1%	4	11.1%
Parasite	380	2.5%	25	6.5%	38	10.0%	39	10.2%

he number of species of different trophic types in the current flora and the proportion that would be out of their climate envelopes with a +3°C temperature change. Trophic type data are incomplete for 444 species.

Wetland and Aquatic Species

Species that occur in wetlands and aquatic habitats, either facultatively or obligately, represent 23.4% of North America's flora, according to the National Wetlands Inventory data. The present climate-envelopes analysis suggests that these species are less likely to be vulnerable to climate change than are upland species (Table 8-4). Obligate wetland or aquatic species are the least vulnerable group; only 2.5% to 4.3% would be entirely out of their climate envelopes in a +3°C climate. The group of facultative wetland species, those which have 33-66% of their occurrences in wetlands, appears to be more vulnerable with 4.2% to 5.9% out of their climate envelopes. Of the upland species, 8.5% to 13.1% would be at such risk.

Table 8-4
Habitats

	Total Species Count	% of Total	Full Range Out+3	Full Range %out	Std. Dev. Out+3	Std. Dev. % out	68% Trim Out +3	68% Trim %out
Obligate Wetland	1546	10.2%	39	2.5%	67	4.3%	66	4.2%
Facultative Wetland	1992	13.1%	61	3.0%	93	4.6%	99	4.9%
Facultative	759	5.0%	32	4.2%	45	5.9%	44	5.8%
Upland	10851	71.6%	928	8.5%	1422	13.1%	1426	13.1%

The number of wetland and upland species in the current flora and the proportion that would be out of their climate envelopes with a +3°C temperature change. All species that do not have a recorded association with wetlands are assumed to be upland species. Wetlands associations are from unpublished data provided by the National Wetlands Inventory, U.S. Fish & Wildlife Service. Obligate = at least 95% of occurrences are in wetlands; Facultative, Wetland = 66-95% wetland; Facultative = 33-66% wetland; Upland = less than 33% wetland.

Dispersibility Considerations

Based on the seven-point dispersal ability scale discussed above, it appears that the majority of the species have an intermediate potential for dispersal (Figure 8-7). Approximately 3,500 species (40.4% of those with full data) received a score of four, indicating that they are neither exceptionally sedentary nor exceptionally dispersible. Data were available for all variables in the seven-point scale of dispersibility characters for 8,668 species, 57% of the native flora.

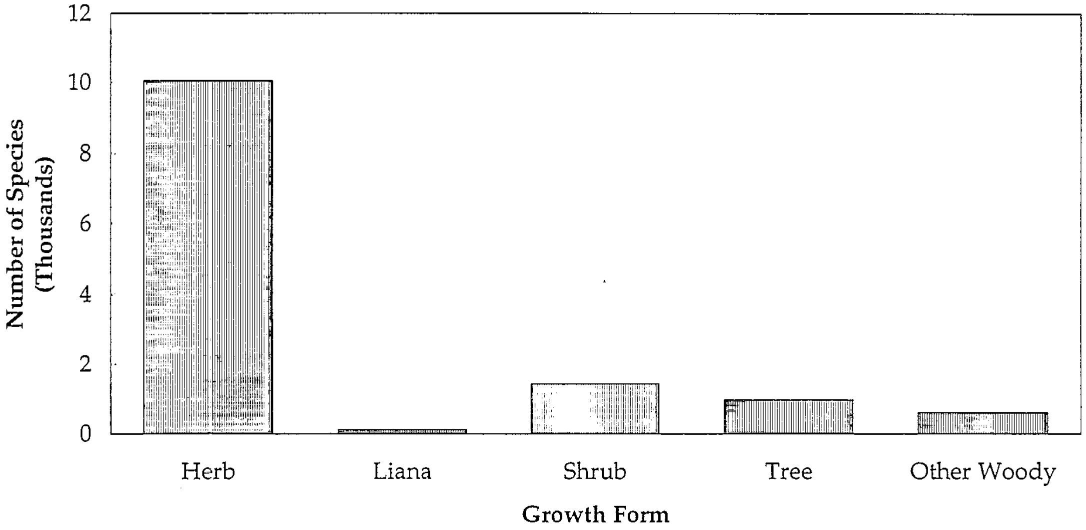

Figure 8-6a
Growth Form—Number of Species

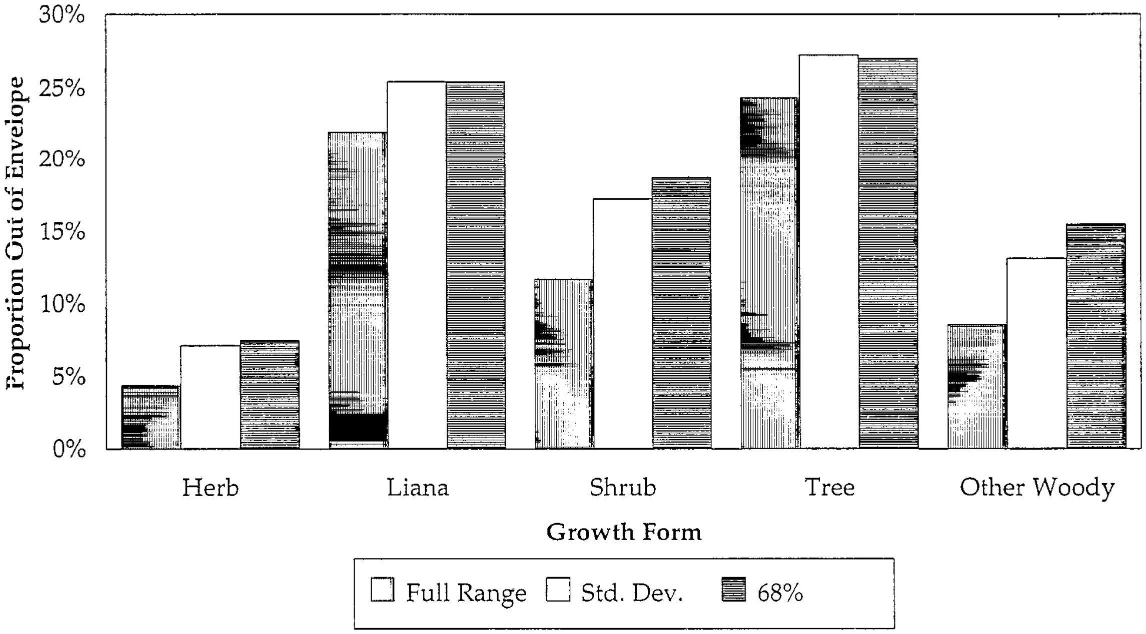

Figure 8-6b
Growth Form—Proportion Out of Envelopes

The proportion of species of different growth forms out of their climate envelopes with a +3°C temperature change. The "other woody" category contains additional woody species not identified as trees, shrubs, or lianas. Growth form data are incomplete for 2,014 species.

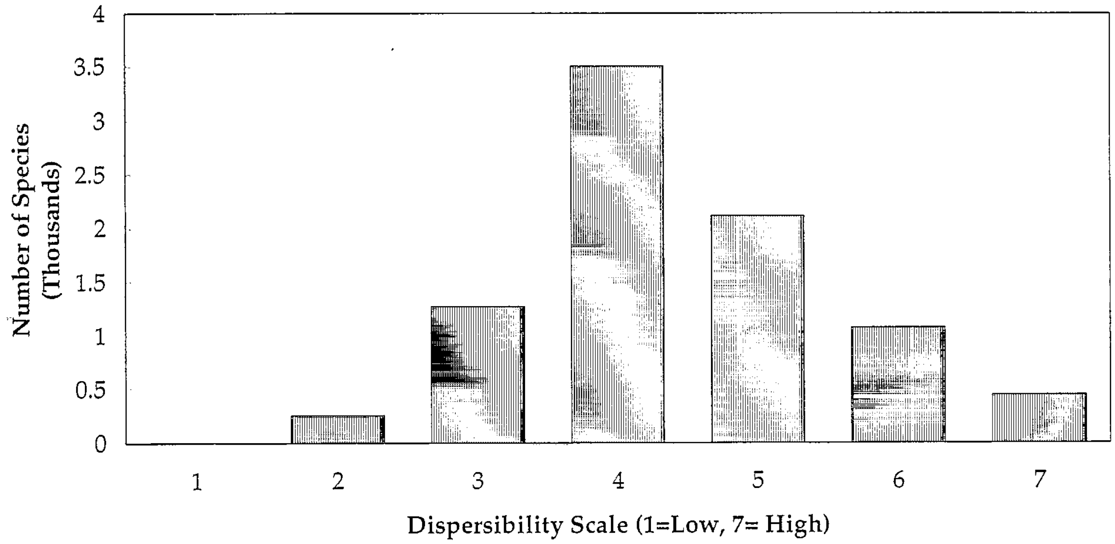

Figure 8-7
Dispersibility

The dispersal and establishment capacity for all species, based on a seven-level scale which indicates the number of mobility (or "weedy") characteristics each species exhibits. On this "weediness" scale, a score of 1 indicates low potential for mobility and establishment at a new site and a score of 7 represents a high potential. Full data were available for 8,668 species.

