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Population Differentiation in Tree-Ring Growth
Responses of White Fir (*Abies concolor*) to Climate:
Implications for Predicting Forest
Responses to Climate Change

by

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by

Deborah Bowne Jensen

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Abstract

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Forest succession models and correlative models have predicted 200-650 kilometer shifts in the geographic range of temperate forests and forest species as one response to global climate change. Few studies have investigated whether population differences may affect the response of forest species to climate change. This study examines differences in tree-ring growth, and in the phenotypic plasticity of tree-ring growth in 16-year old white fir, *Abies concolor*, from ten populations grown in four common gardens in the Sierra Nevada of California. For each population, tree-ring growth was modelled as a function of precipitation and degree-day sums. Tree-ring growth under three scenarios of doubled CO₂ climates was estimated.

Clinal variation in growth responses of white fir populations was found. Populations from cold sources were less plastic in their response to degree-day sums and populations from warm sources (typically lower elevation sites) were more plastic in their response to degree-day sums. Intermediate populations had intermediate responses. Differences between populations were more pronounced under the various warming scenarios than under current climatic conditions. Under the warmest climate scenario, using output from UKMO, the growth response functions predicted that the most responsive population would grow at a rate 40% larger than the least responsive population. Population differentiation will affect forest productivity in the future and make more difficult the task of predicting the responses of forests to climate change.

The substantial scientific uncertainties about the magnitude and rate of climate change and the responses of natural ecosystems to these changes makes formulating policy more difficult. This research indicates that a local phenomenon, population differentiation, may affect predictions of forest responses to climate change, suggesting that further research may increase rather than decrease estimates of uncertainty about the effects of climate change. Policy responses to climate change will have to proceed in the face of such uncertainty.

John Harte

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CHAPTER 1

INTRODUCTION

The magnitude and rate of projected changes in global climate are anticipated to significantly affect ecosystems throughout the world (IPCC, 1990). Ecosystems will be affected by the direct effects of increases in carbon dioxide, by the direct effects of changes in climate that result from increased levels of all greenhouse gases, and by the indirect effects of changes in biogeochemical processes and biotic interactions (Harte, Torn, & Jensen, 1992). Temperate forests are a major focus of current research on ecosystem response to climate change because of the many human uses of forests and because of the role of temperate forests in the global carbon cycle (Schlesinger, 1991). Current research focuses on tree species as the fundamental unit of analysis, overlooking intraspecific variation, and thereby misestimating the response of forests to climate change.

While plants have experienced many past shifts in climate, some species may not be able to tolerate the rapid climatic changes projected for the next century. Species migrated hundreds of kilometers in response to past climatic shifts such as those which accompanied advancing and retreating ice sheets during the Quaternary (see for example Huntley & Webb, 1988). Estimated future changes in climate will occur much faster,

however, than have past climatic changes (Woodwell, 1989). Increases in global average temperature between 2-5° C would require a 200 - 625 kilometer northward migration or a 300-750 meter elevational shift for species to stay within the same temperature isotherm (Peters & Darling, 1985; IPCC, 1990). Because the magnitude and the rate of change are large, researchers anticipate that many forest communities will be greatly affected as tree species begin to migrate in response to the climatic changes (Davis, 1989; Harte, et al., 1992).

Current Approaches to Projecting Forest Responses to Climate Change

Two general approaches are being used to forecast the response of forests to climate change--correlation of climate variables with biomes or individual species' distributions, and simulation models of forest succession.

Climate variables such as temperature, precipitation, and evapotranspiration have long been used by plant biogeographers to explain the global distribution of biomes (Box, 1981; Holdridge, 1967). While the debate continues as to which climatic variables are best correlated with the distribution of vegetation globally (Stephenson, 1990), the large scale patterns of vegetation biomes can be predicted with considerable accuracy using climate variables.

The responses of biomes to climate change have been estimated by correlating the current distribution of biomes with climate variables. Using estimates of future patterns of climate variables from general circulation models (GCM), global patterns of vegetation under scenarios of future equilibrium climates are then predicted by assuming the correlations between climate variables and biomes will remain constant (Emanuel, Shugart, & Stevenson, 1985).

Vegetation-climate correlations have also been used to predict the response of individual species to changed climate. Davis and Zabinski (1992) employed a correlative approach to identify the climate variables that correlate with the existing distribution of specific forest tree species. They then located areas of suitable climate for those tree species in a world with a climate in equilibrium with doubled CO₂ using GCM climate output. For many species they predicted 200-400 kilometer shifts in the location of suitable climate, with only a small overlap between the present range and the estimated future range in a doubled CO₂ world.¹

¹Davis (1981) also calculated tree dispersal rates from paleoecological studies of past climate changes. Jack pine had the fastest estimated rate of Holocene expansion, 400 meters/year. Other species had slower migration rates, and some could not keep up with the climate changes of the Holocene. The rates projected for greenhouse gas induced climate change are much faster, leading to the conclusion that many species will not be able to migrate as fast as the climate shifts.

Forest succession models simulate the establishment, growth, and survival of individual trees in a stand (Botkin, Janak, & Wallis, 1972; Shugart, 1984). Growth of each tree in a forest is estimated using species-specific optimal growth functions modified by environmental factors such as temperature, moisture, and light. Using GCM climate output to derive the environmental variables, forest succession models have projected forest migration poleward in response to climate change (Botkin & Nisbet, 1992a; Solomon, 1986; Solomon, West, & Solomon, 1981). Because each species has a different response to climatic variables, as the climate changes the competitive balance between species is altered, resulting in shifts in dominant taxa.²

Limitations of Existing Approaches

Both vegetation-climate correlations and forest-succession modelling incorporate certain assumptions in order to predict forest responses to climate change. My research addresses two significant assumptions about the relationship between tree distributions and climate used by these current approaches. First, both assume that populations within a species do not differ in their responses to climate. Second, they assume that the existing

²Forest succession models do not explicitly model dispersal. Rather, seeds from all species are assumed to be available at all locations. Migration is therefore solely dependent on environmental conditions, and these models predict more rapid migrations of forests than is consistent with the limited data available on seed dispersal.

distribution of the species represents the climates that the species can tolerate.

Current approaches to estimating forest responses to climate change have not tested the assumption that intraspecific genetic variation in the species' response to the environment is unimportant. Forest succession models include equations that describe each species' growth-response to a collection of climatic variables. By giving each species in the model only a single growth response function, the models assume that each population has an identical growth-response curve. If populations differ significantly in their response to climate change, this assumption is not valid and could lead to systematically biased results when predicting the response of existing forests to widespread environmental change.

The vegetation-climate correlation approaches have less explicitly stated assumptions about population differentiation. Results of these analyses are often presented as a map that shows the current distribution and the anticipated future distribution of acceptable climates (e.g. Davis, 1988). Assumptions about population differentiation are evident in the interpretation of these results. If it is assumed that each population can tolerate the conditions experienced throughout the entire range of the species, then populations occurring within the intersection between the

present and future ranges are predicted to survive.³ If instead, population differences are acknowledged, then the response of the species to climate change cannot be predicted without knowledge of the response of populations.

The second assumption made by each of the current approaches is that the existing distribution of a species adequately represents the climate it can tolerate. Equating the realized niche of the species with the fundamental niche (Pacala & Hurtt, 1993) greatly influences the outcomes of these forecasting efforts. In the general case, trees would be expected to tolerate a broader range of climates than those that correlate with the limits of their present range--the fundamental niche is larger than the realized niche. In topographically diverse regions with complex paleo-histories, such as California, the present geographic distributions may be a poor indicator of species' physiological tolerances to climate variables. For example, Monterey pine (*Pinus radiata*) has a native range restricted to three areas along the central coast of California (Ano Nuevo vicinity, the Monterey peninsula, and Cambria vicinity) (Griffin & Critchfield, 1972). However, this

³The Intergovernmental Panel on Climate Change comes to the unsupported conclusion that the area of overlap between the present and "future" range is "where trees are likely to be found 100 years from now" (IPCC, 1990 p 298). Davis and Zabinski (1992) are careful to mention the importance of ecotypic differentiation in predicting the response of populations to climate change in their correlative study.

tree has been planted and successfully reproduces in large areas of Central California, and Monterey pine is now a major timber species in the Southern hemisphere, particularly Australia and New Zealand. This species' current natural distribution does not appear to be controlled by climate. A growth function derived from the climate of the native distribution of Monterey pine would gravely misrepresent the climates the species can tolerate.

Importance of Population Differentiation for Climate Change Responses

Ecologists and evolutionists have been studying species' adaptations to local environmental gradients for much of this century. Turesson's work in 1922 on Poa alpina plants from alpine, subalpine and lowland sites established the existence of ecotypes, defined as locally adapted populations or races within a species. Clausen, Keck & Hiesey's (1941) classic work with several herbaceous perennials in California established the genetic basis of ecotypic differentiation by showing that reciprocal transplants of several ecotypes grown in common gardens performed differently. This proved that many ecotypic traits were not simply plastic responses to the environment, but rather had a genetic basis.

The evolution of clinal variation as an adaptive response to environmental gradients is a common phenomenon (Schlichting, 1986; Endler, 1977). Most species are a collection of locally adapted populations.

Populations and individual trees therefore do not have the average characteristics of the species. These differences are well recognized in forestry where use of seeds from populations that are poorly adapted to the environmental conditions of the plantation has significant economic consequences. As a result, genetic studies of the growth and performance of populations across a range of environments are commonplace in agriculture and forestry (e.g. Namkoong, Kang, & Brouard, 1988).

Although the importance of population differentiation is well recognized in forestry and agriculture, as yet, few of the insights from this research have been applied to predictions of the effects of climate change on forest trees. Fetcher & Shaver (1990) recently reported on the results of common garden experiments of six ecotypes of tussock grass, *Eriophorum vaginatum* L. Ecotypes from the coldest sites were the least plastic in their responses to warmer climate. This genetic limitation on productivity suggests that tussock grass ecotypes from cold climates may not be able to increase productivity in response to warming to the same degree as ecotypes from warmer climates.⁴ If these results are generalizable, it suggests that the ecotypes now found in the northern or high elevation

⁴Fetcher and Shaver speculate that ecotypes from cold climates cannot take advantage of warmer conditions due to earlier leaf senescence of the northern ecotypes.

portions of a species range may also be least able to take "advantage" of the future warmer conditions by responding with increases in productivity.

Differential population responses could also affect the future range of species responding to rapid environmental change. To use an example from the correlative approach, if populations of a species are locally adapted, the northern-most populations may experience novel climates beyond their range of tolerance, even though that novel climate is not beyond the range of the species as a whole. In this case, it would be wrong to assume this northern population of the species will persist.⁵

Although population differentiation is a commonly occurring phenomena in plant species, and may influence the responses of species to climate change, little research has focused on this question.⁶ Predicting the

⁵The populations may not die because the climate has changed beyond their tolerance, but may instead simply grow poorly. In this case, the species may not persist in the area because it is outcompeted by other species, not because of direct mortality. The new climate may thus be within the fundamental niche of the population, but not within its new realized niche.

⁶Much of the literature on genetic variation and climate change has considered the potential loss of genetic variation in the face of rapid environmental change (see for example, Jackson, Ford-Lloyd, & Parry, 1990). The role of microevolutionary responses to climate change has also generally been overlooked in the belief that species will have to respond more rapidly than mutation and selection can affect adaption (but see Geber & Dawson, 1993; Holt, 1990).

response of a forest tree species to climate change requires knowledge of whether the species as a whole, as well as its component populations, can tolerate a broader range of climates than those now experienced. This can be accomplished by studying population and species climate growth responses.

Investigation of Population Growth-Response Differences in White Fir

To investigate the potential importance of differential population growth responses to climate change, one must first establish that population differences exist, and then determine how these differences may affect species responses to climate change. Transplant experiments are one of the best techniques to examine population differences in adaptive traits (Primack & Kang, 1989). The challenge is then to evaluate how these differences affect population performance across the range of environments likely to be experienced due to climate change.

I investigated the population-level growth-response differences in white fir, *Abies concolor* (Gord. and Glend.) Lindl., by working with 10 populations of white fir reciprocally planted in four experimental plantations in the Sierra Nevada in 1976 and 1977. Two of these plantations are within the existing range of white fir in the Sierra Nevada. The third plantation is at a higher elevation (colder and wetter) than white fir presently occupies. The

fourth plantation is at a lower elevation (hotter and drier) than the present distribution of white fir. Annual radial growth for each population was correlated with climate at each of the plantations. This allowed comparison of growth of these 10 populations across a range of climates greater than those currently experienced by white fir, and, in one plantation, possibly similar to the hotter conditions likely from global warming.

The work is presented in three separate chapters. Chapter two approaches the problem from the perspective of quantitative genetics, documenting the population differences in growth and discussing the importance of phenotypic plasticity in predicting trees' responses to climate change. Chapter three models tree-ring growth-response functions for each population and documents how population differences may lead to changed predictions of forest productivity in the face of climate change. Chapter four discusses the uncertainties in estimating the response of ecosystems to climate change and the policy implications of these uncertainties.

CHAPTER 2

PHENOTYPIC PLASTICITY, TREE RINGS, AND CLIMATE CHANGE

Introduction

Researchers have estimated that temperate forests will need to migrate poleward 200-650 kilometers to keep up with the predicted change in global climate over the next 100 years (IPPC, 1990). Research on forest responses to climate change has focused on species to ecosystem levels of analysis. Intraspecific variation has been overlooked and populations are generally assumed to be interchangeable. The research presented here suggests that incorporating population differentiation and phenotypic plasticity into analyses of responses to climate change may significantly alter our predictions of the effects of climate change on natural ecosystems over the next several centuries.

