Potential effects of climate change on stand development in the Pacific Northwest[1]

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Long-term climate and stand structure records and projections from a simulation model are used to explore effects of predicted changes in temperature on forest development in the Pacific Northwest. Few climate trends have occurred during the past 92 years, although there have been variations in September temperatures. The lack of climate trends makes it impossible to relate past changes in stand development to climate. Measures of stand development from six long-term forest plots over the past 7 decades are typical of Douglas-fir stands: stem density declines, leaf area stabilizes, aboveground biomass increases, and shifts in size distribution occur. These changes are consistent with patterns of natural succession. A computer model projected forest development under two climate scenarios: current temperature conditions and temperature warming (such as that predicted under a doubling of atmospheric CO_2). The model predicted changes in species composition, leaf area, and stem density in response to temperature increases. Total aboveground biomass is not sensitive to the simulated temperature alterations. Predicted biomass stability suggests that the Pacific Northwest forest would continue to store large amounts of carbon in the living trees even with climatic warming. Therefore, the predicted temperature change would not alter the role of the Pacific Northwest forests as a major storage location of terrestrial carbon. Changes in precipitation patterns or in disturbance frequency or intensity that might occur with climatic warming could alter these predictions.

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Des données à long terme sur le climat et la structure des peuplements ainsi que des projections établies à l'aide d'un modèle de simulation ont été utilisées pour étudier l'effet des changements anticipés de température sur le développement des forêts du nord-ouest du Pacifique. Peu de modifications climatiques sont survenues depuis 92 ans même s'il y a eu quelques variations dans les températures du mois de septembre. Il est impossible d'établir un lien entre les modifications passées dans le développement d'un peuplement et le climat en l'absence de changements climatiques. Des données récoltées dans six placettes échantillons permanentes au cours des 7 dernières décennies illustrent le développement typique des forêts de Sapin de Douglas : la densité des tiges diminue, la surface foliaire se stabilise, la biomasse aérienne augmente et la distribution des classes de dimension change. Ces changements sont consistants avec les patrons de succession naturelle. Un modèle programmé sur ordinateur a servi à prédire le développement de la forêt selon deux scénarios climatiques : les conditions actuelles de température et le réchauffement des températures tel qu'anticipé si le CO_2 atmosphérique double. La biomasse aérienne totale n'est pas affectée par les modifications simulées de température. Cette prédiction suggère que les forêts du nord-ouest du Pacifique continueraient d'accumuler de grandes quantités de carbone dans les arbres vivants même si le climat se réchauffait. Par conséquent, les changements climatiques prévus n'affecteraient pas le rôle des forêts du nord-ouest du Pacifique en tant que lieu d'accumulation importante du carbone terrestre. Des changements dans la distribution, la fréquence ou l'intensité des précipitations qui pourraient accompagner un réchauffement du climat pourraient modifier ces prévisions.

[Traduit par la revue]

Introduction

The potential for climate change in the near future mandates a need to understand the range of responses of forests to predicted climate conditions (Trabalka 1985). Increases in atmospheric CO_2 have been measured since 1958 (Bacastow and Keeling 1981; Gammon et al. 1985), with a possible consequence being increases in global average temperature by 1.5 to 4.2°C (MacCracken 1985; Luther 1985; Schlesinger and Mitchell 1987). As the climate changes, trees are exposed to new conditions that can affect their rate of regeneration, growth, or mortality. Changes in patterns of forest development, structure, or composi-

tion would have major ecological and economic consequences (Solomon and West 1985). Understanding how forests respond to changes in temperature is critical in predicting the global impacts of increased CO_2 (Houghton et al. 1983) because forests cover more than one-third of the globe (Olson 1975) and store more than 80% of the global terrestrial organic carbon (Olson et al. 1983). Changes in the carbon storage characteristics of forests could alter atmospheric concentrations of CO_2 and thus have a feedback effect on future climate conditions (Armentano and Ralston 1980).

Research to characterize response of forests to rapid climate change has relied on past shifts in climate and on computer simulations. Historic changes in climate have been

used as a natural experiment to study the response of forests to climate change (e.g., Jozsa and Powell 1987). Pollen analysis studies have shown that shifts in species composition and changes in the spatial distribution of some forest types occur as a result of climate change (e.g., Gajewski 1987). The difficulty of using past climate change to understand future responses is that the relevant data are difficult to obtain and past temperature conditions differ from projected temperatures.