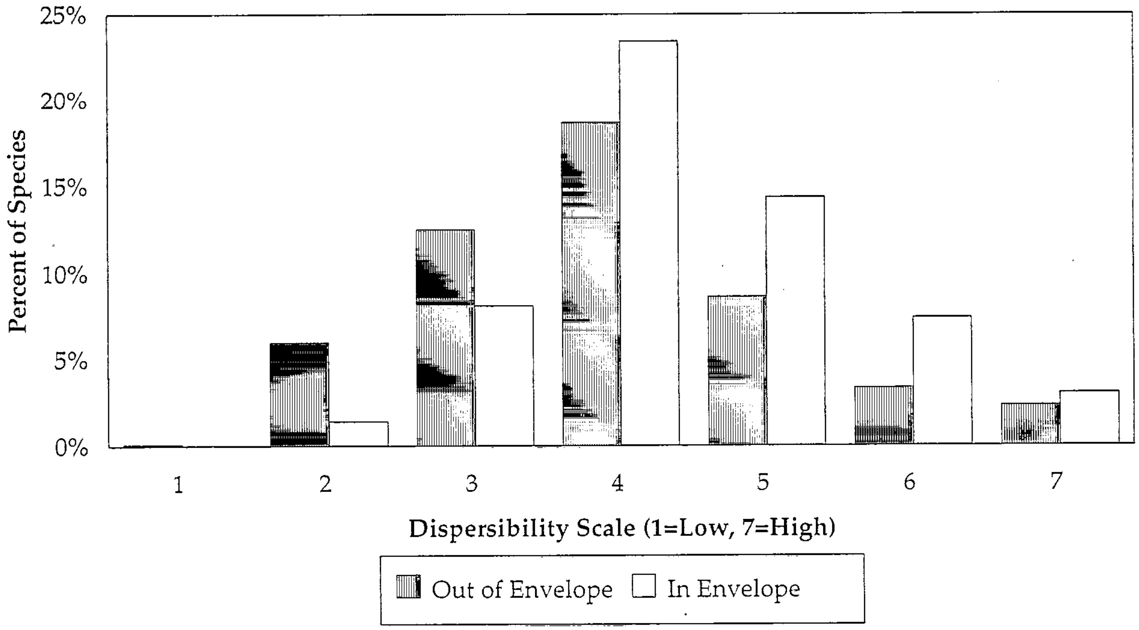

Figure 8-8
Dispersibility - Standard Deviation Envelopes

The proportion of species on the "weediness" scale that are in or out of then climate envelopes for the standard deviation method. Lined bars represent the frequency of species that are vulnerable in a +3°C climate; dot-screen bars are the frequency of species that are not vulnerable (i.e., are within their climate envelope somewhere in their range).

Species that, according to this temperature-envelope analysis, would be globally vulnerable in a +3°C climate (i.e., entirely out of their present climate envelope) tend to exhibit fewer characteristics associated with mobile or dispersive species (Figure 8-8), than do the species here considered resilient. The results presented are from the standard deviation method of analysis; all three methods have similar results. Non-vulnerable species make up the majority of species in all classes of dispersibility. However, vulnerable species have a higher representation among the less dispersible (more sedentary) classes. Of the species that would be out of their temperature envelopes in a +3°C climate, approximately 16% to 19% received low scores of 1-3 on the dispersibility scale. Only 9% to 9.5% of the species that would not be vulnerable in a +3°C climate received scores indicating low dispersibility. While 14% to 16% of the vulnerable species received high scores of 5-7 on this scale, about 25% of the species that would not be vulnerable to climate change are highly dispersible species.

Distribution of Species Vulnerability and Range Limits

The available data on species distributions for the native vascular flora of North America were analyzed to determine the states and provinces which might lose the most species, the areas with the most endemics and near-endemics, and the regions with the highest proportion of species presently at southernmost and northernmost range limits.

Regional Patterns in Species Vulnerability

Figure 8-9 shows the proportion of species that would be out of their climate envelope in each state or province, based on a 3°C mean increase in temperature. This figure presents only the results from the envelope analysis using the standard-deviation method, the *least* conservative model; the results from all three models are presented in Table 8-5. The southeastern states have the highest percentage of potentially vulnerable species. Florida could lose about 14% to 25% of its flora, followed by Louisiana with 0% to 24% of its flora potentially vulnerable. Alabama, Georgia, and South Carolina could all lose as much as approximately 12% of their respective floras. The region that may experience the fewest losses to its flora are the Great Plains states and provinces, including North and South Dakota, Alberta, Manitoba, and Saskatchewan.

Table 8-5
Proportion of species out of each state/province

State or Province	Total Species Count	Full Range Out +3	Full Range % out	Std Dev. Out +3	Std Dev. % out	68% Trim Out +3	68% Trim % out
Alberta	1598	0	0.0%	0	0.0%	0	0.0%
British Coumbia	2168	2	0.9%	25	1.1%	10	0.4%
Franklin	*						
Keewatin	461	0	0.0%	0	0.0%	0	0.0%
Labrador	606	0	0.0%	1	0.1%	1	0.1%
Mackenzie	912	0	0.0%	0	0.0%	0	0.0%
Manitoba	1285	0	0.0%	0	0.0%	0	0.0%
New Brunswick	966	0	0.0%	0	0.0%	0	0.0%
Newfoundland	816	0	0.0%	17	2.0%	0	0.0%
Nova Scotia	1030	22	2.1%	36	3.5%	031	3.0%
Ontario	1926	0	0.0%	0	0.0%	0	0.0%
Prince Edward Island	636	9	1.4%	9	1.4%	9	1.4%
Quebec	1811	0	0.0%	10	0.5%	0	0.0%
Saskatchewan	1180	0	0.0%	0	0.0%	0	0.0%
Yukon	1001	1	0.1%	2	0.2%	1	0.1%
Greenland	449	0	0.0%	42	9.3%	0	0.0%
Alabama	2419	0	0.0%	295	12.2%%	0	0.0%
Alaska	1245	0	0.0%	7	0.5%	0	0.0%
Arizona	3249	0	0.0%	0	0.0%	0	0.0%
Arkansas	2166	0	0.0%	128	5.9%	128	5.9%
California	5094	0	0.0%	419	8.2%	10	0.2%
Colorado	2638	0	0.0%	0	0.0%	0	0.0%
Connecticut	1668	22	1.3%	37	2.2%	49	2.9%
Delaware	1578	27	1.7%	41	2.6%	41	2.6%
Florida	2874	404	14.0%	712	24.7%	643	22.3%
Georgia	2762	116	4.2%	343	12.4%	138	5.0%
Idaho	2313	0	0.0%	0	0.0%	0	0.0%
Illinois	2055	0	0.0%	59	2.8%	0	0.0%
Indiana	1837	0	0.0%	51	2.7%	0	0.0%
Iowa	1385	0	0.0%	3	0.2%	3	0.2%
Kansas	1686	0	0.0%	29	1.7%	17	1.0%
Kentucky	2015	46	2.2%	121	6.0%	119	5.9%
Louisiana	2085	0	0.0%	505	24.2%	403	19.3%
Maine	1488	0	0.0%	14	0.9%	15	1.0%
Maryland	2035	0	0.0%	68	3.3%	0	0.0%
Massachusetts	1648	18	1.0%	44	2.6%	31	1.8%
Michigan	1950	0	0.0%	0	0.0%	0	0.0%
Minnesota	1718	0	0.0%	0	0.0%	0	0.0%

State or Province	**Total Species Count**	**Full Range Out +3**	**Full Range % out**	**Std Dev. Out +3**	**Std Dev. % out**	**68% Trim Out +3**	**68% Trim % out**
Mississippi	2034	0	0.0%	131	6.4%	153	7.5%
Missouri	1886	0	0.0%	37	1.9%	0	0.0%
Montana	2106	0	0.0%	18	0.8%	0	0.0%
Nebraska	1459	0	0.0%	24	1.6%	0	0.0%
Nevada	2679	0	0.0%	0	0.0%	0	0.0%
New Hampshire	1423	0	0.0%	0	0.0%	0	0.0%
New Jersey	1905	20	1.0%	54	2.8%	22	1.1%
New Mexico	2810	0	0.0%	0	0.0%	0	0.0%
New York	2188	0	0.0%	26	1.1%	7	0.3%
North Carolina	2445	0	0.0%	128	5.2%	6	0.2%
North Dakota	1137	0	0.0%	3	0.2%	3	0.2%
Ohio	1915	0	0.0%	29	1.5%	29	1.5%
Oklahoma	2278	0	0.0%	81	3.5%	4	0.1%
Oregon	2932	0	0.0%	13	0.4%	0	0.0%
Pennsylvania	2028	0	0.0%	37	1.8%	0	0.0%
Rhode Island	1350	28	2.0%	39	2.8%	39	2.8%
South Carolina	2194	57	2.6%	266	12.1%	110	5.0%
South Dakota	1403	0	0.0%	5	0.3%	8	0.5%
Tennessee	2111	0	0.0%	168	7.9%	163	7.7%
Texas	4512	0	0.0%	279	6.1%	39	0.8%.
Utah	*						
Vermont	1486	4	0.2%	5	0.3%	16	1.0%
Virginia	2320	1	0.4%	69	2.9%.	22	0.9%
Washington	2331	0	0.0%	197	8.4%	0	0.0%
West Virginia	1727	0	0.0%	54	3.1%	0	0.0%
Wisconsin	1624	0	0.0%	5	0.3%	5	0.3%
Wyoming	*						

The proportion of species in each state/province that would be out. of their climate envelope in that state/province if the unit were 3°warmer.

*Data imprecise, excluded from table.