Current modelling approaches to predicting forest responses to climate change make two assumptions about the relationship between vegetation distribution and climate. The first is that each population in the species has a growth response identical to the average growth response of the species. Secondly, the existing distribution of the species is assumed to adequately represent the climate that the species can tolerate (Chapter 1). The first assumption overlooks the importance of intraspecific variation and

population adaptation, while the second equates the fundamental niche with the realized niche (Pacala & Hurtt, 1993).

Local adaptation of populations and the plasticity of tree growth responses to climatic changes may significantly influence the short term response of forests to climate change. For long-lived species such as trees, individuals alive today will experience the climatic changes. The responses of these individuals and their progeny will constitute the response of forests over the next century or more. Characterizing the degree of differentiation within a species and the tolerance of differentiated units to similar changes in climate will help us understand and predict species' responses to global climate change.¹

Geographic variation in traits is a common phenomena in many species. Often these patterns have a genetic basis, and are adaptive responses to environmental gradients that result in differences in selection across the range of the species. Given the numerous studies of ecotypic

¹Because of the rate and magnitude of the projected changes, species will not be able to evolve quickly enough to adapt to the new climate (Pease, Lande, & Bull, 1989; Holt, 1990; Billington & Pelham, 1991; Geber, 1993). Nevertheless, existing patterns of population differentiation or local adaptation may influence species responses to climate change.

differentiation,² it is reasonable to expect that for many plants there is population differentiation in growth responses to climate.

Populations may differ both in their mean response to the environment and in the flexibility, or plasticity of their response to environmental changes that occur within their lifetimes. Individual plants encounter a range of environmental conditions over their life times. In the short term, plants respond to environmental changes by changing their morphology or physiology in response to these changes. Phenotypic plasticity refers to the "ability of an individual organism to alter its physiology/morphology in response to changes in environmental conditions" (Schlichting, 1986 p.667).³

²Turreson (1922) coined the term ecotype, which refers to genetically differentiated forms within a species that are adapted to local environmental conditions.

³Although phenotypic plasticity is sometimes considered to be a non-genetic response to the environment, there is considerable empirical and theoretical literature that indicates that plasticity (or the lack of plasticity, sometimes referred to as stability) is a trait that can be selected for, and that can evolve (see for examples Bradshaw, 1965; Schlichting, 1986; Sultan, 1987; Via, 1987). The potential exists for the evolution of plasticity as a trait (West-Eberhard, 1989).

Individual traits can differ in their degree of plasticity, with some traits being stable and others being very plastic. For example, taxonomic characters of plants such as petal size and carpel number are stable, whereas there is often great phenotypic plasticity in the number of flowers or the numbers of seeds set. In forest trees, many quantitative characters related to growth such as height, radial growth, and root to shoot ratio are highly plastic (e.g., Zabinski pers. comm.).⁴

Schmaulhausen (1949) called the different phenotypic responses a genotype has to environmental changes its "norm of reaction". Norms of reaction describe the phenotypic response of an organism when it encounters a range of environments. When two genotypes or populations change relative rank in response to an environmental change, a gene by environment interaction can be identified (Figure 2.1). The slopes of the reaction norms can indicate whether or not the genotypes are highly sensitive to the range of environments experienced. In Figure 2.1, the reaction norm of genotype 2 has a steeper slope than that of genotype 1 indicating that genotype 2 is more sensitive (phenotypically plastic) than genotype 1.

⁴In preliminary studies on plasticity in families of Port Orford Cedar, Zabinski found significant plasticity in the root-shoot ratio of seedlings, grown in different types of soils.

Figure 2.1. Reaction norms in three different environments. Environments 1 and 2 produce qualitatively different phenotypes. (from Sterns, 1990).

To investigate the potential importance of differential population responses to climate change, both phenotypic plasticity and population differentiation need to be evaluated. Both the amount of environmental change a population or species can tolerate, and differences in phenotypic plasticity among populations need to be investigated.

This study investigates the potential importance of population differentiation in estimating the effects of climate change on a montane conifer, white fir, *Abies concolor*, in the Sierra Nevada of California. By looking at the changes in annual radial growth of individual trees, I evaluate changes that are due to environmental effects on an individual, as well as characterize the population differences in growth response and phenotypic plasticity.

White fir is found in high mountainous areas in the Rocky Mountains and in California and Oregon. Its range is characterized by humid climates, with long winters and moderate to heavy snow (Fowells, 1965). In California and Oregon, the summers tend to be dry; most of the annual precipitation falls during the winter.

The lower limit of precipitation for the species is 50 centimeters per year, and 50-90 centimeters is common over much of the desert portions of

its range. The best stands develop in areas receiving 100-150 centimeters of precipitation. The species' range encompasses a wide range of temperatures with the extremes going from -29 °C in Colorado to 43 °C in the desert peaks in California (Fowells, 1965).

White fir is considered a variable species, with high levels of genetic variation both within and among populations. Hamrick (1972) identified four taxonomically distinct groups of white fir. All of the populations used in this study are within geographic Group II, which includes the Sierra Nevada, the southern-most Cascades, and southeastern Oregon. Some authors have proposed that the western portion of the range (California and Oregon) contains a separate taxon, *Abies concolor* var. *lowland* which is distinct from the Rocky Mountain form, *Abies concolor* var. *concolor* (Hamrick & Libby, 1972).

This work investigates two questions:

1. Do populations of white fir differ in their mean growth-response when grown in identical climatic conditions?
2. Do populations differ in their phenotypic plasticity to climatic differences?

Materials and Methods

Seed and Plantation Design

White fir provenance tests were established by the U.S. Forest Service Pacific Southwest Forest and Range Experiment Station in 1976 and 1977 using seeds from 10 populations of white fir (Jenkinsen pers. comm.). In each population, seeds were collected from 10 open-pollinated individuals, 100 meters apart along a transect, giving 10 families for each population. Seeds were planted in a common nursery. When seedlings were two years old, fifteen individuals from each of the 10 families per population were planted in 4 geographically separate plantations in a randomized block design (Libby & Cockerham, 1980). The seedlings were watered during the first season of growth to ensure establishment, and the plantations were fenced to diminish losses due to browsing animals.

The four experimental plantations span a broad range of geography and climate (Figure 2.2). The northern most plantation is at Swain Mountain, in northeastern California. The southern most plantation is at Chimney Rock, above the existing distribution of white fir at 2182 meters. The Institute of Forest Genetics (IFG) plantation is below the existing range of white fir at 818 meters. The source populations cover a narrower range of latitude and elevation than do the plantations but represent the center of the range of white fir in the Sierra Nevada. The locations of the white fir

Figure 2.2. Map of white fir distribution in the Sierra, plantation locations (SW = Swain Mountain, IR = Iron Mountain, IFG = Institute of Forest Genetics, CR = Chimney Rock), and source population locations (indicated by numbers).

population source sites and the locations of the experimental plantations are listed in Table 2.1.

Sampling and Measurement

To obtain annual radial growth data for each tree, increment cores (5 mm diameter) were taken 20 cm from ground level.⁵ Twenty trees from each population were cored at each plantation. The trees were chosen using a stratified random design to assure that the range of ecological conditions within the plantation was represented.⁶ The cores were labeled, stored and dried at room temperature. Cores were mounted on a standard wooden mount and sanded to allow the rings to be accurately measured. Cores were then cross-dated to assure that an accurate date could be assigned to each ring in the core.

The ring widths of each core were measured to the nearest 0.01 mm at the Laboratory of Tree Ring Research (TRL) at the University of Arizona, Tucson. To verify accuracy and consistency of measurements, a second person remeasured at least 10 percent of the cores. The computer program

⁵The trees were too small to take cores at breast height.

⁶Each block within the plantation included 10 trees, one per family, from each source population. Each plantation contains 15 blocks. One tree, chosen at random was sampled from each population within each block and then five additional trees were sampled from each population at random with respect to block.

Table 2.1. Locations of the white fir populations and the plantations included in this study.

1976 planting year for Swain, Iron, and IFG 1977 planting year for Chimney Rock					
Seed Source	Plantation	Planting locations	Latitude in degrees	Longitude in degrees	mean elev in meters
Monarch Mine		CR,SW,IF,IR	39° 35.5'	120° 40.5'	1970
Babbet Peak		CR,SW,IF,IR	39° 34.7'	120° 06.2'	2364
Bunker Hill		CR,SW,IF,IR	39° 02.7'	120° 22.6'	2030
Strawberry Canyon		CR,SW,IF,IR	38° 47'	120° 09'	1833
Bryant Springs		CR,SW,IF,IR	38° 50'	120° 27.2'	1500
Pollock Pines		CR,SW,IF,IR	38° 45.7'	120° 35'	1152
Angora Creek		CR	38° 52.2'	120° 03'	1970
Angora Lookout		SW,IF,IR	38° 52.9'	120° 03.2'	2197
Bourland Mountain		CR,SW,IF,IR	38° 06.5'	119° 56.6'	2212
Little Reynolds Creek		CR,SW,IF,IR	38° 03'	119° 58.1'	1856
Rabbit Meadow		CR,SW,IF,IR	36° 42.3'	118° 52.5'	2318
	Institute of Forest Genetics (IF)		38.75°	120.7°	818
	Iron Mountain (IR)		38.7°	120.33°	1758
	Chimney Rock (CR)		36.68°	118.87°	2182
	Swain Mountain (SW)		40.42°	121.08°	1879

Verify was used to compare the accuracy of the measurements (Grissino-Maver, 1990). This program compares the two measurements of the same core and calculates an error term for the differences. If the standard deviation of the difference is greater than 0.10 mm, the core is identified as needing remeasurement. Systematic measurement errors attributable to a particular measurer can be readily identified using this method.

The raw data were then converted into standard measurement format files using TRL program Convert4. Quality control for crossdating and measurement was completed by using the TRL program COFECHA (Holmes, Adams, & Fritts, 1986). COFECHA flags each series that correlates poorly with the corresponding segments of an aggregate of all series. Divergent year-to year change, absent rings, and statistical outliers are identified. A small number of cores were remeasured following these error-checking routines.

Statistical analyses

Repeated measures analysis of variance (ANOVA) was used to document differences between mean annual ring width of populations and interactions between population and other factors in the experiment and to identify the effects of other variables such as year and block on ring width.

Gene by environment interactions identify genotypic differences in phenotypic plasticity (Falconer, 1981).⁷

ANOVAs were completed both within and among plantations using SAS 6.07 (SAS Institute, 1989) for the period 1980 to 1991. The ring widths for the years 1980-1991 correspond to trees 5 to 16 years old at the Chimney Rock plantation and trees 6 to 17 years old at the other plantations.

Multiple contrasts (Tukey studentized range test) was used to determine which populations had statistically significant differences in means. These contrasts were completed by comparing growth in 1986 to growth in 1987. (I assumed if populations differed, these differences would be evident in this two year period because 1987 was an extremely dry year.)

Measurement of phenotypic plasticity at the population level must incorporate both an estimate of responsiveness and an estimate of the similarity of the response among individuals within the population. To compare the phenotypic plasticity among populations, two measures of

⁷Interactions reflect changes in the relative slopes of population growth in response to treatment, in this case plantations or yearly climate. Thus significant interactions indicate that growth responses of populations are not all parallel.

among environment variance were used: coefficient of variation and mean sensitivity.⁸ One measure of responsiveness was estimated: environmental sensitivity (Finlay & Wilkinson, 1963).

Coefficient of variation (CV) was calculated both across years within a population at a site, to determine the population plasticity to the inter-annual variation in climate, and across sites to look at the population plasticity to the regional differences in climate.

Mean sensitivity (MS) measures the average ring width differences between consecutive years. Mean sensitivity (MS) indicates the responsiveness to climatic differences experienced from one year to the next and is a commonly used measure in dendroecology and dendrochronology. In effect, dendrochronologists measure the phenotypic plasticity of each tree when they calculate mean sensitivity.⁹ MS is calculated as:

⁸Phenotypic plasticity is estimated in as many different ways as there are different attributes of interest. Lin et al. (1986) compared 9 different indices and the aspects of phenotypic plasticity each is best suited to estimate. Measures such as variance and coefficient of variation are best suited to measuring the variability of the phenotype among environments. Other indices measure whether the response of one genotype is parallel to the mean response of all genotypes in the trial. Both aspects of plasticity will affect plant responses to climate change.

⁹Mean sensitivity has not been used before explicitly as a measure of phenotypic plasticity. Dendrochronologists do recognize that mean sensitivity changes from individual to individual and across environments, but their focus

$$MS_x = \frac{1}{(n-1)} \sum_{i=1}^{n-1} \left| \frac{2(x_{t+1} - x_t)}{(x_{t+1} + x_t)} \right|$$

Each x_t is a ring width in the series and n is the number of rings. Values of mean sensitivity run from 0 to 2, zero indicating there is no difference between ring widths and 2 indicating a zero ring-width value occurs every other year in the series. Like CV, mean sensitivity is a measure of the variance of the populations' responses among environments. MS was calculated for each population within each site.

Population differences in phenotypic plasticity were also compared by estimating environmental sensitivity (Yates & Cochran, 1938; Finlay & Wilkinson, 1963). The mean performance of all populations at a site is used as a measure of the environment. The performance of a single population is then regressed against the mean performance of all populations. The slope of the regression indicates the performance of an individual population as compared to the other populations in the trial. Those populations that have slope near 1.0 have average responses to the environment. Where the slope is less than one, the performance is less responsive than average. Where

has been on using tree-rings to measure past climate differences. Phenotypic plasticity among individuals or populations has been part of the "noise" they remove from the series.

the slope is greater than 1.0 the population is more responsive (more phenotypically plastic) than the average population to the environmental differences included in the trials. This technique is widely used in the crop science literature to identify crop varieties that have predictable yields across a range of environments.