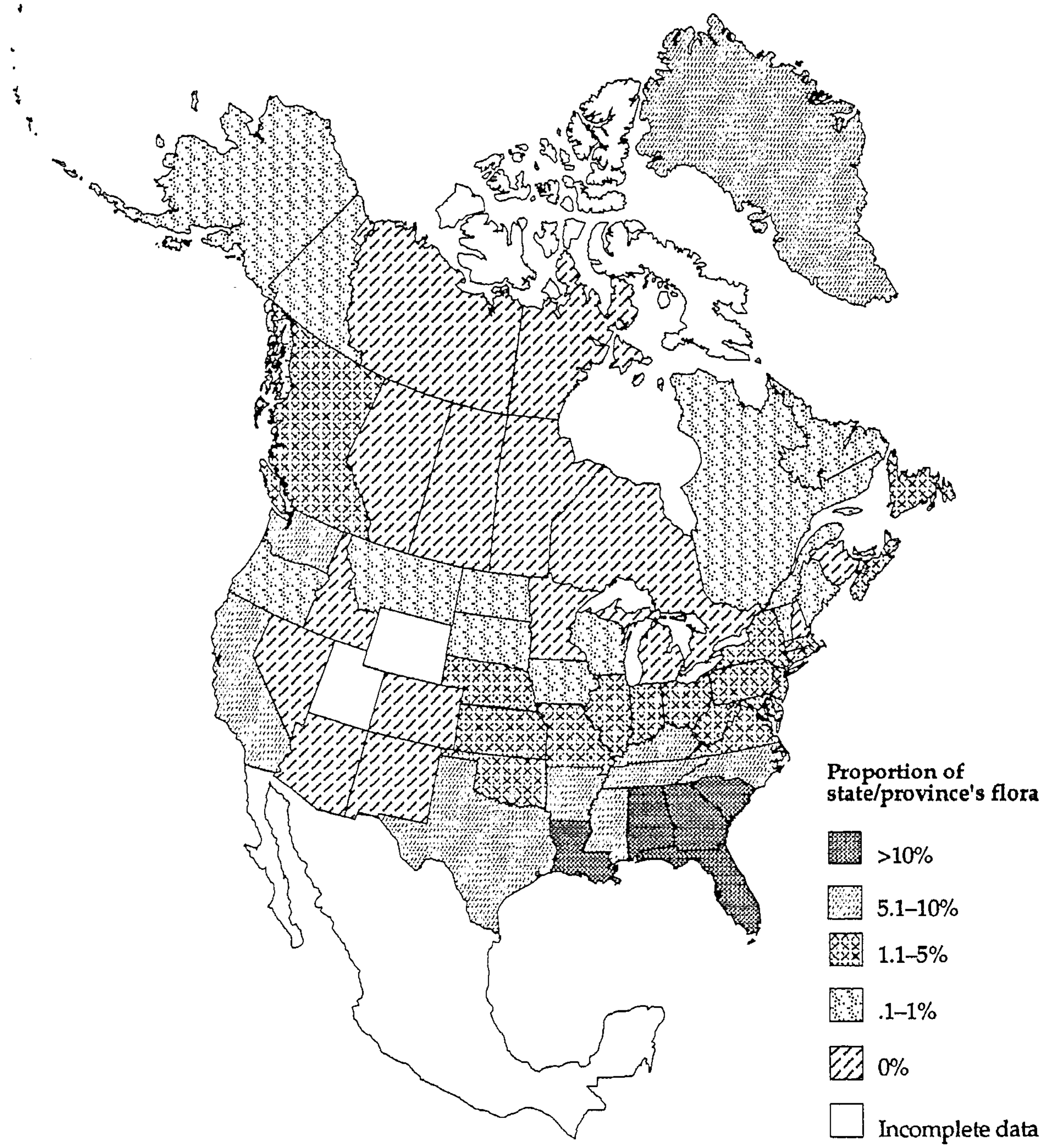

Figure 8-9
Out of Envelope Standard Deviation Method

The proportion of species in each state/province that would be out of their climate envelope in that state/ province with a +3°C temperature change. The results from the climate envelopes calculated by the standard deviation method are presented here. These results are the most extreme of the three methods of analysis.

Distribution of Endemic Species

The number of species endemic to one of the geographic zones used in this study varies considerably across the continent. The proportion of species restricted to one or two states or provinces is presented for each of these areas in (Figure 8-10). The regions with the highest levels of endemism and near-endemism are the southwestern states and Florida. California has by far the most species with limited ranges, with nearly 20% of that state's flora occurring either only in California, or in California and in one other state. The lowest levels of endemism or near-endemism are found in areas of the Great Plains or prairies, such as South Dakota, Iowa, Minnesota, Alberta, and Saskatchewan. The sub-state zones with the highest levels of endemism and near-endemism include the coastal ranges and Sierra Nevada in California, southern Florida, and the Columbia-Snake River plateau and Klamath Mountains in Oregon.

Southern and Northern Range Limits

Regions (states, provinces, and smaller zones) vary considerably in the number of species at their southernmost (Figure 8-11) or northernmost (Figure 8-12) range limit.

The highest proportion of southernmost range limits are found in California, Texas, Arizona, Florida, Louisiana, and Alabama (Figure 8-11). There are several sub-state zones that have remarkably high numbers of species at their southernmost range limits. The most notable are the coastal ranges of California, with about 1,330 species at their southernmost limit in one of the state's three coastal zones; the Gulf prairies and marshes, the southern plains, and the Trans-Pecos area of Texas with over 1,000 species each; and all three zones (Panhandle, Central, and Southern) in Florida with hundreds of species at their southernmost limits.

The areas with the most species at their northernmost range limit include Washington with 1,160 species, Idaho with 1,216 species, Arizona with 1,275 species, and Montana with 810 species (Figure 8-12). Other dramatic examples of such areas are the Canadian provinces Saskatchewan and Manitoba. The Central Valley and the Coastal Ranges of California with 447 and 866 species respectively, as well as central Florida (300 species) and the Trans-Pecos area (408 species) in Texas are some of the sub-state zones with the most species at their northernmost range limits.

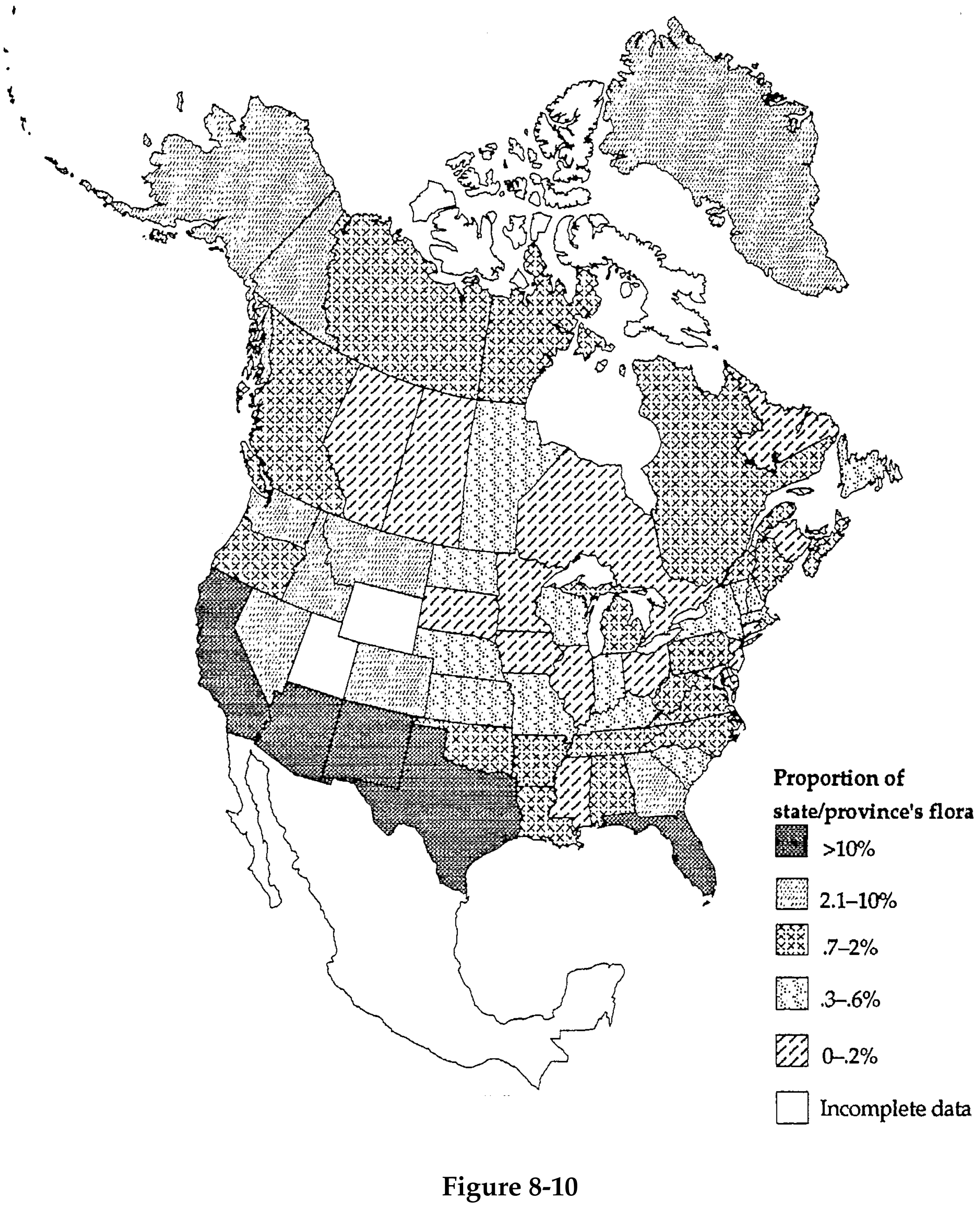

Figure 8-10
Endemics and Near Endemics

The proportion of species in each state or province that are endemics or near-endemics (restricted to one or two states or provinces).

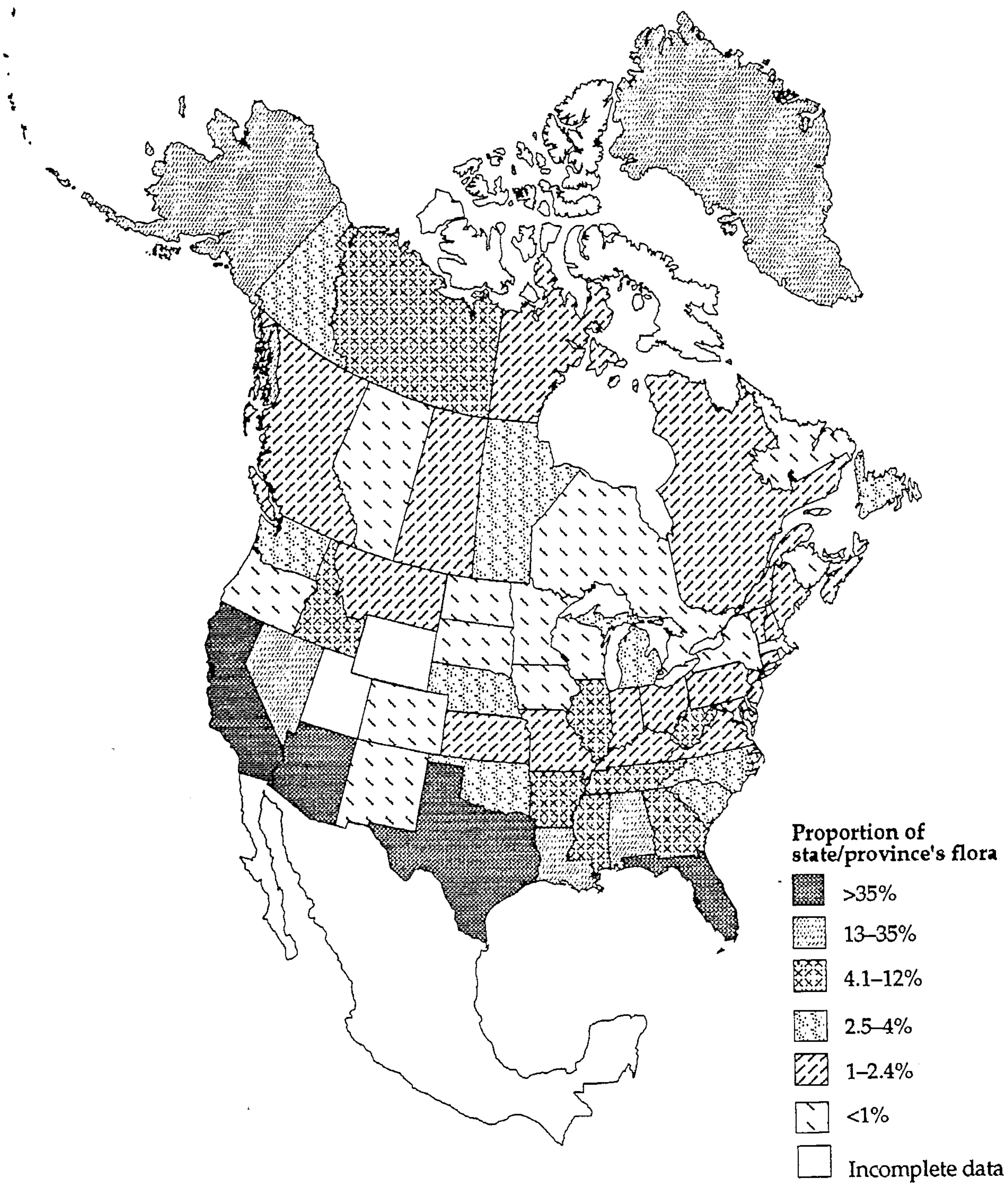

Figure 8-11
Southern Limits

The proportion of species in each of the 49 states in the study and each province in Canada for which that area is the most southern' extension of the species range (by latitude).

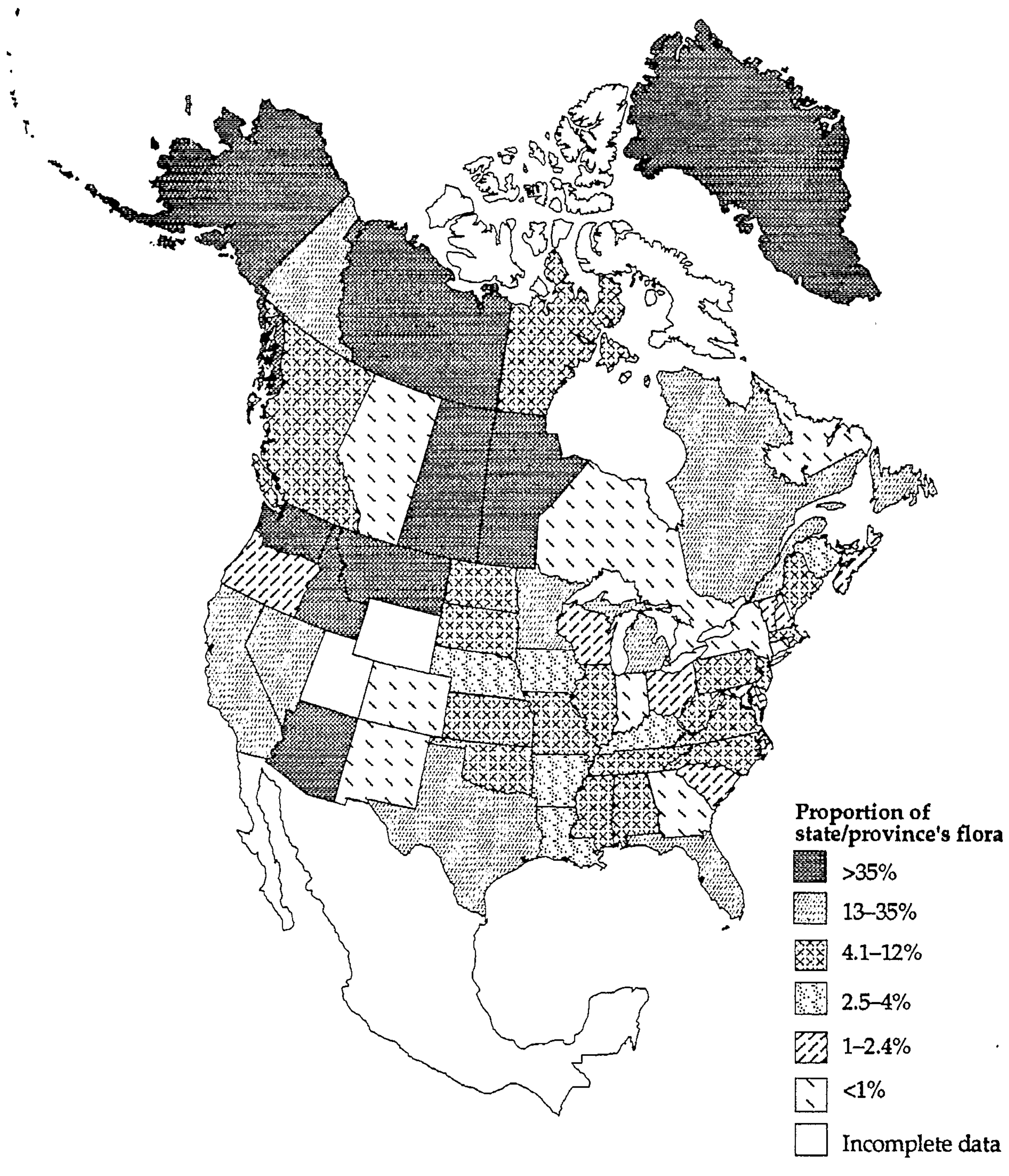

Figure 8-12
Northern Limits

The proportion of species in each of the 49 states in the study and each province in Canada for which that area is the most northern extension of the species range (by latitude).

9

DISCUSSION

The comprehensive database on the classification and distribution of North American vascular plants, developed by John Kartesz, is an immensely powerful tool for biogeographic analysis. These data, supplemented by additional distribution and species-biology data, are here used in conjunction with climate information to develop a climate envelope methodology which can be applied to each of North America's 15,148 native vascular plant species. The envelopes reflect the limits of regional temperatures experienced within the various geographical units of each species' reported current geographic range.

The general association between plant distributions and climate is unquestioned. The present analysis examines climate envelopes based on regional mean annual temperatures, as calculated by three methods, under a scenario of temperature increase that is uniform across the study area. Particular attention is given to the possible 3°C (5.4°F) increase considered by the IPCC (1992) to be likely. Species with small climate envelopes are identified as potentially "vulnerable" to climate change greater than the range of their present climate envelope, since these species may experience temperature stresses that are entirely novel, relative to the conditions in their current distributions.

The climate envelopes methodology used here is flexible and could be based on other (or a combination of) climate variables. The climate envelopes can also be used to predict the potential vulnerability of species under different and/or regional climate-change scenarios. As climate models continue to evolve, they can be used to make more explicit predictions about the effects of climate change on biodiversity. This analytical approach and the plant distribution database provide a tool for further, more refined analyses as improved climate predictions become available.

This preliminary analysis has shown that the impacts of rapid global warming on the flora of North America are potentially large. The results indicate that a mean global warming of 3°C could cause 7.0% to 10.8% of the 15,148 native plant species in North America to be entirely out of their climate envelopes, and hence vulnerable to extinction. For comparison, approximately 90 plant species are believed to have gone extinct in North America in the last two centuries (Russell and Morse 1992). While the timing and extent of climate change are under debate, a future climate averaging 3°C warmer is predicted as likely by various General Circulation Models (GCMs) (cf. Schneider 1989 and 1992, IPCC 1992), if the equivalent atmospheric concentration of carbon dioxide doubles in the next 50 years (Schneider et al. 1992).

As discussed earlier, there is substantial debate over the extent to which the present flora of North America is at equilibrium with the present climate. Some species may still be adjusting their ranges in response to past climate changes. Others are known to have substantial climate tolerances, yet presently occur only in isolated refugial areas. There are also species that persist in areas where they are not known to reproduce. Thus, for an undetermined portion of the plant species considered here, the results of the envelopes analysis would need modification to take into account the discrepancy between a species' present range and its overall climate tolerance. However, the analysis as conducted provides a first attempt to estimate the potential effects of climate change on the entire native vascular flora of North America, north of Mexico.

Species Vulnerability under Various Temperature Increases

Although a mean temperature increase of 3°C is anticipated by many GCMs, the results of this study suggest that significant numbers of plant species could be lost with smaller temperature increases, and perhaps even at the minimum of those predicted in current modelling scenarios (Figure 8-1). For example, 4.9% to 6.9% of the North American flora appears vulnerable to a 2°C increase in mean global temperature, and 7.0% to 10.8% vulnerable to a 3°C increase. In all three methods of analysis, the proportion of vulnerable species rises even more with slightly greater increases in global mean temperatures. A total of 11.1% to 17.5% of the native North American flora would be out of their temperature envelopes with +4°C mean global warming. Although the distribution of temperature envelopes is clearly not linear, no temperature thresholds, above which significantly more species are vulnerable to climate change, are readily detected.

Possible Effects of a Uniform 3°C Temperature Increase

Analyses of species vulnerability with respect to characteristics such as taxonomic group, rarity, habitat, and factors affecting dispersibility were based on the scenario of +3°C mean global temperature change.

Vulnerability within Taxonomic Groups

Most studies of the potential effects of climate change have focused on a few individual species, vegetation types, or entire ecosystems. There has been little work on possible patterns of vulnerability to climate change among higher taxonomic units, particularly entire genera or families, and impacts on biological diversity. Higher taxonomic units appear in this analysis to have substantially varying proportions of vulnerable species that are not related to the number of species in that taxonomic unit. No large family or major genus in North America, however, is composed entirely of species that would be out of their climate envelopes with +3°C mean temperature change (Tables 8-1 and 8-2).

The observation that genera or families vary in the proportion of species vulnerable to climate change suggests that whole lineages may vary in their susceptibility, possibly resulting in significant impacts on biodiversity. If entire genera are decimated or lost, it could signify critical losses to the genetic resources and evolutionary potential of the North American flora.

Potential Impacts on Rare Species

The species in the North American flora most vulnerable to climate change are almost invariably the rarest, both in terms of The Nature Conservancy/Natural Heritage Network conservation priority ranking system and the U.S. Fish and Wildlife Service's statuses under the Endangered Species Act (Figures 8-3b and 8-4b). Many rare species (by either standard) are restricted to few populations over a small geographic area and are regional or local endemics. Species with small ranges tend to have narrow climate envelopes and are likely to be identified in this analysis as vulnerable to potential climate change.