The various measures of plasticity were correlated with latitude and elevation of the source populations to identify geographic patterns in the distribution of phenotypic plasticity in white fir.

Results

Mean radial growth of the white fir saplings differed across the plantations. The mean radial growth during the period 1980-1991 was smallest (34.46 mm) at Chimney Rock, the high elevation plantation in the Southern Sierra and was largest (67.28 mm) at Iron Mountain, the mid-elevation plantation in the Central Sierra (Figure 2.3, Table 2.2). Ring width varied from year to year within populations in a plantation and between populations in a plantation and varies between plantations (Figures 2.4-2.7).

Factors Determining Ring Width Variation

The repeated measures analysis shows that site is the overwhelming source of variation in ring width (Table 2.3). Population and the interaction

10 Year Radial Growth Grown in Four Plantations

Figure 2.3.

Table 2.2. Total Mean Radial Growth of White Fir from 1980 - 1991 at four plantations. Measurements are in hundredths of millimeters (10^{-5} m).

<u>SOURCE</u>	<u>Pop No.</u>	SWAIN	IRON MOUNTAIN	INSTITUTE FOREST GENETICS	CHIMNEY ROCK
Monarch Mine	1	4484 ± 974	6639 ± 1557	5683 ± 1352	2852 ± 959
Babbitt Peak	2	3966 ± 531	6299 ± 1365	5312 ± 1536	2399 ± 507
Bunker Hill	3	4945 ± 1158	7425 ± 847	6350 ± 1179	2514 ± 1220
Angora Lookout	4	3098 ± 1221	7088 ± 1024	7712 ± 816	4026 ± 956
Bryant Springs	5	4788 ± 1188	6866 ± 1446	6943 ± 1095	4131 ± 1393
Strawberry Canyon	6	3953 ± 1106	6698 ± 1243	6194 ± 1037	3476 ± 487
Pollock Pines	7	3848 ± 620	6597 ± 1290	5939 ± 1491	3099 ± 1275
Bourland Mountain	8	4380 ± 1730	6446 ± 1082	7246 ± 1765	4340 ± 1128
Little Reynolds	9	3571 ± 1347	6811 ± 1664	7144 ± 1460	4298 ± 1662
Rabbit Meadow	10	4142 ± 1097	6410 ± 1054	6955 ± 1119	3334 ± 809
Mean for all trees		4118	6728	6548	3447

Mean Ring Width at Swain Mountain

Figure 2.4.

Mean Ring Width at Iron Mountain

Figure 2.6.

Mean Ring Width at Chimney Rock

Figure 2.7.

Table 2.3. Repeated measures analysis of variance of ring-widths across four sites and 11 years.

	F	Pr > F
<u>MANOVA (Wilk's Lambda)</u>		
Time	61.54	.0001
Time*Site	125.23	.0001
Time*Pop	1.60	.0005
Time*Site*Pop	1.76	.0001
Time*Bloc(Site)	2.25	.0001
Time*Bloc*Pop(Site)	1.28	.0001
<u>GLM between subjects</u>		
Site	309.19	.0001
Pop	5.78	.0445
Site*Pop	2.50	.0002
Bloc(Site)	2.88	.0001
Bloc*Pop(Site)	1.27	.0309
<u>GLM within subjects</u>		
Time	55.16	.0001
Time*Site	168.88	.0001
Time*Pop	1.85	.5617
Time*Site*Pop	1.91	.0001
Time*Bloc(Site)	3.72	.0001
Time*Bloc*Pop(Site)	1.43	.0001

between site and population are also significant sources of variation in ring width. Populations differ in their ring width; the relative performances of populations also change at the different sites. For example, the populations with the highest growth at IFG (the warmest site) are not the populations with the highest growth at Swain (the northernmost site) (see Figure 2.3). Blocks within sites also are significant sources of variation in ring width, suggesting that trees are responding to microenvironmental variation present among the blocks. In addition, the significant interaction between block and population, and among year, block, and population, indicates that populations respond differently to the microenvironmental variation present in the blocks. These responses also differ across years.

All analyses show that age is a significant factor explaining the differences in ring width measurements. This is not surprising since young trees typically have increasing ring widths at this stage of their growth (Husch, Miller, & Beers, 1982). The within-subjects analysis shows there are also significant interactions between year and the other factors in the experiment. Both sites and populations change their relative rank over time, and in complex ways as indicated by the significant year*site*population interaction term. In addition, there are significant year*population*block

interactions indicating that there are year-to-year differences in the relative performance of populations within each block.

No effort was made to further explore the importance of microenvironmental variation. However, the importance of block and the significant interaction of block with other factors implies that ignoring block underestimates the importance of environmental variation in explaining population differences in ring width.

Within-plantation Effects

Repeated measures ANOVA for each plantation examined the importance of year, population, and block as factors explaining the ring width variation of individual trees within a plantation. Within each plantation year, year*population, and year*block are highly significant factors in explaining the variation in ring width (Table 2.4). This indicates that populations perform differently over time, and that the influence of blocks also changes over the eleven years. These results are consistent with the complete ANOVA discussed above.

Population is a significant source of variation in ring width at three of the four plantations: Swain Mountain, IFG, and Chimney Rock ($P < .075$, $P < .0001$ and $P < .022$ respectively). However, at Iron Mountain, the mid-

Table 2.4. Repeated measures analysis of variance on ring-widths within sites.

Manova (Wilk's Lambda)	Swain		Iron		IFG		Chimney Rock	
	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F
Time	144.53	.0001	143.76	.0001	189.04	.0001	40.38	.0001
Time*pop	1.60	.0069	2.38	.0001	1.52	.0064	1.57	.0049
Time*bloc	1.94	.0001	3.43	.0001	2.43	.0001	1.76	.0001
Time*pop*bloc	1.33	.0054	1.52	.0001	1.34	.0002	1.25	.0080
<u>GLM between subjects</u>								
Pop	2.01	.075	1.54	.152	6.11	.0001	2.48	.0218
Bloc	1.13	.37	6.33	.0001	1.94	.042	3.84	.0003
Pop*bloc	1.23	.27	1.54	.0231	1.01	.502	1.04	.4464
<u>GLM within subjects</u>								
Time	43.94	.0001	273.0	.0001	184.2	.0001	118.8	.0001
Time*pop	1.67	.0014	2.34	.0001	2.12	.0001	1.7	.0005
Time*bloc	2.23	.0001	6.9	.0001	4.00	.0001	2.63	.0001
Time*pop*bloc	1.44	.0002	1.66	.0001	1.52	.0001	1.27	.0032

elevation site in the Central Sierra and in the heart of the current range of white fir, the populations did not differ significantly in annual ring widths ($P < .152$).

Block is also a significant source of variation at three plantations: Iron Mountain, IFG, and Chimney Rock ($P < .0001$, $P < .042$ and $P < .0003$ respectively). This suggests that microenvironmental variation with the plantation was large enough to significantly affect growth, except at Swain Mountain. Only at Iron Mountain was there a significant interaction between population and block.

Identifying Populations that Differ

Because of the overwhelming importance of site and year in explaining ring width variation, populations do not have significantly different ring widths when comparing only one year to the next. Rather, these differences are only evident over time as the repeated measures tests show. There are, however, some pairs of years where populations differ in ring width (Table 2.5). These years correspond to years of extreme weather. Population was a significant source of ring width variation between one year and the next (at $P < .05$) only when comparing 1986 to 1987 (SAS repeated measures profile transformation). An unusually dry year compared to the long term historical average, 1987 was the driest year during 1980 to 1991.

Table 2.5. Sources of interannual variation in ring width. Values given are F values and Pr > F. (** indicates that population is a significant source of variation at .05 level between these two years, *** indicates significance at .01).

YEARS		81-82	82-83	83-84	84-85	85-86	86-87	87-88	88-89	89-90	90-91
					***		**				
<u>Source of variation</u>											
Mean	F	278.4	5.21	22.54	156.4	14.89	21.98	19.31	76.65	48.46	73.42
	P	.0001	.0237	.0001	.0001	.0002	.0001	.0001	.0001	.0001	.0001
Site	F	68.37	147.0	97.18	36.21	154.8	336.8	95.05	173.5	402.9	184.7
	P	.0001	.0001	.0001	.0001	.0001	.0001	.0001	.0001	.0001	.0001
Pop	F	1.07	0.44	1.47	1.89	1.24	2.85	1.68	1.40	0.96	0.80
	P	.3883	.9107	.1611	.0558	.2741	.0036	.0956	.1926	.4757	.6155
Site*Pop	F	1.42	1.70	1.28	0.98	1.18	3.61	2.24	1.46	0.87	2.11
	P	.0941	.0221	.1755	.4961	.2612	.0001	.0010	.0770	.6529	.0022
Bloc(Site)	F	2.13	2.40	1.91	2.16	2.25	3.44	1.91	2.61	1.81	1.30
	P	.0001	.0001	.0008	.0001	.0001	.0001	.0110	.0001	.0018	.1037
Pop*Bloc(Site)	F	1.33	1.28	1.22	1.02	1.54	1.67	1.35	1.29	1.00	0.85
	P	.0151	.0283	.0633	.4385	.0005	.0001	.0001	.0245	.5023	.9015

When climate varies greatly from one year to the next, as in 1986 to 1987, populations have significantly different ring widths (although year still explains most of the variation) (Table 2.6). Surprisingly, no plantation showed significant population by year interactions suggesting that all populations responded similarly to the drought. Tukey's studentized range test with $\alpha = 0.05$ (SAS Institute, 1989) was used to determine which population's performance was significantly different from the others. At each plantation only one or two populations differ significantly (see Figures 2.8-2.11).

Measures of Plasticity

Mean Sensitivity

The significant population*year interactions and population*site interactions indicate that the populations differ in their plastic responses to the plantations and year, and therefore to the same environmental change. Mean sensitivity (MS) is a statistic that I used to compare the plastic responses of populations (or trees) to the inter-annual variation in climate at a single plantation. A larger MS indicates a greater response to climate. The average mean sensitivity of populations ranged from 0.22 to 0.40 (Figure 2.12, Table 2.7).

Table 2.6. Analysis of variance of ring width in white fir during 1986 and 1987.

	Swain Mtn		Iron Mtn		IFG		Chimney Rock	
	F	Pr > F	F	Pr > F	F	Pr > F	F	Pr > F
WITHIN A SITE								
Pop	3.19	.0010	2.86	.0028	4.402	.0001	3.29	.0007
Year	17.70	.0001	2.36	.1249	179.9	.0001	14.94	.0001
Pop*Year	.57	.8214	.61	.7894	0.93	.4972	0.49	.8791
OVER ALL SITES								
Site	358.9	.0001						
Pop	5.51	.0001						
Year	10.45	.0013						
Site*Pop	2.81	.0001						
Pop*Year	0.48	.8862						
Site*Pop*Year	9.51	.0001						

Ring width at Swain Mountain in 1986 and 1987

Figure 2.8. Symbols mean that population 7 is different from populations 1 and 3, and that populations 3 and 4 are different.

Figure 2.9. Symbols mean that population 4 differs from populations 7, 8, and 9, and that population 2 differs from populations 8, 9, and 10.

Ring width at Iron Mountain in 1986 and 1987

Figure 2.10. Symbols mean that population 10 differs from populations 1 and 3.

Ring width at Chimney Rock Plantation in 1986 and 1987

Figure 2.11. Symbols mean that population 5 differs from populations 2 and 4.

Table 2.7. Analysis of variance in Mean Sensitivity within and across sites

	Swain Mtn			Iron Mtn			IFG			Chimney Rock		
	F	Pr > F	Pr > F	F	Pr > F	Pr > F	F	Pr > F	Pr > F	F	Pr > F	Pr > F
<u>WITHIN A SITE</u>												
Pop	6.29	.0004		0.21	.9916		2.26	.0367		2.02	.0600	
Bloc	2.98	.0142		2.82	.0030		2.18	.0264		4.41	.0001	
Pop*bloc	1.28	.2814		1.00	.5053		1.15	.3097		1.99	.0062	
<u>OVER ALL SITES</u>												
Site	12.22	.0001										
Pop	1.56	.1253										
Site*pop	2.77	.0001										

Mean Sensitivity at each plantation (pops ordered by decreasing elevation)

Figure 2.12. Populations marked with a double symbol differ from each population marked with a single identical symbol of the same type.

Populations differed in mean sensitivity at three plantations: Swain, IFG, and Chimney Rock ($P < .004$, $P < .0367$, $P < .060$ respectively). Populations differ in their mean sensitivity when grown in extreme circumstances; most populations do not differ in their mean sensitivity (Figure 2.12). Mean sensitivity of trees from Pollock Pines (number 7), the lowest elevation source population, is distinctly higher than MS of 5 other populations when grown at Swain mountain, the northernmost plantation. Trees from Little Reynolds (number 9), a source from the southern Sierra, also have higher MS than trees from two other populations when grown at Swain Mountain. At IFG, the lowest plantation, trees from Babbit Peak (number 2), a high elevation source north of Lake Tahoe, had higher mean sensitivity than two of the three sources from the southern Sierra. At Chimney Rock, the highest plantation, only two populations differed in MS. Population 2 had higher MS than population 6, a mid-elevation population from the Central Sierra at Angora Creek.

Mean sensitivity at the Swain Mountain plantation is negatively correlated with the elevation of the source plantation (Pearson correlation coefficient (R) = -0.767 , $P < .01$). Mean sensitivity at the IFG plantation is positively correlated with the latitude of the source plantation (R = 0.74 , $P < .01$). There are no significant correlations between MS and elevation or latitude at the other two plantations.