Since the distribution of narrowly endemic species varies considerably across the continent, certain areas would be likely to experience more dramatic changes to their floras due to loss of endemic species (Figure 8-10). For example, about 17.5% of the 15,148 native species in the study area are found in only one state or province, and slightly more than 13% are endemic to one within-state zone. Another 6.6% of the flora is restricted to two states or provinces and 11% are restricted to two zones. The majority of the species restricted to one or two zones occur in either California or Texas.

Several of the undivided regions, particularly Alabama (cf. Thomas 1976), Arizona (Kearney and Peebles 1951), and Nevada (Kartesz 1988), are rich in endemic plants with fairly narrow distributions. Notable among these are the several endemic plants of Ash Meadows in southern Nevada which are found only in a single desert spring system a few thousand hectares in area (cf. USFWS 1985). These species are considered resilient because they were credited with Nevada's entire temperature range, 7.1°C to 12.7°C (depending on the method of calculating the climate envelope).

Potential Impacts on Common Species

Common species tend to have wider geographic ranges, occurring in more populations or sites. They thus experience a wider range of current temperature (larger climate envelopes), and are presumably less vulnerable to potential climate changes. Even so, 7.5% to 9.8% of the species that are potentially vulnerable to a climate change of +3°C are considered common species (ranked G4 or G5). By Conservancy standards, species ranked G4 are considered relatively secure, and G5-ranked species demonstrably secure. Such plants have many populations (hundreds or more) over a substantial geographical range. The vulnerable G4-ranked species are more likely to be those species that are extremely common within a relatively restricted area, rather than those sparsely distributed over large areas. For such plants to be considered vulnerable to climate change, their ranges must be contained in a narrow band of climates, as for *Quercus inopina* (Florida Scrub oak), endemic to central Florida but locally abundant there (Johnson and Abrahamson 1982).

The more common (ranked G4 or G5) species identified by this analysis as vulnerable currently receive little or no conservation attention except in local areas where they are uncommon. Some of these species are widespread tropical plants with small U.S. ranges, but are not yet identified as such in the data used here. Since many tropical species are presently at their northernmost limit in places such as Florida, climate change may not be a significant concern for them. Other species currently ranked G5 but here identified as potentially vulnerable to climate change may need reassessment of their ranks since the G5 rank indicates an absence of significant known threats.

For all species that consist of local populations with relatively narrow climate tolerances, the climate-envelope analysis of whole species de-emphasizes the possibility that some populations may be out of their idiosyncratic population-level climate envelopes. For widespread species, however, the differences between populations may be more significant. One of these species may actually be sensitive to climate change because, in terms of climate tolerance, it is not one widespread entity, but a collection of narrowly distributed entities with small temperature envelopes. If there are genetic variations between populations, then the loss of several populations could have a notable impact on the genetic diversity of the species.

For example, *Pinus ponderosa* (ponderosa pine) occurs throughout most of western North America, with a quite large climate envelope (20.9 to 26.8°C, depending on method). However, as discussed previously, this species is composed of several population groups with genetically distinct characteristics (cf. Millar and Libby 1991), each presumably having a climate envelope far narrower than 20°C.

Many of the species identified by this study as not vulnerable to extinction may nevertheless become significantly more rare–a G4-ranked species may become a G2-ranked species, for example–if range contraction at the southern range limit is not matched by expansion at the northern range limit. Additionally, many of the approximately 1,450 to 1,630 species ranked G1 and G2 and identified as "not vulnerable" are likely to lose populations from the southern portion of their ranges. Such losses would further endanger these already rare species. Warming temperatures at the southern edges of species ranges may necessitate increased management efforts in these zones, in an attempt to protect the species there and save past investments in protection.

Vulnerability of Wetland and Aquatic Species

The analysis suggests that both facultative and obligate wetland species, including aquatics, are less likely to be vulnerable than are upland species. For example, only

2.5% to 4.3% of the obligate wetland species would be out of their climate envelope in a +3°C world, while 8.6% to 13.1% of the upland species would be similarly affected (Table 8-4).

This difference reflects the wide distributions that many wetland species–even rare ones–tend to have along coastlines or watersheds, resulting in large climate envelopes. There are several reasons, however, why wetlands species may be interesting and complex cases relative to the limited notion of "vulnerability," based solely on temperature, developed in this study.

Discontinuous Habitats.

Many wetland species occupy specialized habitats that are discontinuous on the landscape, more so than for most upland species. This distribution may prevent these species from readily dispersing from one wetland to another. Extensive destruction of wetlands in North America, and especially in the contiguous United States, has further fragmented wetland habitat. Losses from the matrix of wetlands increase the distances that species must migrate to find the nearest appropriate habitat area.

Hydrologic Changes.

Warmer temperatures increase evapotranspiration and may cause soils and habitats, particularly wetlands, to become drier, unless local precipitation increases. Even in some areas that are predicted to experience increased precipitation, increased evaporative losses may exceed gains from precipitation. Marginally drier conditions can radically alter the suitability of habitat for some species. Although all species may be threatened by climate-change effects on their habitat, wetland species are likely to be the most vulnerable, even though they may remain within their temperature-based climate envelope.

For example, the previously discussed *Ptilimnium nodosum* (harperella) is a rare but widely distributed aquatic plant species that occurs in a narrow range of water depths in streams and coastal plain ponds in the eastern United States. *Ptilimnium* is eliminated both from areas that are too dry (the species is sensitive to desiccation and competition) and from areas with late summer water too deep for these plants to complete their life cycle (Maddox and Bartgis 1991). Although this species is not considered vulnerable in any of the three methods of temperature-envelope analysis used here, modest changes in local hydrology would significantly threaten it.

Relation to Sea-Level Rise.

Many North American wetlands are associated with seacoasts and related estuaries, including salt marshes, dune swales, mangrove swamps, and freshwater-estuarine intertidal shores. Not only has post-Columbian development interrupted these habitats along all but the Arctic coast, but development immediately upslope in many places would also prevent these habitat types from shifting to slightly higher ground if sea levels rise significantly, as expected in most climate-change scenarios (IPCC 1990). Rare plants of coastal wetlands are thus unusually susceptible to losses of populations if sea level changes as a result of climate change (Reid and Trexler 1991).

Dispersal and Establishment Abilities

Species will vary in their abilities to move northward (Figure 8-8). This analysis does not allow projections concerning which species will be able to migrate. However, based on knowledge about their ecological and biological characteristics, some suggestions can be made.

The majority of rare species, and especially of critically endangered ones, are less likely to successfully migrate for three reasons. First, many (but not all) rare species lack the migration-enhancing characteristics of mobile species. Secondly, most rare species tend to occur in few populations, and often in low numbers, resulting in few sources of colonists for new northern populations. Thirdly, many of them are species that are restricted to wetlands, unusual substrates, or other specialized habitats, and may have difficulty migrating to comparable new sites due to the highly fragmented landscape and the distance between suitable sites, regardless of their dispersibility.

The relative scarcity of weedy or highly mobile species among those identified as vulnerable suggests that the classes of species potentially most vulnerable to climate change are, in general, also the species least equipped to respond with range shifts. About 25% to 28% of the vulnerable species are quite rare (ranked G1 and G2). Such species have already shown themselves in general to be either sensitive to environmental disturbance or poor colonizers of new habitats, either because of specialization to habitat types that are fragmented across the landscape or because they are especially sedentary.

During the glacial advances and retreats of the Pleistocene, there were immense changes in the distribution of plant species as climates changed. However, these migrations occurred over thousands of years, in conditions of more continuous natural landscape. In the next 50-100 years, climate may change much more rapidly and the current landscape is highly fragmented by human development. Even those species which exhibit considerable mobility may not be able to bridge habitat gaps within the available time.

Possible Effects on Species Composition of Local Floras

According to the taxonomic classification in the revised checklist by Kartesz (1993), the native vascular flora of North America, north of Mexico, numbers 15,148 extant species, ranging from single-site endemics to plants abundant transcontinentally. As shown in Table 9-1 (adapted from Kartesz 1992), species richness is greatest in the southern and western portions of the continent, particularly California, Texas, Arizona, Oregon, and

Florida. Species numbers are low in Greenland, northern Canada, and Alaska, and relatively low in central Canada, the midwestern United States, and New England.

Table 9-1 Total Species Counts

UNITED STATES	
Alabama	2,419
Alaska	1,245
Arizona	3,249
Arkansas	2,166
California	5,094
Colorado	2,638
Connecticut	1,668
Delaware	1,578
Florida	2,874
Georgia	2,762
Idaho	2,323
Illinois	2,055
Indiana	1,837
Iowa	1,385
Kansas	1,686
Kentucky	2,015
Louisiana	2,085
Maine	1,488
Maryland	2,035
Massachusetts	1,648
Michigan	1,950
Minnesota	1,718
Mississippi	2,034
Missouri	1,886
Montana	2,106
Nebraska	1,459
Nevada	2,679
New Hampshire	1,423
New Jersey	1,905
New Mexico	2,810
New York	2,188
North Carolina	2,445
North Dakota	1,137
Ohio	1,915
Ontario	1,926
Oklahoma	2,278
Oregon	2,932
Pennsylvania	2,028
Rhode Island	1,350
South Carolina	2,194
South Dakota	1,403
Tennessee	2,111
Texas	4,512
Utah	2,590
Vermont	1,486
Virginia	2,320
Washington	2,331
West Virginia	1,727
Wisconsin	1,624
Wyoming	2,080
CANADA	
Alberta	1,598
British Columbia	2,168
Franklin	340
Keewatin	461
Labrador	606
Mackenzie	912
Manitoba	1,285
New Brunswick	966
Newfoundland	816
Nova Scotia	1,030
Prince Edward Island	636
Quebec	1,811
Saskatchewan	1,180
Yukon	1,001
GREENLAND	449

The number of native vascular plant species in each of the states or provinces in the study.

In addition to possibly causing species extinctions, climate change could profoundly affect the species composition of local floras. If temperatures increase enough to shift the local climate beyond species' tolerances, the ranges of most North American species would probably retreat from their southern and/or downslope edges. They would thus be vulnerable to local extirpation regardless of how secure they might be elsewhere. Consequently, populations near the southern range limits of species and at low elevations would be most likely to be lost. Northward range expansion of some species may eventually balance the number of species lost from an area, but the local flora and communities may be composed of unique assemblages.