When all sites are included in a single ANOVA, site and site*population interactions explain some of the variation in mean sensitivity but population does not. Trees at IFG had higher MS values than at Iron Mountain or Chimney Rock (Tukey alpha = 0.05). Swain also has higher MS values than Iron Mountain or Chimney Rock, a result greatly influenced by the unusually high MS value of population 7 at Swain Mountain (Tukey, alpha = 0.05).

Coefficient of Variation

Using coefficient of variation (CV) as a measure of plasticity (Jain, 1978; Schlichting & Levin, 1984) allows a comparison of populations across all plantations (Figure 2.13). CV of ring width is negatively correlated with the elevation of the source population ($R = -0.67$, $P < .03$) indicating that individuals from high elevation populations are more similar in their response than individuals from low elevation populations. If plasticity is evaluated only within a plantation, it is negatively correlated with the elevation of the source plantation only at Iron Mountain ($R = -0.63$, $P < .05$) and Swain Mountain ($R = -0.72$, $P < .02$). At IFG and Chimney Rock no significant correlations were found between either source population latitude or elevation and CV.

Comparison of CV for populations
(ordered by decreasing elev of source)

Figure 2.13.

Environmental Sensitivity

These results all indicate that phenotypic plasticity differs among white fir populations. The Finlay-Wilkinson (1963) approach to estimating environmental sensitivity (ES) uses the trees themselves to create a measure of the environmental gradient experienced by the trees. Table 2.8 lists the ES of each population within each plantation and across the 4 plantations. Populations from lower elevations have higher sensitivity (slopes > 1.0) than do populations from high elevations when all plantations are considered ($R = -0.649$ $P < .04$). In addition, the ES of each population differs from one plantation to the next. ES values for all populations are most similar at IFG (range = 0.93-1.10) and least similar for Chimney Rock (range = 0.71-1.33). Both of these plantations are outside the current distribution of white fir. IFG is a lower elevation, hotter site and Chimney Rock is a cooler, higher elevation site than the current distribution of white fir in that part of the Sierra.

Discussion

The results show that these ten populations of white fir differ in mean ring width when grown in a common environment. Furthermore, populations differ in phenotypic plasticity of ring width growth. These results are consistent with other studies of gene by environment interactions in trees and with the theory of norms of reaction. Populations differed in ring width

Table 2.8. Environmental sensitivity as measured by regressing population mean ring width against site mean ring width. Comparisons are made both within plantation (using different years as different environments) and across four plantations and 12 years.

Source population	Swain Mountain		Iron Mountain		Institute Forest Genetics		Chimney Rock		All sites compared	
	slope	r^2	slope	r^2	slope	r^2	slope	r^2	slope	r^2
Monarch Mine	0.96	.84	0.77	.74	0.93	.91	0.87	.85	0.88	.91
Babbitt Peak	0.91	.81	0.90	.91	0.93	.95	1.01	.95	0.86	.91
Bunker Hill	0.99	.86	1.15	.97	1.02	.98	1.07	.97	1.03	.95
Angora Creek	0.92	.85	1.09	.84	0.99	.99	0.71	.90	0.95	.94
Bryant Springs	1.01	.75	1.11	.92	1.02	.83	0.91	.93	0.98	.94
Strawberry Canyon	1.23	.79	0.97	.94	1.05	.96	1.06	.98	1.02	.97
Pollack Pines	1.02	.65	1.09	.91	1.10	.83	0.95	.96	1.22	.90
Bourland Mountain	0.93	.95	0.87	.90	1.02	.94	1.33	.97	1.00	.94
Little Reynolds Creek	0.86	.85	1.12	.94	0.99	.95	1.16	.98	1.04	.93
Rabbit Meadow	1.10	.95	1.04	.94	1.00	.82	1.02	.98	1.04	.94

at the three plantations that are near the edge of or beyond the existing range of white fir. Population ring widths were not different at Iron Mountain, a plantation in the middle of the geographic range of white fir and at an average elevation for white fir. Referring back to Figure 2.1, this suggests that Iron Mountain is analogous to environment 2, the intersection of the norms of reaction.

The populations of white fir in this study also differ in the variability of their response to different environments. Comparisons of coefficients of variation showed that some populations are significantly more variable in their ring width than others, and that this variability changes when environment changes. Populations also differ in their sensitivity to year-to-year fluctuations in climate, as was shown by the measures of mean sensitivity. The regression analysis approach of Finlay and Wilkinson (1963) also showed differences in plasticity.

All estimates of phenotypic plasticity were inversely correlated with the elevation of the source population. This implies that high elevation populations will be less able to respond with increased radial growth to the warmer conditions resulting from global warming than lower elevation populations.

The Finlay-Wilkinson environmental sensitivity analysis suggests that the norms of reactions of the populations are strongly non-linear for at least some of the populations. For example, the slope of the Bourland Mountain population regression changed from 0.87 at Iron Mountain to 1.33 at Chimney Rock. Because these regressions are the performance of one population in relation to the others they cannot be used to draw the true norm of reaction for the population. Nevertheless, the variation in slopes serves as a reminder that although straight lines are used to graphically represent norms of reactions, real norms of reaction are complex integrations of the genotypes' response to the many environmental factors that change between sites.

Although climatic factors are only a few of the environmental factors that differ among the plantations, it is evident that climatic factors are important variables driving differences in ring width. Climatic differences are included in this study at several scales, from one plantation to the next, the inter-annual variation within a plantation, and the microenvironmental variation from block to block. The inter-annual variation in ring width is persuasive evidence of the importance of climatic factors, as it is the main treatment between any two years at a single plantation. Given the wealth of research in dendrochronology any other result would be quite surprising.

This study shows that these populations of white fir, though geographically close together compared to the total range of the species, have significant differences in their response to climate. A range-wide study could be expected to show larger differences in relative measures such as mean sensitivity.

Conclusions

Mean Sensitivity as a Measure of Plastic Responses to Climate Change

Mean sensitivity is a statistic frequently collected by dendrochronologists and dendroecologists. Although these data are rarely available for individuals or populations with known genetic relatedness, they still provide insight into the phenotypic plasticity of trees.

Dendrochronologists have long used the responsiveness of tree ring growth to climate as a tool for understanding past climates. Because these researchers seek to untangle the climate signal from the tree-ring growth series, they prefer to work with trees that are very sensitive to climate changes, and trees from extreme sites where climate is the predominate environmental factor influencing tree growth. Dendrochronologists prefer to work with trees of high mean sensitivity. They refer to trees that have little ring width response to inter-annual variation in climate as trees with "complacent" series (Fritts, 1976). Mean sensitivity is a measure of the

year to year variation in response to the tree's environment. Thus, mean sensitivity is a good measure of plastic responses to climatic changes.

Advantages of Long-term Studies

Multiple years of data cannot always be obtained for ecological or evolutionary studies. Yet many years of data may yield different results than a single year or even a pair of years. Differences that are not detectable over a short period of time may be evident over a longer period. For example, in this study, population was rarely a significant source of the year-to-year variation in ring width. If, however, the trend of many years were included, then population did explain a significant proportion of the ring width variation. These differences are in part due to the response of populations to years with extreme weather such as 1987. To address questions such as the effects of climate change on species responses to climate change, understanding both long-term responses and the importance of extreme events is critical.

Implication of Results for Understanding the Effects of Climate Change

This study shows that white fir populations' responses to environmental change are not identical. To the extent that plantation and year (the most significant factors in explaining variation in ring width) are surrogates for climate, populations differ in both their mean responses to

climatic changes and the plasticity of their responses. Further, high elevation populations were less plastic than low elevation populations.

These results contain several lessons for climate change research. Assuming that all populations have the same norm of reaction to climatic variables will misrepresent the growth response of the species. The wealth of research in forest genetics could be used to evaluate the ecotypic differentiation and the phenotypic plasticity of many of the major forest tree species for use in studies modelling the effects of climate change on forests.

Including population differentiation in studies of climatic change effects will be particularly important for species with significant trends in phenotypic plasticity along latitudinal gradients or elevational gradients. If northern populations or high elevation populations are less phenotypically plastic, using a species model of growth rather than population models will overestimate the growth response of existing stands. For example, the growth of existing stands of white fir at high elevations cannot be expected to respond to warming with the same annual growth now found in lower elevation populations because of the less plastic response of the high elevation populations.

This study did not find correlations between phenotypic plasticity and the latitude of the source population in white fir, perhaps due to the confounding effects of elevation. The climate of high elevation sites in the southern Sierra is more similar to moderate elevation sites in the northern Sierra. To adequately interpret the patterns of plasticity, the climate variables themselves rather than the surrogate treatments of plantation and year used in this study, are needed. If population growth response could be correlated with common climate variables, rather than with ES as estimated by tree responses (Yates & Cochran, 1938; Finlay & Wilkinson, 1963), the results would be more relevant for climate change studies. This analysis is presented in Chapter 3.

Many contemporary efforts to model the effects of climate change on forest trees make a starting assumption that the present range of the species is an adequate estimate of its climatic tolerances (examples include Shugart, 1984; Botkin & Nisbet, 1992b; Davis & Zabinski, 1992). (This assumption is not restricted to research on plant species. See, for example (Root, 1988).) This study shows that trees can grow very well outside their current range. The plantation at IFG is well below the natural distribution of white fir; yet trees there were very large and robust, and their annual growth rate quite high.

Tree growth and the range of a species depend on numerous environmental factors of which climate is just one. Other factors such as disturbance are often the critical factors limiting the range of a species. In the case of white fir, a fire-intolerant species, it is very likely that forest fires help determine its lower elevational limit (Fowells, 1965; Parsons & DeBenedetti, 1979). Changes in climate variables such as precipitation and temperature are but the simplest of the direct and indirect effects of climate change. If the indirect effects such as changing disturbance regimes or altered runoff patterns are ignored, significant effects will be overlooked (Harte et al., 1992).

Finally, reaction norms also differ for different life history stages of an organism. The reaction norm of young trees is possibly quite different from that of seedling white fir or of mature trees. It is possible that seedlings would not have survived at the IFG plantation if they had not been watered during their first summer. Norms of reaction also describe the response of a genotype to a particular range of environments. The estimates of environmental sensitivity suggest the reaction norms in white fir are strongly non-linear. Unless the real shape of the reaction norm is understood (which would require a level of knowledge of physiology rarely, if ever, available) caution is merited when extrapolating results to different age classes or to novel conditions.

Understanding forest responses to climate change is an important applied research question that requires insight from many areas of basic research. This study refutes two assumptions common to current modelling approaches: that populations are identical in their responses to climate, and that the distribution of a species adequately reflects the climates it can tolerate. The results presented here demonstrate that incorporating population differentiation and differences in phenotypic plasticity within a species may significantly alter our predictions of the responses of forests to climate change.

CHAPTER 3

CLIMATE CHANGE, FOREST TREES AND POPULATION DIFFERENTIATION IN GROWTH-RESPONSE FUNCTIONS: A LESSON FROM WHITE FIR

Introduction

Global climate change is projected to have significant effects on the distribution and composition of boreal and temperate forests (Smith & Tirpak, 1989; IPCC, 1990). Studies correlating the current range of forest trees to today's climate and then contrasting this to the expected future climate suggest that North American forests may need to migrate hundreds of miles north in order to stay within suitable climatic zones (Davis & Zabinaki, 1992). Forest succession models, using species-specific growth functions also project substantial changes in the range of eastern North American trees due to global climate change (Solomon, et al. 1984). These studies predict that in the eastern United States significant areas will be dominated by a different collection of species than those now present. While these approaches provide insight into the possible impacts of global change, they make many assumptions that reduce their usefulness for understanding the effects of global warming on particular species of trees or for shorter time scales.

First, approaches to evaluating the response of forests to climate change assume that the populations of a species do not differ in their growth responses to climate. Forest succession models use a single optimal growth curve for each species, therefore overlooking any population-level differences that may be present within the species. Scenarios of forest responses to climate change that compare range maps to current and future climates do not contain explicit assumptions about population differentiation. Implicit assumptions are made, however, when predicting the growth and performance of existing forests in new climatic conditions (Chapter 1). Although some researchers have acknowledged the limitations of assuming that populations of a species have the same growth-response functions (Solomon, et al., 1984), few efforts have been made to evaluate the importance of population differences in growth response to understanding the effects of climatic change on forests.

Because of the long lives of forest trees, the forests now standing will experience significant changes in climate if greenhouse gas emissions continue as projected. If growth-response functions differ significantly among the populations of a species, range-wide predictions of the effects of global warming will need to incorporate these subspecific differences.

Second, current modelling approaches assume that the existing distribution of a species is an adequate description of the climate the species can tolerate. This assumption, too, is acknowledged to be an oversimplification (Shugart, 1984), yet few studies have empirically investigated the growth of trees in climates beyond those now experienced. Future climates will in many cases be beyond the conditions now experienced by existing forests. Without some knowledge of the performance of tree species in novel conditions, predictions of future performance is speculative.

This study investigates population differences in growth-response functions of white fir by comparing the growth of ten populations growing in four plantations in the Sierra Nevada of California (Figure 2.2). These ten populations of white fir differ in their phenotypic plasticity when grown in the four different sites (Chapter 2). The objectives of this study are: 1) to correlate differences in ring-width growth with climatic variables; 2) to quantify the populations' growth-response functions; 3) to evaluate patterns in growth responses of populations; and 4) to evaluate and discuss the implications of population level differences in growth response for projection of forest responses to climate change.

Material and Methods

White fir, *Abies concolor* (Gord. and Glend.) Lindl., is a widely distributed conifer of the montane regions of the western United States. The species occurs over a broad range of climates with populations in high elevations of the desert mountain ranges of California, Arizona and New Mexico, and populations in cool, moist, montane sites in the Sierra Nevada, Oregon, and the Rocky Mountains. Fowells (1965) reports that stands are best developed on moist sites with long winters and heavy snowfall. The species experiences temperature extremes, however, that range from -39 °C to 43 °C (Fowells, 1965).