Regional Patterns in Species Vulnerability.
As shown in Figure 8-9 and Table 8-5, the proportion of species that would be out of their climate envelopes in each state or province, according to this analysis, varies regionally. The figure presents only the results from the climate envelopes calculated by using standard-deviations, the *least* conservative method. Areas that would be most affected by species loss are those that contain many species at the southern edges of their ranges (Figure 8-11)–that is, areas that appear to be "ecotonal" with respect to climate.

The more detailed patterns detected for the various subdivided states and provinces presumably also would occur in many of the jurisdictions that were not subdivided in the present study. For example, Georgia was divided into several zones, allowing specific analysis of the set of Appalachian plants with their southern range limits in northern Georgia. Many Alabama species, similarly, occur only in the northern, mountainous part of the state (cf. Clark 1971), but specific analysis of these was not possible here since data on within-state distributions were not developed for Alabama, a state still poorly known floristically. The Great Basin is another area that may contain many plant species that are particularly sensitive to climate change (cf. Wharton et al. 1990), although not identified as such in the present study due to the great elevation ranges (and hence large climate ranges) in the geographical units analyzed here.

Losses from Southernmost Range Limits.
A number of regions in North America are ecotonal with respect to the southern distribution of species. These areas contain an unusually large number of species for which the given area is the southern limit of the species range (Figure 8-11). The floras of these areas will tend to experience more species losses because populations at the southern ends of species ranges would be outside of their climate envelopes if temperatures increase.

The southernmost ends of north-south mountain ranges often have many species at their southern limit. For example, the southern end of the higher Appalachians, in the area where Georgia, North Carolina, and South Carolina adjoin, is the southern range limit of about 150 species that do not extend downslope into the warmer climate of the adjacent Piedmont. Similarly, the Sierra Nevada in California is the southernmost zone for about 250 species. The southern Rockies also contain unusually high numbers of species at their southern range limits.

Other dramatic examples of sub-state regions that include the southernmost extent of many species ranges, and thus are likely to be most significantly affected by climate change, are found in California, Texas, and Florida. In California, the coastal ranges contain about 1,330 species (almost one third of the state's native flora) that reach their southern limit in one of the state's three coastal mountain zones, as defined here. In Texas, the Gulf Coast prairies and marshes, the southern plains, and the Trans-Pecos area each have over 1,000 species that are at their southernmost limits. In Florida, all three zones (Panhandle, Central, and Southern) have hundreds of species that are at their southernmost limits. Some of these plants, however, may actually have ranges that extend into Mexico or tropical areas, although not recorded as such here, reducing the potential impact on the floras of the above areas.

There are two major consequences of this phenomenon of local concentrations of species at their southern range limits. First, such species are generally most likely to be lost from local floras if the climate warms. Many of these species are already rare in states along their southern limits, due to ecological stresses or limited habitat. Such species are generally inventoried and monitored by Heritage Programs, are considered during environmental reviews and conservation planning (Hoose 1981, Jenkins 1985, Morse 1987), and are often protected by state law or regulation (cf. Kartesz and Kartesz 1977, McMahan 1980). Range contraction, the process of progressive loss of the more vulnerable populations within a species' distribution, is a major means by which currently secure species may become endangered, in this case due to climate change.

Secondly, gains and losses in the local flora would greatly affect the composition of plant communities in these floristically ecotonal regions. Weedy species (native or exotic) new to the local flora could become established, and may become dominant. Ecotonal areas contain more species that are vulnerable to climate change, increasing the probability of large changes in community structures. Their elimination would bring greater changes than in areas with fewer vulnerable species. For example, if forest-tree species are lost from an area (as when a forest becomes a savanna or prairie), many herbaceous species may be lost secondarily due to loss of canopy and change to the microenvironment.

Northward Migrations into New Areas.

Species currently limited by intolerance of cold conditions may migrate northward if the climate warms. This process is likely to be most significant at the northern range limits of species ranges. As with southern range edges, certain areas contain more species at the northern edge of their range than others (Figure 8-12). For example, Washington contains about 1,160 species for which this state is the northernmost range limit. Other dramatic examples of such areas are the Canadian provinces Saskatchewan and Manitoba, and the Central Valley and the Coastal Ranges of California, as well as central Florida and the Trans-Pecos area in Texas.

The less vulnerable and more dispersible species would be the most likely to expand their ranges northwards as climatically marginal areas become more suitable. If suitable habitats are present, substantial additions to the local floras can be expected in regions immediately north of areas presently rich in species at their northernmost range limits. The presence of more resilient species in new locations may offset (in terms of numbers of species) the regional loss of species which are now at their southern range limits in that area. The overall effect of these northward migrations may be to replace vulnerable, less dispersible (and often rare) species with resistant, dispersible (and widespread) species in each region.

Since Mexican or Caribbean plant species that are not already known from the United States were not considered, this analysis does not address the likelihood that some, or even many, such species may move northward into the United States if the climate warms. An important point concerning northward range extensions is that the species must have the capacity to migrate and establish in new habitats.

Habitat Fragmentation and the Limits to Species Migration

The overwhelming changes to the American landscape over the past five centuries suggest that species' capabilities of adjusting to changing climates would, in general, be substantially more limited than in past glacial cycles. Native populations, particularly for rare or non-weedy species, are generally assumed to be fewer and smaller now than before European exploration and settlement. Reduced populations provide fewer sources of propagules for dispersal, and genetic variation in some species may also be depleted. Since many of the rare or peculiar habitats and substrates have been altered, developed, or destroyed, there are fewer novel places available for colonization by habitat-constrained species, even if they can disperse fast enough to follow rapid changes in the climate.

Extensive habitat destruction and fragmentation increases the dependence of many species on the relatively rare events of long-distance dispersal, since appropriate colonization sites are likely to be fewer and more isolated. Furthermore, species often must disperse across an unnatural landscape of hostile habitats, which include roads, cities and suburbs, and farmland. These developed areas tend to limit the possibilities for incremental landscapes where many of the open or disturbed areas are increasingly colonized by aggressive weedy exotics, rather than being available for less aggressive native species. range expansion by short-distance dispersal. Finally, newly arriving propagules would need to establish themselves in landscapes where many of the open or disturbed areas are increasingly colonized by aggressive weedy exotics, rather than being available for less aggressive native species.

A corollary to the suggestion that highly mobile, or weedy, species are less vulnerable to climate change is that many species of exotic weeds may be favored over native species under a warmer climate. Invasive exotic species, on the whole, have the generalist characteristics that may make them even more prevalent in the future. Most such species are widespread (with large climate tolerances), prolific and fast growing, and capable of establishing in disturbed habitats. New work identifying native or exotic weed pests that are likely to move into new areas would be especially important to agriculturalists, foresters, and other land managers.

Potential Resilience of Apparently Vulnerable Species

Since climate stations are mostly in flat, open areas and are distributed broadly across the landscape, the regional climates used here can not completely reflect the full range of microclimates present in any climate zone. Within an otherwise warmer area, certain species may occur only in cool habitats, such as north-facing cliffs or areas near waterfalls. Other species may occur only in warm habitats, such as south-facing slopes or drifting sand deposits. In either case, the estimation of the climate envelopes for such species is either wrong or too large.

Of the 1,060 to 1,630 species that this analysis suggests would be outside of their climate envelopes, some might prove resilient, or actually benefit from local warming. Under the right conditions, some rare species might become more common. Species may respond to changing climate by moving locally among sites with marginally different microclimates.

Rare Plants of Presently Warm Microclimates

The use of regional climate averages, rather than exact microclimate data, in the climate-envelopes analysis may incorrectly assess the potential vulnerability of species found only in specific microclimates. The most serious limitation suggested here is that species endemic to warm microclimates in zones with narrow climate-station temperature ranges would be considered vulnerable in the present analysis. These species instead could be expected to spread and prosper if the regional climate warms to resemble more closely these species' present microclimates. This would require the availability of appropriate habitat nearby, and survival of the original population until successful expansion could occur.

The characteristic plants of the Appalachian shale barrens, for example, may be quite resilient to substantial regional temperature increases, and might even become more abundant in a warmer climate. As discussed earlier, these species currently occur in the warmest local microhabitat, steep south-facing shale talus slopes. At many sites, these barrens grade into adjacent open woods, with a gradual and patchy transition dependent on local topography. With global warming, these adjacent woods may become even more open, providing expansion space for the shale-barren species even if the original sites becomes too warm (or too dry) for these plants. Dispersal requirements would be modest, perhaps a hundred meters, well within the normal incremental dispersal capabilities of most species.

Upslope and Aspect Shifts in Species Distributions

To some extent, where topography permits, species may follow their temperature requirements by dispersing and establishing upslope to higher elevations, a phenomenon well documented in species responses to past climate change. At mid-latitudes, an altitude shift of 500 meters is the equivalent in terms of temperature to latitude shift of 250 km (MacArthur 1972), or about 1000 feet of elevation to 100 miles of latitude. In areas with significant elevational variation, this process may help many species persist, if they are able to adapt to potentially different moisture conditions.

Another possible ecological response is that some species could move locally from relatively hot and dry south-facing slopes to presently cooler and moister north-facing slopes, if these latter slopes become warmer and drier as the south-facing slopes become less hospitable.

Refugial populations in the current flora demonstrate that species can often persist within their original range, despite changes in the regional climate which make it less suitable, by finding microhabitats (refugia) within which the original climatic conditions still exist. The transformation of widespread species into refugial species, and vice versa, could represent an unpredictable yet substantial impact on the flora of a given area.

Alpine species and others found exclusively at the highest elevations within an area cannot move further upslope, and may be extirpated by climate change. The alpine floras of New England, for example, contain many species at their southern range limits, plus a few endemics (Zwinger and Willard 1972, Graber 1980). These floras could be severely stressed by further warming of the climate there, and occurrences of some taxa already appear extirpated there (Steele 1982, Zika 1992).

Limitations of the Present Analysis

Several specific aspects of the data and analysis in the present study place further constraints on the interpretation of the results obtained. These concern the level of geographic precision, weaknesses in the distribution of climate stations, and uncertainties in the botanical data. Improvements in any of these areas would refine the reliability of the results presented here.

Areas with Sparse Climate Data

Some of the geographic units used here, selected for floristic purposes, had too few climate stations in the datasets used for meaningful analysis. Additional climate data, either from more observing locations or from regionalized climate maps, could be used to provide better estimates of the ranges of present climates in these geographical areas. Higher elevations tend to be under-represented in the climate-station data.