In California, white fir is a common component of the highly productive mid-montane conifer zone of the Sierra Nevada, occurring at elevations ranging from 1250-2200m (Rundel, 1977). At the upper end of its elevational range, white fir is replaced by red fir, an upper montane species. The upper montane forests experience more severe winters and shorter growing seasons and are less productive than the mid-montane forests (Barbour, et al., 1990; Westman, 1987). Barbour et al. (1990) and Kunz (1988) suggest that the boundary between white fir and red fir is determined by the duration of snow pack, with red fir dominating sites with heavy snow pack, and white fir dominating sites with moderate snowpacks. On dry sites, or at lower elevations, white fir typically occurs in mixed

stands with a number of other conifer species. Mid-montane forests of California frequently burn, and fire may be a factor influencing the lower elevational limits of white fir. White fir is a shade-tolerant species and fire suppression has been implicated in the increasing cover of white fir in the Sierra Nevada (Kilgore & Taylor, 1979; Parsons & DeBenedetti, 1979).

White fir is an excellent subject for investigating population differentiation in growth-response functions because is a highly variable species and covers a broad geographic range (Hamrick & Libby, 1972). In particular, Hamrick's (1976) study of genetic variation in needle growth and morphological characteristics of white fir found significant ecotypic differentiation among populations from an elevational transect in the Sierra Nevada.

In this study, both the experimental plantation and the year were important factors explaining the variation in ring-width in these ten populations (Chapter 2).¹ Climate is an important component of both these factors suggesting that population-level growth responses can be investigated directly.

¹I have shown in Chapter 2 that 10 populations of white fir, when grown in a common environment, differ in their annual radial growth, and when grown in different environments these populations differ in their phenotypic plasticity.

As Fritts (1976) and others (Cook & Briffa, 1990) have shown, a tree-ring series can be modeled as a linear aggregate of several subseries: age; climate; disturbances endogenous to the stand; and exogenous stand disturbances.² The commonly used of variation in ring-width is:

$$R_t = A_t + C_t + D1_t + D2_t + E_t$$

where R = observed tree-ring, A = age, C = climate, $D1$ = local disturbances, $D2$ = stand-wide disturbances, and E = unexplained variation, or error.

These authors include environmental factors such as climate, and disturbances (both at a local or microenvironmental scale, and at a larger scale) in models of ring-width growth. However, they rarely explicitly include genetic differences among populations of a species. Rather, genetic differentiation is simply part of the unexplained error in their models. In Chapter 2, I show that the genotype of the tree affects its growth response, but my work indicates that population differences alone explain only a small

²Disturbance is not explicitly defined in these models, but Pickett and White's (1985) definition will suffice: "A disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (p. 7). Extreme weather events might be considered a disturbance by Pickett and White, but would not be lumped with disturbances by dendrochronologists.

portion of the ring-width variation. To more fully understand the population differences of ring-width variation in white fir, it is essential to investigate the role of climate more carefully, and then examine the gene by environment interactions.

Seed Sources and Plantation Design

Twenty individual trees from each of ten populations at each plantation were cored 20 cm above the ground. The ring-widths for each year were measured to the nearest 0.01 mm. These annual growth measurements could then be correlated with climatic variables for individual years. (See Chapter 2 for a complete description of the plantations and tree core methods).

The plantations span a wide array of climates typical of the Sierra, as is reflected in the surrounding native vegetation. Chimney Rock plantation, within a red fir forest, is typical of sites that are colder or at a higher elevation than those dominated by white fir. While Swain Mountain plantation is surrounded by a native forest of mature red fir, there is significant recruitment of white fir in the immediate area of the plantation, suggesting that this plantation may be at or near the edge of the range of white fir in this portion of the species range. Iron Mountain plantation is in the mixed conifer zone of the central Sierra, where white fir is a common

component of the forest. These three plantations will be referred to collectively as "fir-zone" plantations. The Institute of Forest Genetics (IFG) plantation is below the natural distribution of white fir in the Sierra, and was chosen to investigate the response of white fir to warmer conditions.

Ring-width Indices

In very young trees the annual growth increment increases with age, and in old trees the annual increment decreases with age. Thus, to understand the relationship between ring-width growth and climate, it is necessary to isolate the age-dependent growth trend from the tree-ring series. This allows comparison of different age trees (or the comparison of ring widths of a single individual across years). If all variables except climate could be quantified in the series, then it would be possible to compare the growth of different populations in different climates.³

To compare white fir population growth as a function of climate across the four plantations, I used a common expected growth function to standardize the ring-width series. Mean ring-width at the Chimney Rock plantation was the smallest (Chapter 2), and trees here exhibited the typical trend of increasing annual increment growth (see Figure 3.1). Therefore, I

³Only age trends were removed from the tree ring series. Many other factors such as nutrition and day length differ among plantations.

Mean Ring Width at Chimney Rock

Figure 3.1.

used the growth at this site as the standard against which to compare the other sites. A linear regression of annual growth with age was calculated for Chimney Rock, using all trees on the site. Ring-width indices were calculated as the ratio of actual ring-width to expected ring-width for each tree for each year. This was done for all trees at all sites. Thus, for example, ring-width indices for the IFG plantation indicate how much larger these trees are than those at Chimney Rock. (Figure 3.2 shows the ring-width index series for one population at the four plantations as an example).

Climate Data

Climate data were obtained from the National Climate Data Center. Data for minimum temperature, maximum temperature, and precipitation from eight climate stations during the years 1976 to 1991 were used in the analysis. Stations were chosen to represent the climatic conditions of each of the four plantations.

Climate data are collected on site at the Institute of Forest Genetics, providing an excellent record of the climate the trees experienced. None of the other three plantations had on-site climate data. For the Chimney Rock plantation in the southern Sierra, one climate station at Grants Grove was used to represent the climatic conditions. For the remaining two plantations, no single climate station was suitable. Therefore, composite climate records

Ring Width Indices for Population 1 at Four Plantations

Figure 3.2.

were created using climate stations that were similar in elevation, latitude and longitude to each plantation. After each station's record was error checked and adjusted (as described below), the data were averaged to produce a regional record representative of the climate at Swain Mountain and at Iron Mountain. Table 3.1 shows the elevation, latitude and longitude of each climate station, and indicates the stations used to represent each of the four plantations.

Missing Data

Monthly data were compiled for each climate station. Most of the stations were missing monthly data for one or more months. No station was missing more than 5 months over the period the trees were growing (1976-1991). To fill gaps in the monthly data, the values from one station were regressed against those of the nearest station. These regression equations were then used to estimate the values for the missing months. A separate regression equation was derived for each variable (monthly average minimum temperature, monthly average maximum temperatures, and monthly total precipitation) for each pair of stations. For most of the regression equations, the fit between the two stations was quite good, with R^2 values between 0.91 and 0.98.

Table 3.1. Climate stations used to make composite records for each plantation, and plantation locations. Climate values are annual means.						
Station	Plantation	Precip (cm)	Degree day sum	Latitude	Longitude	Elev (m)
Manzanita Lake	Swain Mtn	102.1	2636	40° 32'	121° 34'	1742
Canyon Dam	Swain Mtn	86.9	3156	40° 10' 19"	121° 05' 13"	1380
Calaveras Big Trees	Iron Mtn	135.9	3562	38° 17'	120° 19'	1423
Blue Canyon	Iron Mtn	156.9	3842	39° 16' 42"	120° 42' 28"	1600
Lake Spaulding	Iron Mtn	176.8	3239	39° 19'	120° 38'	1562
Institute of Forest Genetics	IFG	97.0	5568	38° 44' 24"	120° 44' 28"	835
Placerville (for missing data at IFG)	IFG			38° 43' 45"	120° 47' 51"	573
Grants Grove	Chimney Rock	104.7	3569	36° 44' 29"	118° 57' 40"	1994
	Swain Mtn			40.42°	121.08°	1879
	Iron Mtn			38.7°	120.33°	1758
	IFG			38.75°	120.7°	818
	Chimney Rock			36.68°	118.87°	2182

Adjusting for Lapse Rate

Given the sparse distribution of climate stations at high elevations in mountainous regions, the stations chosen to represent Chimney Rock, Swain Mountain, and Iron Mountain are all at lower elevations than the plantations themselves. Therefore, the mean monthly temperature data were adjusted to account for the cooler temperatures experienced at the plantations (relative to the climate stations) due to an elevational lapse rate.

Adjustments were made by decreasing the average monthly temperature data for each station using the lapse rates estimated by Alexander (1981). Alexander used data from 130 weather stations to develop regression equations for predicting mean monthly temperature at different elevations between the latitudes of 35 and 42 °N in the Sierra Nevada. He calculated a different regression equation for each 0.5 degree of latitude. His work shows that lapse rates differ from month-to-month and across latitudes in the Sierra.

Degree-Day Sums

Once the gaps in the data had been filled, degree-day sums were calculated using a base of 0°C.⁴ For each station, the average monthly

⁴Using monthly averages to estimate degree days underestimates the actual degree-day sums, and is not as good an estimator for hot sites as for cool sites. Faced with substantial missing daily values for several sites, I used monthly averages to estimate annual degree-day sums.

temperature was calculated from the average monthly minimum and average monthly maximum temperatures. If this average monthly temperature was less than or equal to 0°C, the degree-day sum for the month was tabulated as zero. The degree-day sum for months warmer than 0°C was calculated as the difference between the average monthly temperature and zero, multiplied by the number of days in the month.

Potential Evapotranspiration

Values for potential evapotranspiration were calculated using Thornthwaite's (1948) method. For each weather station, the long-term average monthly temperature (NOAA 1991) was adjusted for lapse rate as described above and then the heat index for the site was calculated using the formula:

$$I = \sum_{m=1}^{12} \left(\frac{T_m}{5} \right)^{1.514}$$

where: I is the heat index; m is the month; T_m is the long-term average monthly temperature. Monthly evapotranspiration (in centimeters) is then calculated using the formula:

$$E_o = 1.6 \left(\frac{T}{I} \right)^2$$

where: E_0 is monthly potential evapotranspiration; T_j is the average temperature of a given month in Celsius; and

$$a = (0.6751/T_j^3 - 77.1/T_j^2 + 17920/T_j + 492390) \times 10^{-6}$$

These monthly unadjusted potential evapotranspiration figures were adjusted for latitude and duration of sunlight using tables from Thornthwaite and Mather (1957).

Annual Climate Data Summaries

Finally, these monthly data were summed by hydrologic year, from October 1st to September 30th. Hydrologic year was used rather than calendar year to model growth because tree growth in the summer is affected by the water supply made available by the previous winter's precipitation.⁵ Table 3.1 shows the climate stations, their average precipitation, their average degree-day sums for the period of the study, and their locations and elevation. Table 3.2 shows the average values of climate variables for the composite record created for each plantation.

⁵Dendrochronologists use monthly data to build their models, and often include 4 months from the previous year. They work with long time series and have enough degrees of freedom in the regression models to have many independent variables in the model. I work with short series and therefore cannot run regressions using monthly data, so I used annual data.

Table 3.2. Average annual climatic conditions at four plantations during the years 1979-1991. Means for the hydrologic year Sept - Oct.

	Swain Mountain	Iron Mountain	Institute of Forest Genetics	Chimney Rock
Precipitation (in cm)	101.52 $\pm$ 32.3	168.95 $\pm$ 69.2	106.6 $\pm$ 45.1	107.07 $\pm$ 43.1
Degree days (base 0 °C)	2317.3 $\pm$ 224.4	3208.9 $\pm$ 250.4	5701.1 $\pm$ 306.2	2965.8 $\pm$ 253.6
Potential Evapotranspiration (in cm)	225.01 $\pm$ 17.3	303.8 $\pm$ 12.8	648.3 $\pm$ 24.3	254.55 $\pm$ 17.1

Climate of Population Source Locations

The average climate of the ten source populations was estimated from Rantz's (1972) isohyet map, and Alexander's (1981) regression equations for mean monthly temperature. Table 3.3 also shows the estimated long-term average climate for the ten source populations.

Estimating Climate for Fir-zone Plantations Due to Doubled CO₂

Output from general circulation models (GCM) was used to estimate the expected change in climate of the fir-zone plantations due to doubled CO₂. The predicted percent change in climate was calculated from monthly temperature and precipitation from control and doubled CO₂ runs using three GCMs: NASA Goddard Institute of Space Sciences (GISS); Geophysical Fluid Dynamics Laboratory (GFDL); and United Kingdom Meteorological Organization (UKMO).⁶ The composite climate records for 1979-1991 were then adjusted by the expected change to produce estimates for doubled CO₂ climate for Swain Mountain, Iron Mountain, and Chimney Rock. The doubled CO₂ climate for the fir-zone plantations was compared to the actual 1979-1991 climate at IFG.

⁶The grids used centered on the following latitude and longitude: GISS, 36° 120°w; GFDL 37.8°, 120°w; UKMO 37°, 117°w.

Table 3.3. White Fir seed sources and average climate values at source locations.
(Data from long-term averages, see text).

Source		Latitude	Longitude	mean elev m	expected degree days base = 0°C	expected precip in cm
Monarch Mine	1	39.59	120.68	1970	2407	165
Babbit Peak	2	39.58	120.10	2364	1849	69
Bunker Hill	3	39.05	120.38	2030	2341	165
Angora Creek	4	38.87	120.05	1970	2431	165
Bryant Springs	5	38.63	120.45	1500	3421	140
Strawberry Canyon	6	38.79	120.15	1803	2681	140
Pollock Pines	7	38.76	120.58	1152	3877	107
Bourland Mountain	8	38.11	119.94	2212	3011	114
Little Reynolds Creek	9	38.05	119.99	1856	3479	114
Rabbit Meadow	10	36.71	118.88	2318	2512	114

Modelling Growth

To model tree-ring growth as a function of climate, ring-width index was regressed against precipitation and degree-day sums (SAS Institute, 1989). The independent variables came from the composite climate record created for each plantation. All four plantations were included in the analysis, and the 12 years of record (1980-1991) were used. A separate growth equation was calculated for each population. Multiple contrasts were used to determine if populations differed in their dependence on particular climatic variables.

To determine whether populations were adapted to the climate typical of the origin of the population, regression coefficients for precipitation and degree days were correlated with the climate of the seed source for each population. Regression coefficients also were correlated with elevation and latitude of the source of the population. Correlations between growth-response equations and source climate or elevation were expected to reveal population differentiation based on climatic differences. Correlations between growth-response equations and latitude were expected to reveal differentiation based on geography.

2 of 2

Differential Population Response to Climate Change

Once population differences in growth-response equations had been identified, population growth differences under current and future climates could be estimated. Using regression equations derived for each population and 5 different climate scenarios (fir-zone plantations, UKMO, GISS, GFDL, and IFG) ring-width indices for each population were estimated. Differences in population ring-width indices were then compared.

Results

Plantation Climate

The three fir-zone plantations experienced similar temperatures during the study (Table 3.2). Swain Mountain was the coldest plantation with an average annual degree-day sum of 2317 ± 224 during the study. Iron Mountain and Chimney Rock were slightly warmer with average annual degree-day sums of 3210 ± 250 and 2966 ± 254 respectively. Institute of Forest Genetics was much warmer than the fir-zone plantations with an average annual degree-day sum of 5701 ± 306 .

Precipitation varied greatly over the twelve years and four plantations in the study. 1982 and 1983 were very wet years, whereas 1987-1991 were drought years throughout the Sierra. The extremes in precipitation in the study range from 290 centimeters at Iron Mountain in 1982 to 55

centimeters at Chimney Rock in 1987. Figures 3.3-3.6 show the annual precipitation and degree-day sums as estimated for the plantations.

The white fir source populations are from locations with similar temperature and precipitation to those occurring at the fir-zone plantations during the study (Figure 3.7). Nine of the ten populations are from locations with degree days sums greater than 2000 and with average annual precipitation greater than 100 centimeters. The Babbit Peak population, is from a cooler (1849 degree days), drier (69 cm) site than any other population in the study. The Swain Mountain plantation is slightly cooler than most of the source population locations; whereas the Institute of Forest Genetics plantation is substantially warmer than any of the source population locations.

The IFG plantation is warmer and somewhat drier than the climate projected for the fir-zone plantations from doubled CO₂ scenarios. Figure 3.8 plots the estimated average doubled CO₂ climate for the fir-zone plantations and contrasts them with the actual average climate at the fir-zone plantations and IFG.

Swain Mountain Climate

Figure 3.3.

Institute of Forest Genetics Climate

Figure 3.4.

Iron Mountain Climate

Figure 3.5.

Chimney Rock Climate

Figure 3.6.

Climate at 4 Plantations During the years 1979-1991

Figure 3.7. Climate of plantations and seed source locations. Climate of seed source locations indicated by population number.

Comparison of 2XCO₂ Climate with climate of Fir-zone and IFG

Figure 3.8.

Correlating Ring-Width Index with Climate

White fir growth-response functions were modeled using annual precipitation and degree-day sums. Multiple regression incorporating all the populations found the following partial R^2 s: precipitation, 0.26; degree days, 0.15; degree days squared, 0.0085 (SAS 6.07 Stepwise multiple regression). Although tree-diameter growth models often include the square of degree-days as a growth factor, in this study, degree-days squared explained only a small portion of the variation and was not included in the growth-response models.⁷ For many of the regressions for individual populations, degree days squared was not a significant factor in the model. Potential evapotranspiration did not improve the regression model of growth and was not included in any of the analyses.

Comparing Population Growth Responses

Growth-response functions modelled with multiple regressions show that both precipitation and degree days are important predictors of growth for all the populations. The relative importance of the two climatic factors varies, however, across populations. Table 3.4 shows the results of the multiple regressions for each population, as well as the regression for the aggregate of all populations. The coefficients of determination for these

⁷As would be expected, the coefficient for the degree-day squared term is negative.

Table 3.4. Regression equations of ring-width index as a function of degree days and precipitation for each population. The first regression is for all populations together. The rest are regressions for each population alone. P values for all regressions < .0001. (Coefficients have all been increased by 10⁵, so RWINDX equals 100,000 x ring width index).

All populations	RWINDX = 653.7PRCP + 19.20DEGDY + 377	R² = 0.42
Monarch (1)	RWINDX = 528.9PRCP + 12.94DEGDY + 29301	R² = 0.42
Babbitt Peak (2)	RWINDX = 570.0PRCP + 9.23DEGDY + 29496	R² = 0.35
Bunker Hill (3)	RWINDX = 692.9PRCP + 13.18DEGDY + 24479	R² = 0.38
Angora Creek (4)	RWINDX = 725.3PRCP + 15.14DEGDY - 1264	R² = 0.44
Bryant Springs (5)	RWINDX = 657.9PRCP + 20.66DEGDY + 1357	R² = 0.45
Strawberry (6)	RWINDX = 655.5PRCP + 19.92DEGDY - 2171	R² = 0.41
Pollock Pines (7)	RWINDX = 789.1PRCP + 31.92DEGDY - 54310	R² = 0.55
Bourland Mountain (8)	RWINDX = 575.4PRCP + 21.44DEGDY + 12055	R² = 0.45
Little Reynolds Creek (9)	RWINDX = 707.6PRCP + 26.04DEGDY - 27278	R² = 0.55
Rabbit Meadow (10)	RWINDX = 633.4PRCP + 21.47DEGDY - 7476	R² = 0.43

equations (R^2) ranged from 0.35 to 0.55. Precipitation is the more important variable for explaining the variation in ring-width index, with partial R^2 values ranging from 0.22 to 0.34 (Table 3.5). The importance of degree days in explaining the variation in ring-width index ranged from a partial R^2 of 0.05 for the population from Babbit Peak, the coldest source population, to a partial R^2 of 0.30 for the population from Pollack Pines, the population from the warmest source site.

The climate of the origin of the population is a better predictor of the similarity of population growth-response functions than is the geographic proximity of the source populations. Populations from source locations with similar climates had regressions that were not distinguishable statistically. In contrast, populations from source locations with the least similar climates had regressions that differed significantly. However, only those populations from the extremes of the climate space sampled (see Figure 3.7) had significantly different regressions. Furthermore, these regressions differed only with respect to the coefficient for degree-days. For example, populations 3 and 4, Bunker Hill and Angora Creek, both cool, moist source sites, have different coefficients for the degree-day variable than do Populations 7 and 9, from Pollack Pines and Little Reynolds Creek, the warmest source sites ($p < 0.04$). In addition, Population 2, from Babbit Peak, the coolest, driest source site, had significantly different degree-day

Table 3.5. Partial R^2 for Degree day sum and precipitation in the regressions.

	PRCP R^2	DEGDY R^2	Total Adjusted R^2
Population			
Monarch (1)	0.30	0.12	0.42
Babbit (2)	0.30	0.05	0.35
Bunker (3)	0.31	0.07	0.38
Angora (4)	0.34	0.10	0.44
Bryant (5)	0.26	0.18	0.45
Strawberry (6)	0.25	0.16	0.41
Pollock (7)	0.25	0.30	0.55
Bourland (8)	0.22	0.23	0.45
Little Reynolds (9)	0.28	0.27	0.55
Rabbit (10)	0.24	0.19	0.43

coefficients in the regression than Populations 7 and 9 ($p < 0.03$). Other contrasts were explored, but no other significant contrasts were found for degree days. Although the coefficients for precipitation in the regressions varied from 570 to 789.1, they were not statistically different.

High-elevation source populations are less responsive to changes in precipitation and degree-days than are lower elevation populations. The elevation of the population's source location was negatively correlated with both the regression coefficients for precipitation and for degree days ($R = -0.66$). Thus, for a given change in temperature or precipitation, higher elevation populations will show less change in ring-width. This finding is consistent with the results of Chapter 2 which showed that higher elevation populations have flatter norms of reaction and show less phenotypic plasticity in response to changes in climatic variables. No significant correlation was found between the latitude of the source population and the coefficients of the growth-response regressions (Table 3.6).

Populations from warmer sites have larger growth responses to degree-days than do populations from cold sites. The average degree-day sums of the population source locations were positively correlated with the degree-day coefficient in the regression ($R = 0.92$, $p < 0.0002$). This trend suggests that for a given change in temperature, populations from cold sites

Table 3.6. Correlation between coefficients of growth response regressions (or partial R^2) and attributes of the source of the population. R = Pearson Correlation Coefficients.

		Coeff. PRCP	Coeff. DEGDY	R^2 PRCP	R^2 DEGDY
Attributes of Population Source Locations					
Latitude	R	-0.16	-0.52	0.58	-0.53
	p	0.65	0.12	0.08	0.10
Elevation	R	-0.66	-0.66	0.14	-0.55
	p	*0.04	*0.04	0.70	0.10
Precipitation	R	0.10	-0.22	0.42	0.27
	p	0.79	0.55	0.23	0.49
Degree days	R	0.57	0.92	-0.50	0.91
	p	0.08	**0.0002	0.14	**0.0003

will show less change in growth than populations from warm sites. This trend in increasing response to temperature as the source locations are warmer is reinforced by the finding that the portion of the variation in ring-width index explained by degree-day is positively correlated with the degree-day sums of the population's source location ($R = 0.91$, $p < 0.0003$).

These results suggest that white fir growth responses vary clinally. Populations found at the ends of the climate gradient have statistically different growth-response functions, but intermediate populations cannot be differentiated from each other or from the end points. Nevertheless, there is a trend for populations from warmer sites to have a larger response to temperature (modelled here as degree-day sums).

Populations have differentiated more in response to the environmental gradients in temperature than to gradients in precipitation. Precipitation is a very important factor in explaining ring-width growth, but populations do not differ significantly in their growth responses to precipitation. (There is, however, a trend for precipitation to be an increasingly important factor in growth as the elevation of the source population declines ($R = -0.66$, $p < .04$)). In the Sierra, the annual degree-day sum of a given site is much less variable than the annual precipitation of a site. Populations may have experienced both selection for adaptation to the average degree-day sum of

their source site and selection for the ability to tolerate a wide range of variation in precipitation.

White fir populations from high elevation sites or cold sites are less responsive to climate than those at lower elevation and warmer sites. As discussed in Chapter 2, these results are consistent with the quantitative genetics literature and evolutionary theory which suggest that there is an evolutionary trade off between ability to tolerate adverse conditions and the ability to take advantage of favorable conditions (Schlichting, 1986).

These results also are consistent with other studies of white fir in the Sierra Nevada that found genetic differentiation in needle attributes among populations along an elevational transect (Hamrick, 1976). Westfall and Conkle (1990) analyzed geographic patterns in allozyme data in white fir in the Sierra and found both latitudinal patterning and elevational patterning in allozymes. My results suggest that white fir is responding to selection gradients in temperature that correlate with elevation.

Population Responses Under Differing Climate Scenarios

Population differentiation in responsiveness to temperature provides an indication of how populations may perform differently due to climate change. Populations showed greater differences in growth in the warmer

climates predicted by the GCMs than in the climates they experience now (Figure 3.9). Using the population-specific regressions and the current average climate of the fir-zone plantations, the Pollack Pines population (number 7) was predicted to be, on average, 7% larger than the Babbit Peak population. In contrast, under the GISS or GFDL doubled-CO₂ scenarios of fir-zone climate, the Pollack Pines population has a predicted ring-width index 28% larger than Babbit. Under the hotter and dryer conditions predicted by UKMO, Pollack Pine ring-width index is 40% larger than Babbit.⁸ Comparisons between other populations show similar though less dramatic results (Table 3.7).

These results suggest that climate change could amplify population differences in growth because of differences in growth-response functions. The magnitude of population differences, like other response of forests, will certainly depend upon the magnitude and nature of the climate change. If climate gets significantly hotter and drier, then future conditions for white fir will be more like the UKMO or even IFG. In the case of white fir, population differences in growth response will be most pronounced if the climate change is also large, and in the direction of hotter and drier conditions.

⁸Note in Figure 3.9 that populations differ even further in growth response at the IFG plantation which is warmer and drier than any of the doubled-CO₂ scenarios.

Estimated ring width indices for five populations in five climate scenarios

Figure 3.9.

Table 3.7. Estimated ring width indices for 5 different climate scenarios. Fir-zone is the current climate averaged over three plantations. IFG is the current climate at IFG. The other three are estimates of doubled-CO₂ climate using output from the noted GCM to extrapolate from the Fir-zone climate. All ring width estimates use average annual precipitation and degree day sums, and the empirically derived population growth-response regressions.

	Climate Scenario				
	Fir-Zone	GFDL	GISS	UKMO	IFG
Population					
1	1.317	1.599	1.678	1.689	1.557
2	1.267	1.511	1.598	1.566	1.391
3	1.482	1.804	1.908	1.888	1.689
4	1.320	1.674	1.782	1.774	1.575
5	1.418	1.828	1.923	1.981	1.849
6	1.358	1.759	1.854	1.905	1.769
7	1.353	1.939	2.050	2.187	2.074
8	1.443	1.845	1.927	2.010	1.918
9	1.343	1.832	1.933	2.031	1.916
10	1.322	1.738	1.828	1.900	1.784

Discussion

Implications of Population Differentiation

Recognition that population growth differences may be greater under future climates than under current conditions has important implications for research on forest responses to climate change. Prevailing approaches to modelling forests assume that populations are interchangeable, but white fir populations show significant differences in ring-width when grown in a common environment. Furthermore, these growth responses vary clinally along climatic gradients. Projections of growth under three doubled-CO₂ climate scenarios found that population differences in ring-width could reach as much as 40-50%. In fact, population productivity differs more under the various scenarios of warming than under the climatic conditions white fir naturally experiences.