Accordingly, narrowly distributed species with broad elevation ranges may be incorrectly categorized as vulnerable if the climate ranges for mountainous zones are too narrow and do not adequately represent the altitudinal relief of the zone.

For species restricted to mountaintops, elevation-based subzones with narrower climate envelopes might be a more accurate representation. It was not feasible, however, to obtain species-distribution data by narrow elevation zones for many regions, so this possibility was not pursued here. The climatically broad zones in mountainous regions attribute a larger temperature range to these mountaintop species than they actually experience. These high-elevation species may thus be considered resilient, based on the current analysis, when they really may be quite vulnerable to climate change.

Limitations in the Botanical Data

Uncertainties in the taxonomic classification affect the results in two ways. If, for example, two geographically restricted species were treated by Kartesz as a single, broader, species, they might individually be vulnerable to climate change, while the collective species appears resilient. Conversely, if what in reality is one species was treated here as two (or several) more narrowly defined species, they may have individually appeared more vulnerable than the more broadly defined species would be, considered under the same method of analysis. While significant in individual cases, these two effects tend to counterbalance each other when general patterns are considered.

As a rough extimate, less than 5% of currently accepted North American vascular plant species are taxonomically questionable, suggesting perhaps half those might be combined into other species upon further study. Conversely, perhaps 2% of currently recognized species will be found by future studies to be composed of more than one species. Of course, botanists will also continue to find additional species completely new to science that were not previously confused with known species.

Uncertainties in the geographical distribution data also affect the results obtained here. If states or smaller geographic units in which a species occurs were omitted from the distributions data, that species' climate range would have been underestimated if the missing area represented a climate limit for the species. Similarly, erroneously crediting a species to an area could have resulted in overestimation of its climate range.

While not determined for all the species considered, the species-biology data are presumably sufficiently representative to provide a basis for the patterns detected here. Further refinements on these data would add confidence to these findings.

The states and provinces selected to be subdivided were chosen on the basis of relatively large climate ranges, as well as the availability of sufficiently detailed plant distribution data. Not all climatically or topographically diverse areas were subdivided, leaving some very broad climate zones. If the climate range of a state or province exceeds the 3°C interval used for most of the present analysis, then any species recorded as occurring in one or more of these areas is automatically determined to be resilient to climate change. For example, *Erythronium propullans* (Minnesota dwarf trout lily) is known from only a small portion of Minnesota, but it was here given the state's entire temperature range (3.2 to 5.4°C difference between minimum and maximum mean annual temperatures), thus appearing resilient to a +3°C climate change. Two other significant effects of using distribution data at the state and province level are misrepresentation of the actual climate ranges of narrowly endemic species and crediting an additional broad range of climate to species whose range only enters a small part of the area.

Since the climate-envelope analysis is based on climate station data from whole zones, the inclusion of any area with a broad temperature range would makes some species appear resilient to climate change. Most widespread species occur in at least one of the large states or provinces that were not subdivided, and are hence automatically considered resilient. Since widespread species usually experience a broad range of climate, no major error is introduced by this overestimation of their climate envelopes. However, species with narrow geographic distributions that include a portion of an undivided area do not experience that area's general climate range, even as represented by weather-station data. The postulated temperature envelopes of these species are large, greatly reducing their potential vulnerability to climate change in this analysis. Use of additional geographical areas in the analysis would lead to more accurate climate envelopes but would require better botanical data than are often available.

10

CONCLUSIONS AND RECOMMENDATIONS

This study is a climate-envelopes analysis of the geographic ranges of the 15,148 native North American vascular plant species. The North American distribution by states, provinces, and within-state or within-province geographic units (194 units altogether) of the native North American vascular plant species was matched with climate data for these same geographic units to estimate the "climate envelope" for each species. The envelope is based on the upper and lower limits of temperature currently experienced by each species within its present range.

To provide a range estimate of possible vulnerability to different amounts of temperature change, three methods were used to determine the climate envelope characterizing a species' present distribution. Each area's climate was recalculated on the basis of projected increased mean temperature. For purposes of this analysis, it was assumed that a species would be eliminated from areas expected to have future regional climates outside the species' present calculated climate envelope.

Biological assumptions implicit in this analysis include that species' current climate envelopes are equivalent to their physiological tolerances of climate variation, and that current species distributions are in equilibrium with climate. While these assumptions do not hold for all species, they provide a consistent frame of reference for identifying groups and regions which might need further attention.

Conclusions

1. If the mean annual temperature increases by +3°C (5.4°F), an amount considered likely by the IPCC (1992), a significant number of North America's native vascular plant species may be vulnerable to climate change. About 7% to 11% of the flora would be entirely out of its present climate envelope (i.e., none of the species' current range would exhibit a climate within the species' envelope) with this magnitude of warming. In a +5°C climate, about 15% to 20% of the species would be entirely out of their envelopes; between 28% and 44% would be out in a +10°C climate.

2. Rare species would be disproportionately affected by a warming trend. While approximately 10% to 18% of the rare species (ranked G1, G2, or G3 by The Nature Conservancy and the Natural Heritage Network) would be totally outside their temperature envelopes in a +3°C climate, only 1% to 2% of "common" species (Conservancy/Heritage ranks G4 and G5) are at such risk. Many of these presently

common species may become rare, however, creating a new generation of endangered species. Approximately 17% to 33% of the 354 species that are protected, or candidates for protection, under the U.S. Endangered Species Act would be out of their climate envelopes in a +3°C climate. Rare species tend to have narrow geographic distributions, and are potentially more sensitive to climatic changes.

3. The impact of potential climate change on species not globally at risk (i.e., species whose entire current range will be not out of their climate envelope), will be seen in local floras. If temperatures warm and the southern portion of these species' current ranges falls outside their climate envelopes, these populations could be eliminated from these areas. Geographic regions of North America vary in the number of species they are likely to lose. The areas that are most likely to be affected would be regions that represent the southern edge of many species ranges. The states with the highest proportion of southernmost range limits include California, Texas, Arizona, Florida, Louisiana, and Alabama. In addition, there are several smaller geographic areas that include the southernmost extent of many species' ranges. These sub-state regions include the southern Appalachians (Georgia, North Carolina, and South Carolina); the Coast Ranges in California; the Gulf prairies and marshes, the southern plains, and the Trans-Pecos areas of Texas; and all three zones (Panhandle, Central, and Southern) in Florida. The range of some species in these regions may actually extend into Mexico or tropical areas, thus reducing their potential vulnerability to climate change.

4. If climate warms, there may be a significant northward shift of species ranges. Range shifts may cause additions and changes to the floras of regions adjacent to areas that contain many species at the northern limit of their distributions. If northward range expansion keeps pace with climate-stress-induced range depletion further south, a species may not be vulnerable to extinction due to projected climate change. Species vary in their abilities to disperse. Rare species (especially critically endangered ones) tend to have low dispersal rates and/or poor establishment abilities, thus are less likely to successfully migrate to new areas. The migratory ability of many rare species is additionally limited by habitat restrictions. Species survival by northward migration is limited by the projected rates of climate change, which exceed known effective dispersal rates of almost all plant species, and the large gaps between areas of potential habitat for most species in North America. Past Pleistocene migrations typically occurred over periods of several thousand years and in conditions of more continuous natural landscape. Today, suitable habitat is highly fragmented in many areas by human development. Even species that exhibit considerable mobility may not be able to bridge these habitat gaps.

5. In terms of local or regional effects, less vulnerable and more dispersible species may be expected to expand their ranges northwards. As these resilient species colonize new habitats, their presence in new locations may offset (in terms of numbers of species) the regional loss of species that are now at their southern range

limits there. This would have an overall effect of replacing vulnerable, less dispersible (and often rare) species with resistant, dispersible (and widespread) species in each local area.

6. The possibilities for local plant populations to persist through climate change at their present sites could make some species more resilient to climate change than the present analysis indicates. Such climate tolerance may be particularly significant for habitat-limited rarities that appear to have narrow climate ranges (based on their present distributions) yet presumably have survived past climate changes at or near their present sites.

7. Since the effects of significant global warming on biodiversity could be large, and furthermore could vary by region, the selection, design, and management of nature preserves should take into account the possible implications of climate change on species distribution and survival. Land management organizations, such as the National Park Service, the U.S. Forest Service, many state and provincial agencies, and The Nature Conservancy, may need to revise their strategies accordingly.

8. The results of a climate-envelopes analysis such as the present preliminary study must be interpreted carefully. There is no question that climate determines broad patterns of vegetation and plant species distributions. However, when considering individual species and more local patterns of distribution, additional factors often become important. Climate envelopes cannot reflect this complexity, especially when envelopes are being determined for over 15,000 species. The incomplete botanical and phytogeographic knowledge of the North American flora places additional limitations on this type of analysis. Therefore, the present findings are of interest primarily for the broad patterns detected rather than for their applicability to individual species. Using an arbitrary definition of vulnerability, this analysis provides an initial estimate of the magnitude of the threat imposed by climate change and a means to determine which species might be the most vulnerable. Without further species-specific information, it should not be concluded that any particular species will definitely be either threatened by or resilient to climate change.

Recommendations

Rapid climate change may pose a substantial threat to plant species diversity in North America as we know it today, both in terms of its potential negative effects on rare species and on the native flora generally. Further study is needed to refine the nature and scope of these possible effects. Climate change, especially rapid change, would also present difficult biological and ethical challenges to species conservation efforts.

Conservation Implications

Rapid climate change could place novel demands and constraints on plant species conservation. Vulnerability to climate change could affect selection and design of new preserves and management procedures in existing preserves, especially in southern portions of species ranges. Management of species threatened by climate change could involve restoration and transplantation of species among preserves or into new northern locations and/or ex situ propagation of critical species (cf. Falk and Walter 1986). Possible management actions such as exotic species removal or hydrological management may not be qualitatively different than those that are currently required of land managers, but climate change may increase the intensity and frequency of threats from exotic species, drought, and fire. In the absence of clear evidence that the predicted climate changes will *not* occur, preliminary plans for conservation actions should be developed.

Recommendations for Further Study

Further attention should be given to two areas of research relevant to maintaining populations of rare species in areas which, according to this analysis, are out of their climate envelopes. Where resources are available, the actual climate tolerances of representative examples of these species under natural conditions should be determined. Second, the potential for species to survive in microclimates during regional climate changes should be examined. This research would help determine which species would be most severely affected because of the inadequacy of existing mechanisms to maintain them and will assist in habitat management.