Productive forests provide society with forest products and, by sequestering carbon, influence the global carbon cycle. Estimating the future productivity of white fir in the Sierra requires a knowledge of population-level growth responses, the degree of climate change that occurs, and the fate of the low elevation white fir populations. All populations in this study grew larger in climates warmer than their source site, suggesting that climate change will increase growth in all white fir populations. However, productivity will increase only if white fir's climate

range extends, so that the species as a whole experiences warmer climates. On the other hand, if the lower elevation limit of white fir advances uphill at the same pace as, or faster than, the climate isotherms, then the region-wide productivity of white fir will decrease because the populations lost at the lowest elevations are the more productive ones. At present, some limiting factor (perhaps fire, seedling requirements, moisture availability or predation) prevents white fir from occupying warmer sites where it grows quite well. Whether the balance between white fir and that limiting factor will change under doubled CO₂ remains to be seen, but it appears to control future productivity of the species. Improving the prediction of future productivity in white fir depends in part on understanding the controls on both the lower and upper elevational limits of white fir, topics now poorly understood. Future productivity also depends upon the growth responses of those populations which survive.

Including population differentiation in forest succession models is necessary in order to obtain geographically explicit predictions of forest responses to climate change. Forest species often have large ranges which span significant environmental gradients either from north to south or in elevation. Frequently, the species have ecotypes that have differentiated in response to these environmental gradients. Because population differentiation is a common phenomenon, it is reasonable to anticipate that

many forest trees will have changes in growth responses across their range. In these cases the use of a single growth function in forest succession models will not accurately reflect the growth of that species throughout its geographic range. Although this study included trees from only a small portion of the geographic range spanned by white fir, growth differences between two populations resulted in as much as a 40% difference in ring-width index under some warming scenarios.

This study is consistent with other quantitative genetics studies of forest trees that show smaller average growth in populations from northern latitudes when compared to southern populations. For example, the study by Roberds' et al. (1990) of white ash provenances found that the mean height of five-year old trees from northern provenances was less than half that of the trees from the southernmost provenance studied.

Generalizing patterns of population differentiation in forest trees for use in broad-scale analyses will not be an easy task. Populations of trees are not necessarily optimally adapted to their location of origin. Because of past migrations of trees in response to climatic shifts, trees may still be adjusting to the climate they presently experience. As a result, some populations may actually grow better if subjected to a degree of warming. The reverse may also be true. The white fir population from Babbitt Peak

grew largest under the average climatic conditions predicted using the output from the GISS model, conditions significantly warmer and wetter than Babbitt Peak. In contrast, the study of Roberds et al. indicates that some southern and central provenances of white ash grew best at locations to the north of their location of origin (Roberds et al., 1990).

Provenance tests, in combination with genetic and dendroecological techniques, as applied in this study, can provide a source of relevant data for estimating range-wide patterns of differentiation in population growth responses. Measured clines in growth-response functions, could be incorporated into stand simulation models, perhaps by calibrating the growth function for each geographic region defined by the provenance and climate gradient analysis. As a first approximation it might be possible to use seed transfer zones (Namkoong et al., 1988) already identified by forest geneticists to define geographic areas that could be adequately represented by a single growth-response function.

Although other researchers have proposed using tree-ring analyses to improve the accuracy of predictions of forest response to climate change, they have only proposed improvements to species-level models, not consideration of population-level differences (Cook & Cole, 1991; Graumlich, 1989). Nevertheless, using tree-ring analysis of trees in native stands,

Cook and Cole (1991) found a geographic trend in the growth-response function of eastern hemlock across its range in North America. Growth was more strongly correlated with March temperature in trees from the central and northern portions of the range, than for trees from eastern portions of the range. This suggests that eastern hemlock populations differ in their growth response across the range of the species.⁹

Extrapolating Beyond the Range of the Species

The successful growth of trees at IFG undercuts the common practice of using the existing range of a species to approximate the climatic tolerance of the species. If the current range is equivalent to the climate the species can tolerate, it follows that if the climate changes the range of the species changes accordingly. As Pacala and Hurtt (1993) point out, this equates the realized niche with the fundamental niche, and therefore tends to underestimate the range of climates a species will be able to tolerate. Certainly white fir can grow outside of its natural range; it does quite well at IFG.

⁹Their study did not use reciprocal transplants, and therefore cannot clearly distinguish between the differences in climate across the range of the species and the difference among populations. Nevertheless, trends in the correlations of monthly climatic variables with tree rings should be expected in range-wide dendroecological studies because population differentiation is common in trees.

Equating the realized and fundamental niche raises two distinct concerns with regard to estimating the response of forests to conditions beyond those they now experience: climate is only one of many factors limiting the range of species; and extrapolating beyond known conditions can often lead to unexpected results.

One reason a species can often tolerate a broader range of climatic conditions than those experienced within its range is that climate is rarely the limiting factor for all of a species' range. To accurately predict how forest trees will respond to climate change it is necessary to understand both how climate affects regeneration, growth, and mortality, as well as what other factors determine the existing geographic range of the species. Knowledge of the responses to climate alone is not enough. In this study, white fir grew quite well at IFG, a plantation which is warmer than the temperatures mid-Sierran populations of white fir are predicted to experience (on average) due to an atmosphere with doubled CO₂. This result might not have been expected from a model that considered only the responses of white fir within its range, and then extrapolated outward.

A variety of reasons may determine why white fir is not found naturally at IFG although it grows well there. Perhaps seedlings cannot survive due either to climatic conditions or competition with other plants. Or

white fir may not occur naturally at IFG because the fire frequency is too high to allow the development of mature regenerating stands¹⁰. Predation or disease may be more prevalent in the warmer, dryer sites.

One of the challenges of predicting the effects of climate change is the necessity of extrapolating beyond the known boundaries of the system. In any type of modelling, extrapolation beyond the known range of values is a speculative exercise because it assumes that the form of the functional relationship does not change in a new set of conditions. Ideally, empirical data would be available to test the extrapolations needed for climate change research. For forest trees, provenance tests provide a fortuitous opportunity to test responses to a broad range of conditions. Plantations in sites warmer than the current range of the species may be a good source of empirical data to validate some of the predictions of responses to global warming.

Often researchers create alternative models to evaluate the importance of different sets of assumptions. Here I have argued that

¹⁰Particularly in regions or community types where disturbances such as fire are common, models need to include a more complete understanding of the many factors controlling tree growth and distribution before reliable predictions of the effects of climate change on forests are possible. Fire is an important factor in many of the forests in the western United States and fire frequency and intensity will also be affected by climate change (Torn & Fried, 1992).

overlooking populations in analyses of forest trees' responses to climate change will provide biased results. Others argue for inclusion of missing elements in hopes of better estimating the effects of climate change on forests and thereby on society. Ironically, without some understanding of how the species or ecosystem will respond to novel conditions, adding more detail to our models, whether by incorporating population differences or by adding disturbance as a factor controlling range limits, may increase the precision of our analysis without decreasing the uncertainty.

CHAPTER 4
POLICY MAKING UNDER UNCERTAINTY:
IS THERE ANY ALTERNATIVE FOR
CLIMATE CHANGE POLICY ?

Three broad policy responses to the problems posed by global climate change are available: wait and see if the problem really needs attention; take actions that will avoid or reduce the expected impacts; or take actions that will allow human society and ecosystems to adapt to the expected impacts. Although the scientific community generally agrees on the potential magnitude of the change in the *average* climate of the world (IPCC, 1990) there are huge uncertainties about the direction, magnitude and timing of impacts that will be experienced in any particular region, nation, industry or ecosystem. Similarly, there are large uncertainties about the costs and benefits of proposed policy alternatives.

Various calls for policy responses to climate change (e.g. NAS, 1991; IPCC, 1990; Jager & Ferguson, 1991; Mintzer, 1992) argue for additional scientific research to reduce uncertainty about the estimates of the climatic changes anticipated from a doubling of greenhouse gases (GHG), and to reduce uncertainty in the consequences of doubling GHG for human societies and ecosystems. Clarifying the consequences of climate change,

these authors argue, will help decision-makers choose among policy options by elucidating the risks of various actions or inactions (Turner, O'Riordan, & Kemp, 1991).

At this time, and for the near future, estimates of climate change, and the ecological impacts of that change, on a scale relevant to human activities, are inherently uncertain. Moreover, it is not evident when, if ever, research results will be reliable enough to inform policy choices about climate change. Scientific research on climate change is better suited to the identification of potential problems than to the comparison of policy prescriptions based on such estimates. Therefore, policy prescriptions which implicitly or explicitly depend on reliable estimates of climate change and its impacts will be precluded. Policy prescriptions must instead acknowledge the limitations of the available information, and that improvements in information may never be adequate to eliminate uncertainties in policy-making. This suggests the need for a new, adaptive policy prescription, one I call "take your best shot", as an alternative to the existing prescriptions that assume that more information, when available, will reduce the uncertainties and will inform better decision-making.

Policy Responses to Climate Change

"Wait and See" Versus "No Regrets"

In the face of uncertain impacts from climate change, two different schools of thought have attracted the most attention in the debate over appropriate policy responses to the suite of potential impacts from climate change. One group of scientists and policy-makers argues that because the adverse consequences of climate change may be grave, actions should be taken now to avoid and mitigate the impacts. However, recognizing the uncertainty in current estimates of climate change impacts, they urge implementing policies likely to mitigate the impact, such as increases in energy efficiency, that can be justified today on other bases. This policy prescription is termed "no regrets". Others disagree with this approach, arguing that the impacts and consequences of climate change are so uncertain that decisions made without complete information will lead to costly, inefficient, and likely ineffective policies. Proponents of this second view argue that we should "wait and see" what further research tells us before taking action.¹

¹"Wait and see" proponents argue the merits of this policy proposal based on their ability to solve the problems posed by climate change. "No regrets" often argue for policy proposals based on their ability to address "other" problems. In a sense these two schools argue past each other, each addressing somewhat different concerns.

Some of the distinctions between advocates of the "wait and see" policy response and the "no regrets" policy responses can be explained by different tolerances of risk, by different evaluations of the costs and consequences of a particular action (Turner, et al., 1991), and by different views of the need for certainty in policy-making. The argument for "wait and see" is usually based on avoiding excessive or ineffective current costs; it assumes that additional information will allow the design of more efficient and less costly solutions in the future. The "no regrets" proponents argue that the opportunity costs of inaction are too high.²

Pachauri and Damodaran (1992) characterize these two different policy prescriptions as "acting, then learning" and "learning, then acting", emphasizing the importance of information to the decision-making process. "Wait and see" proponents appear to want higher quality, more reliable

²These two schools are really extremes in the debate. A school closely aligned to "no regrets" advocates risk reduction or policies that provide "insurance" against catastrophe. This school argues that the consequences of climate change may be so extreme that we should "insure" ourselves against the worst outcomes by taking action now to reduce the likelihood of their occurrence. The extreme proponents of "no regrets" argue only on economic grounds, whereas the "insurance" proponents use a broader array of values to bolster their position.

To focus this discussion on the interaction between action and information in the climate change policy-making arena, I include the "insurance" school into the "no regrets" position rather than restricting the "no regrets" school to only those using solely economic analyses.

information before designing and implementing policy responses.³ They argue that because global climate change does not have certain significant and adverse impacts, it does not merit precautionary policy measures, nor the high costs of implementing such measures. They urge further research on both climate change and new technologies. In contrast, because the potential impacts of climate change are severe, the "no regrets" proponents argue for precautionary policies today as insurance against grave misfortunes tomorrow. The "no regrets" proponents anticipate that future research will reinforce and clarify the need for actions to reduce GHG emissions and to mitigate the impacts of climate change. While the "wait and see" school appears⁴ to want more certainty from the science, both groups acknowledge that existing information is incomplete and look to the scientific community to provide improved assessments of the types of impacts that will result from climate change and the likelihood of their

³Pachauri and Damodaran argue that the proponents of "learn then act" want "perfect information" -- "complete, correct and exact predictions of the future" p. 238.

⁴I use the word "appear" because an alternative explanation is that the two schools use the uncertain scientific results to support their pre-existing positions on policies. Thus the "wait and see" school uses uncertainty to argue for maintaining the status quo, while the "no regrets" school uses uncertainty to argue for changes in energy and environmental policy that they favor for other reasons. This alternative explanation makes the role of scientific information in the policy debate a bit more complex. To the basic question "Can science provide the answers the policy-makers seek"? is added the further question: "Do policy-makers really want the answers they say they do?" Exploration of this second question awaits a different paper.

occurrence. In the long run, both the "wait and see" and the "no regrets" groups anticipate increased certainty about the likelihood and consequences of climate change. Justifications for future policy prescriptions are expected to be based on better information than present policy prescriptions. There is a low probability, however, of ever achieving the certainty both schools seek.

Certainty is Unlikely

Resolution of uncertainty in two separate but interconnected areas of scientific inquiry is needed to understand climate change impacts.

Uncertainty in the climate predictions has already received significant discussion (IPPC, 1990). Less discussed is the probability and speed with which uncertainty will be reduced in predictions about the effects of climate change on biogeochemical processes and biological systems.

Uncertain Future Climates

Climatologists cannot yet make confident predictions of the climatic changes anticipated from increased levels of GHG. To date the best estimates available are global, or broad regional assessments based on differing scenarios of GHG emissions and the different assumptions imbedded in the general circulation models of global climate. Regional, mesoscale and local predictions of climate are significantly less certain than

are global averages, and resolving the uncertainties at regional scales will take many more years of research than resolving some of the uncertainties in the global models (Schneider, Mearns, & Gleick, 1992). Finally, estimating climate variability, in contrast to climatic averages, is inherently more difficult at any scale, from global to local. Yet these measures of climate variability at local and regional scales may be the most important factors for predicting impacts, particularly to ecosystems.

The limitations of the predictions from climatologists necessarily constrain the ability of other researchers to predict the responses of ecosystems. Yet, reliable climate predictions are not the only stumbling block to resolving the uncertainties of the impacts of global warming. Researchers' ability to predict the responses of ecosystems is also greatly limited by incomplete knowledge of the fundamental mechanisms that affect ecosystem structure and function. An examination of the many impediments to understanding the ecological impacts of climate change will help us evaluate the possibility that science can diminish the uncertainties in a way and time-frame helpful to policy-making.

Uncertain Impacts to Biological Systems

Research on the impacts and consequences of climate change on biological systems is particularly problematic for three reasons. The systems

being studied are highly complex, and not all of the important components, mechanisms, feedbacks, or interactions that determine the structure and functions of biological systems are identified or understood. Secondly, in modeling the effects of climate change, simplifications are made which limit the scale of the analysis (omitting phenomena known to occur at different scales) and which limit the components and interactions considered. Simplifications are necessary in modeling, yet the choices which make the analysis tractable may profoundly skew the results. Finally, ecosystems are expected to experience novel environmental conditions as a result of climate change; no analogous conditions are present today for comparison.

Many Pieces of These Complex Systems are Unknown

Predicting the impacts of climate change on a species or ecosystem requires knowledge of many environmental and biotic factors that influence the growth, regeneration, and survival of the species or the ecological processes characteristic of the ecosystem. Often many features of the biological system being examined are not known. Surprising results can be uncovered by research, some of which may be important for predicting the impacts of climate change. However, until these surprises are discovered, scientists do not even know to look for them. Because biological systems are complex and incompletely understood, research to understand climate change impacts may overlook important components or interactions.

Studies of the implications of increased carbon dioxide levels on agricultural productivity provide an example of new research findings leading to awareness of new potential impacts. In general, increased levels of CO₂ allow plants to have higher photosynthetic rates and, when nutrients are abundant, can lead to increased productivity.⁶ Increased productivity is only likely, however, when there are no other factors limiting growth. Therefore, plants in low nutrient or low moisture conditions may not show increased productivity (IPPC, 1990).

Additional studies (e.g. Sionit, Mortensen, Strain, & Hellmers, 1981) have found that plants grown in enriched CO₂ atmospheres have higher carbon to nitrogen ratios (C:N) than plants grown in normal levels of CO₂. Changes in C:N ratios in plants were a logical result that led to the discovery of some unexpected consequences. Insects eating plants grown in enriched CO₂ conditions grow slower and have higher mortality (Fajer, Bowers, & Bazzaz, 1989) or eat more leaf biomass to obtain nitrogen (Lincoln, Couvet, & Sionit, 1986) than insects grown in normal CO₂ levels. Thus, not only will plants change in response to increases in CO₂, but insect herbivores will

⁶This simple understanding led some analysts to predict that increased CO₂ would lead to increased agricultural productivity. These analyses left out basic knowledge of the role nutrient availability plays in plant productivity. When nutrients are scarce, increased plant productivity is not found. This is an example of misleading predictions due to omission of critical components of the analysis--a problem discussed in the next section.

change their feeding behavior in response to the changes in plant nutrient content.

Predicting the implications of climate change on agriculture in light of these studies of the effects of increased CO₂ levels on plants and their herbivores is quite difficult. Without additional research, it is not yet possible to make generalizations about herbivore responses to the changed nutritional content of plants that may result from increased levels of CO₂.⁸ Nor is the potential importance of changes in herbivore survival or behavior limited to agriculture--both the forest products industry and natural ecosystems may be affected. Furthermore, if vertebrates change their feeding patterns in response to changes in plant nutritional content, the livestock industry also could be affected.

Because natural ecosystems have many interacting ecological processes, it is difficult to predict which interaction or which mechanism will be most important in determining the response of biological systems to the multifaceted changes brought about by climate change. Until biological

⁸Insect herbivores will be directly affected by the changes in climate as well as indirectly affected by changes in plant nutrient content. Predicting the likely results in any specific circumstance requires understanding the interactions among many components of the system. See Ayres (1993) for a discussion of plant, herbivores, and climate change.

systems and interactions are better understood, predictions of ecological consequences of climate change will remain uncertain.

Simplified Analyses Can Overlook Important Components

Even in circumstances where the components and interactions of the biological system are known, models to understand climate change impacts will, of necessity, omit some scales of analysis or pieces of the system to make the analysis tractable. By choosing what to include in the analysis and what to omit, the researcher may affect the findings of the study.

Completeness is not a realistic goal for analyses of climate change impacts, yet when the omissions affect results important to the policy-making process, the results of the analysis are unreliable. Two types of simplifications will be discussed below: choosing the scale of analysis; and choosing the components.

Scale matters. Many current predictions of the impacts of climate change on natural ecosystems rely on broad, regional analyses of models that, of necessity, simplify ecosystem processes. Broad-brush studies have predicted that entire biomes may move poleward in response to changes in climate (Emanuel, et al., 1985). Using similar analyses other researchers have shown that changes in the distribution of biomes will result in changes

in the carbon storage of the vegetation and of the soils (Lashof, 1989) with resulting feedbacks to the global carbon cycle and to global climate.

Ecologists and paleontologists have found that forest tree species respond individualistically to climate changes (Hunter, Jacobson, & Webb, 1988; Webb, 1987). Therefore the image of biomes moving around as a unit is a simplification that may lead to false conclusions. Rather than the same biomes occurring in new places, new communities of tree species will occur. The biomes themselves will be different. Whether the newly constituted biomes will have different carbon storage characteristics is not known. Using the biome as the unit of analysis is troublesome in part because it overlooks attributes of the biome (for example, the component species) that are of interest and concern to society.⁷

My research on white fir suggests population-level responses to climate change also may have significant consequences both for white fir and for society. This case study suggests that examination of population-level responses results in a picture of forest responses to climate change that is not consistent with analyses completed at the species level.

⁷Forest succession modelers include individualistic species responses in their models explicitly. They argue the species is the appropriate unit to model to understand forests.

Overlooking population-level analysis may mean overlooking important distinctions in the way the biological system works, and overlooking the value of the resource to human society. For example, if low elevation, high productivity populations of white fir (or other species with similar population responses) are lost due to the direct or indirect effects of climate change,⁸ the ability of these species to mitigate global warming by storing carbon dioxide maybe diminished. Futhermore, all populations are not equally valuable for reforestation efforts; the best seeds for high productivity might be from the low elevation populations.

Which pieces are included in the analysis? Another challenge researchers face is evaluating how complete the model must be to make predictions of acceptable accuracy. Even when all the components and interactions are recognized, the researcher must choose among the processes and components because everything cannot be included. Usually the analysis includes strategic choices, intending to capture characteristic patterns and processes representative of the larger picture from the pieces chosen. Because the patterns and interactions are not all known or understood, as discussed above, the analysis will perforce be incomplete.

⁸Low elevation populations of white fir may be able to tolerate warmer conditions, but increased temperature will likely lead to increased fire frequency and therefore losses of low elevation white fir forests.

The white fir study also provides an example of the importance of these research choices in terms of the uncertainties that remain when only a subset of the species biology is included (even within a chosen scale of analysis). Populations of white fir differ in tree ring growth-response functions, with populations from colder sites being less responsive to changes in temperature than populations from warmer sites. However, to understand how white fir will respond to climate change throughout its range, many other differences among populations must be investigated.

Studies on other forest trees have shown that populations differ in traits related to adaptation to cold hardiness and phenology. For example, the proportion of seedlings damaged by cold decreases with the latitude of the source population in black walnut, yellow birch and green ash (cited in Li et al. 1992). Genetically controlled differences in phenology of bud burst or leaf flush is also commonly found in trees. Northern populations tend to start growing later than, and stop growing earlier than, southern populations (Li, MacKay, & Bousquet, 1992). In species where the timing of growth is controlled by day length, northern populations will not start growing earlier in the spring, even though the climate is appropriate. In these cases, northern populations will not be able to take advantage of the longer growing season likely to occur due to climate change.

No single study can incorporate all the relevant details. To predict the future growth and persistence of trees in a given area requires a knowledge of population differentiation in many traits relevant to growth, regeneration, and survival. Much as the species in a community respond individually to the environmental changes they experience, traits can evolve individually in response to different selective pressures and history. Although this suggests a need to study every single trait in every species of tree, many traits are correlated and common responses to the similar selection pressures of cold winters or changing day lengths can be expected. Nevertheless, the question remains whether the correlated responses of trees similar enough among species or populations that generalizations can be made.

Although no analysis can include all the components and interactions of an ecosystem simultaneously, the choice of simplification can determine the results of the analysis. This raises a troubling issue of completeness. How much detail is needed to understand "adequately" the changes that climate change may bring? The appropriate level of simplification in the analysis depends in part upon the mechanisms and feedbacks of the biological system being studied and in part on the attributes of the system of interest or value to society. Scientific analyses must make assumptions and

simplifications, the challenge is to make judicious choices that retain the attributes of the system of interest to those looking at the outcome.⁹

The scientific community typically develops multiple models with alternative simplifications. Real progress in scientific understanding that can inform policy-making occurs when the differing models with their different assumptions produce similar results. If, however, alternative models produce conflicting results, policy-making may be side-tracked by the argument over which result is correct.

Novel Conditions May Mean Surprises

Understanding the impacts and consequences of climate change for even a single ecosystem is a multi-year, multi-disciplinary research challenge. Nevertheless, experts could estimate what research agenda would be needed and how long it would take to diminish the uncertainties in evaluating how known components of the ecosystem will respond. A more troubling predicament is posed by those impacts or responses that fall into the category of surprises. Many biological systems are expected to be experiencing novel environmental conditions due to doubled GHGs. Because

⁹This raises a tough question about whether scientists and policy makers have similar or at least compatible definitions of what are interesting "outcomes" or if they would make different simplifications and assumptions in their models because they want to "know" different things.

many ecological systems have important non-linear responses to environmental factors, extrapolation beyond the known is at best a speculative exercise.

The Outlook for Resolving Uncertainties Is Grim

An integrated, coherent understanding of the consequences of climate change is unlikely because of the dilemmas in modeling and predicting impacts of climate change on biological systems. Rather there will be areas of inquiry where predictions are believable and other areas where, because of unknowns and potential surprises from extrapolating beyond current conditions, predictions will be unreliable. Moreover, because of the gaps in knowledge, and the frequent occurrence of non-linear responses in biological systems, testing the validity of predictions of the impacts of climate change will be difficult. Ironically, the experience to date indicates that research will provide only incremental progress on understanding the impacts and consequences of climate change while concurrently generating more uncertainties as surprises are uncovered, previously overlooked areas of inquiry are incorporated, and the need for more complex analyses are acknowledged.

Policy-making Must Expect Continued Uncertainty

Both of the current policy prescriptions for climate change, "wait and see" and "no regrets" hope for reliable, certain answers from scientists in the future. Both also assume that new information might support different policy actions in the future. They differ, however, in their recommendations about how to proceed in the present and how much additional information they want before changing their policy prescription. Implicit in the "wait and see" prescription is the notion that a threshold of understanding must be crossed before action is taken. (The degree to which predictions would have to be more reliable has not yet been addressed.) Implicit in the "no regrets" prescription is the notion that future research will support the need for the recommended policy remedies. In effect, both schools believe that learning more about the impacts of climate change will inform better policy decision-making in the future.

Resolving scientific uncertainties will not necessarily result in better policy-making. Because of the impossibility of quickly resolving the uncertain estimates of climate change impacts, a mismatch exists between the information science can provide and the information policy-makers want. Policy-makers desire information about the attributes of ecosystems that society cares about which are at risk, what the consequences are of loss, and what the likelihood is that these losses will be experienced. In addition,

they want a means of measuring the benefits gained against the cost of the program. Finally, they seek confidence that any new policy implemented will succeed in reducing the risks associated with any particular adverse impacts.¹⁰ In short, the scientific uncertainties are only a small portion of the unknowns.

I conclude that the belief that policy-making can await the resolution of uncertainties in estimates of climate change impacts is unfounded. Instead, policy prescriptions are needed that acknowledge that decisions about policies to mitigate or avoid climate change (or to adapt to its impacts) must be made in the face of substantial uncertainties. A new policy prescription is needed that allows for improved data and analysis, but neither assumes it will be there, nor waits for its arrival. This approach might be called "take your best shot". The name acknowledges that although the predictions aren't highly reliable, decisions that affect the magnitude and rate of climate change will be made nonetheless. It encourages policy-makers to get the best current evaluation of needed actions, and not assume research will necessarily be able to supply all the answers. Implicitly it assumes that if the first shot misses, the best thing to do is try to figure out

¹⁰This adds a new dilemma -- all new policies can be considered socio-economic experiments, but we are gravely ignorant of how socio-economic systems work, or how new policies may affect them (see for example (Corcoran & Wallich, 1993).

what went wrong, and shoot again. Furthermore, it acknowledges that new information can sometimes increase uncertainty in the estimates of climate change impacts. "Take your best shot" is a policy prescription that returns the debate to the fundamental questions of societal goals for the world's future. The options each of us favor depend, in part, on our hopes and expectations of what the future holds. The technical information being generated by the researchers of climate change and its impacts suggests we have good cause to aim wisely.

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