As noted above, many rare plant taxa are physiologically capable of surviving much greater extremes of climate than are reflected in their current distributions. The ability of individual plants to adjust physiological characteristics that control transpiration rates, efficiency of water use, and allocation of resources, for example, in response to changes in temperature and moisture conditions, should be viewed as instrumental to resilience to climate change (Shugart et al. 1986). Selected mechanisms for persistence under temperature and moisture stress should be investigated further, along with the effects on interspecific competition of the effects of climate stress on species with different tolerance abilities.

Research on local microclimates should include assessments of the extent to which the climate in a given microhabitat would vary with changes in the surrounding regional climate, and investigations of why the species of interest occur at this site. If the species is restricted to the microhabitat primarily because of competitive pressures from species that cannot tolerate the local conditions, then the mere fact that the microclimate continues to differ from regional conditions may be sufficient to maintain the species there. If, on the other hand, the issue is absolute tolerance of climatic conditions, then a cool refuge that warms by 3°C in parallel with regional temperature increases may become unsuitable for heat-intolerant species it previously supported.

An additional research activity that may provide an effective early warning system would be monitoring several of the most sensitive populations of vulnerable plants. Local populations of rare species at their southern range limits could be selected as possible indicators of regional changes in climate. Regular monitoring would assess identifiable threats such as new competitor species or hydrologic changes; the populations' responses to these threats (such as visible drought stress or die-off); and increased establishment of new populations in similar habitats upslope or northwards.

11

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A

APPENDIX: NOTES ON THE PLANT DISTRIBUTIONS DATA

This appendix provides further background on the subdivision of various states and provinces into the geographical units or 'zones' (Figure 6-1) for which the climate envelopes were developed. Sources of the botanical data on species distributions within the subdivided areas are also summarized here. The basis for the zones and the sources of plant distribution information used are listed below for each subdivided state or province. For some of these areas, the within-state zones are those used in recent floristic publications, such as Hatch et al. (1990) for Texas. In other cases, the zones were developed for this study by Conservancy staff, using sources specific to each state or province as well as various general references.

Most of the geographical units developed here are adapted from the physiographic regions of *Natural Regions of the United States and Canada* (Hunt 1974), or an appropriate regional source. Adjustments were made first to distinguish important floristic regions, and second-to separate mountainous regions more clearly from topographically more uniform regions. A third consideration was to divide large areas latitudinally or longitudinally to follow climate patterns. Other major references regularly consulted include the WMO climate atlas (Steinhauser 1979); landform texts by Hunt (1967) and Thornbury (1965); the Raisz (1957 and 1965) landform maps; and vegetation maps by Bailey (1976, 1989), Küchler (1964), Omernik (1986), and Rowe (1972). Patterns in published distribution ranges in the state or province in question were also examined, and botanists familiar with each region's biogeography were also consulted.

Standard floristic references, especially those offering dot maps of species distributions, were then used to assign species to zones. The taxonomy used in the numerous sources of local distribution data were reconciled with the Kartesz (1993) species classification by using a synonym index derived from the Kartesz checklist database file. Species reported for a state by Kartesz but not readily found in the standard floristic works for that state were left in the geographical data file at the state level of resolution, without indication of within-state zones (i.e., as if it occurred throughout the state).

The sources for geographic zones and species distributions used for this study are summarized below.

Canada

Four province-level areas of Canada were further divided here. Also, the province of Newfoundland and Labrador was divided into its two geographical components, and the three administrative districts of the Northwest Territories (Franklin, Keewatin, and Mackenzie) were treated as province equivalents. Data for distinguishing plant distributions of insular Newfoundland and mainland Labrador were developed by Kartesz from various sources, particularly Rouleau (1978) and Rousseau (1974). For the Northwest Territories, species distributions for the three administrative districts were developed by Kartesz from numerous floristic references, primarily Porsild (1957) and Porsild and Cody (1980).

British Columbia. The twelve zones, and the data on species distributions by zone, follow the biogeoclimatic zones in the *Vascular Plants of British Columbia* (Taylor and MacBryde 1977). These divisions incorporate vegetation, substrate, and elevation information, and are shown only approximately on the map in Figure 6-1.

Quebec and Labrador. Ten zones for Quebec, and four for Labrador, were developed by Conservancy staff, drawing on landforms, Bailey's (1989) ecoregion map, the WMO climate atlas (Steinhauser 1979), and floristic patterns in the distribution maps by Rousseau (1974). Customary usage was followed in the floristically complex Gulf of St. Lawrence region, with separate units for the Gaspé Peninsula, the North Shore (Côte Nord), Anticosti Island, and the Magdalen Islands. The Clay Belt in southwestern Quebec (Baldwin 1958) is also treated as a separate unit. Species distributions for Quebec were based primarily on the flora by Rousseau (1974), with additional data from the rare plants study by Bouchard et al. (1983), and the fern flora by Cody and Britton (1989).

The Yukon. Two zones were developed by Conservancy staff, to divide the more mountainous southern region from the relatively flat (and generally treeless) Arctic slope. Distribution data were primarily obtained from maps in the flora by Hultén (1968).

United States

Fourteen U.S. states were selected for subdivision. Thirteen of these are floristically well-known states having significant mountainous areas. Florida, the fourteenth, was subdivided due to its high number of endemics and great latitudinal extent, despite its low topography.

Alaska. Twenty-five units were developed by Conservancy staff. Hultén (1968) describes five broad floristic regions of Alaska: Coniferous forest in the southeastern mountains, boreal forest in the lowlands of much of central Alaska, the Arctic tundra of the North Slope, the lowland Arctic tundra near the Bering Sea, and the Aleutian Islands. Each of these large areas is further subdivided here, resulting in 19 mainland units, Kodiak Island, two units in the Aleutians, and three units for island groups in the Bering Sea (St. Lawrence, St. Matthew, and the Pribilofs). Species distributions data for Alaska were primarily obtained from Hultén (1968), with additional data on trees and shrubs from Viereck and Little (1975).

California. Twelve zones were developed by Conservancy staff based on physiographic provinces, climates, and floristic patterns from the *California Flora* by Munz and Keck (1968) and the California Native Plant Society's rare plants report (Smith and Berg 1988). The Coast Ranges were divided into northern, central, and southern zones. The Channel Islands area is separately recognized, as are the Central Valley, Cascades, and Sierra Nevada. California's two areas of Basin and Range topography are each recognized, one in the state's northeastern corner, and the other east of the Sierra Nevada. The Mojave Desert region (including the Colorado Desert), the Salton Trough, and a coastal zone in the San Diego region complete coverage of the state. Data collection for California emphasized distribution data on rare species (ranked G1, G2, and G3). Data were obtained primarily from Smith and Berg (1988) and Munz and Keck (1968).

Colorado. Five zones were developed following physiographic regions: Great Plains, Rocky Mountains, Wyoming Basin, Colorado Plateau, and New Mexico Plateau. The Wyoming Basin is represented by three disjunct areas in Colorado, along the northern boundary, and the New Mexico Plateau is represented by two areas along the southern boundary. Distribution data for Colorado draw upon Weber's Western Slope (1987) and Eastern Slope (1990) floras and other sources.

Florida. Three zones were used, based on the geographical coverages of the three current regional floras: Clewell (1985) on plants of the Panhandle, Wunderlin (1982) on central Florida, and Long and Lakela (1971) on southern Florida. Species distribution data came primarily from these references. A fourth area, northeastern Florida, is not considered by any of these floras; species occurring there were left at the state level of precision.

Georgia. The three zones draw upon the physiographic provinces used in the checklist by Duncan and Kartesz (1981), from which species distributions data were also obtained. Two zones (the Coastal Plain and the Piedmont) follow their usage, while their small Blue Ridge, Cumberland Plateau, and Ridge and Valley provinces are here combined into a single 'Mountains' zone.

New Mexico. The five generalized zones (Chihuahuan Desert, Great Basin, Great Plains, Mogollon Plateau, and Rocky Mountains) are the floristic regions recognized in the flora by Martin and Hutchins (1980), from which species distribution data were also obtained.

New York. Seven zones were developed by Conservancy staff. Southern and northern portions of the lake plains were distinguished, the upland areas of the Adirondacks, Catskills, and Hudson Highlands were each recognized as zones, Long Island (with Staten Island) was treated separately, and the remainder of the state (primarily the Southern Tier counties) form the seventh zone. Species distribution date were based on the 1990 edition of the New York Flora Association's *Atlas.*

North Carolina. Seven zones were developed by Conservancy staff, based on the three physiographic provinces used in the flora by Radford et al. (1968), from which species distributions data were obtained. The three provinces (Mountain, Piedmont, and Coastal Plain) were each divided into northern and southern portions, and a seventh unit was added for the floristically distinctive Sandhills region.

Oklahoma. *The* westernmost zone were selected from the checklist by Taylor and Taylor (1989), from which species distribution data were also obtained. Other Oklahoma species were left at the state-wide level of resolution.

Oregon. Seven zones were developed by Conservancy staff, based largely on Hunt (1974) and Peck (1961). Species distribution data are from Peck's (1961) flora.

South Carolina. The three zones are the three physiographic provinces recognized in the flora by Radford et al. (1968), from which species distributions data were also obtained. While tiny, the Blue Ridge Mountains portion of the state is floristically (and topographically) distinctive (cf. Barry 1980), and provides continuity with the comparable regions in adjacent Georgia and North Carolina.

Texas. The ten zones, and the species distributions data, follow the vegetational areas used by Hatch et al. (1990) in their checklist.

Utah. Four zones were developed by Conservancy staff based on physiographic provinces and floristic patterns in the *Atlas* by Albee et al. (1988), from which the species distribution data were obtained. The Colorado Plateau was accepted unchanged, the Great Basin region was divided into northern and southern zones, and a single unit combines three mountainous areas in northeastern Utah (Wasatch, Uintas, and Wyoming Basin).

Virginia. Nine units were developed by Conservancy staff, drawing on the four physiographic provinces recognized in the *Atlas* by Harvill et al. (1986), from which species distribution data were also obtained. The small Cumberland Plateau area was recognized unchanged. Northern and southern zones are distinguished within the mountains and Piedmont provinces, and four zones were recognized in the Commonwealth's Coastal Plain.