Computer simulations allow researchers to specify climate scenarios and examine the simulated response of individual trees and forests over long time periods and at various locations. Simulations can incorporate the major factors affecting species compositions and turnover, although the details specific to sites are often not included. Using a forest succession model, Davis and Botkin (1985) showed that a shift in species of the eastern United States could occur as long as 100 to 200 years subsequent to a decrease in mean annual temperature. Solomon (1986) projected forest development in eastern North America following a doubling and quadrupling of atmospheric CO_2. The predicted response of forests to the CO_2-induced climate change occurred as long as 300 years after the climate shift and depended on the species composition of the forests. On a global scale, large changes in plant biome distributions are predicted to result from CO_2-induced climate changes (Emanuel et al. 1985).

Combining long-term climate and stand records with computer models can take advantage of both historic information and computer simulations. The long-term records allow researchers to assess the past and current relationships between climate and stand development. Computer simulations allow researchers to examine predicted consequences of specific climate scenarios.

Consideration of the global impacts of CO_2-induced climate change on forest systems can best be achieved by disaggregation of the forest biomes. Prediction of climate effects can be accomplished on a biome by biome basis for two reasons. First, each area is likely to experience unique climate changes. Second, the species composing each biome have distinct limitations concerning temperature and moisture conditions. Thus far, research has concentrated on forests of eastern North America (e.g., Solomon 1986; Davis and Botkin 1985; Pastor and Post 1988).

The Pacific Northwest was targeted for this study because of the high productivity of the forests (Franklin and Waring 1980) and the relatively small impact of air pollution on Northwest forests (thus eliminating potential confounding effects). The high biomass results from both high growth rates and the sustained growth and longevity of the trees of the Pacific Northwest. The dominant early successional species (Douglas-fir (*Pseudotsuga menzeisii* (Mirb.) Franco)) can live for as long as 1000 years. Thus, in the classical paradigm of succession (Whittaker 1953), the climax forest may not be attained for over a millennium.

There have been no studies of the response of the coniferous forest ecosystems of the Pacific Northwest to predicted climate change. Considering the physiological response of coniferous species to prevailing climate conditions, Leverenz and Lev (1987) suggest that the ranges of six major Northwest species can shift with climate change. However, the ecosystem response of the full complex of species depends on the feedbacks between species limitations, species interactions, and environmental conditions.
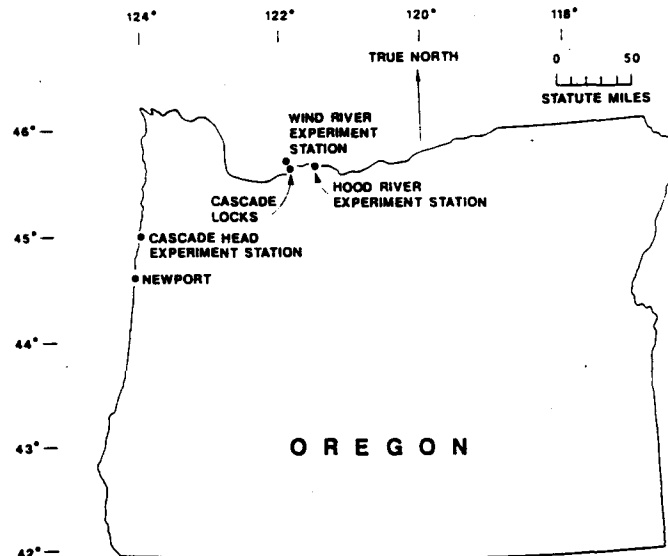

FIG. 1. Map of Oregon showing locations from which vegetation and climate data were obtained (1 mi = 1.6 km).

The objective of this study was to examine temporal patterns in carbon storage and release by Pacific Northwest forest ecosystems under changing temperature. We used (*i*) long-term records of climate and forest growth to evaluate changes in climate and stand development over the past century and (*ii*) a forest succession simulation model (Dale et al. 1986) to predict potential future trends in forest development for the complex forest ecosystem. Monthly measures of temperature and precipitation for the past 92 years were analyzed for trends in climate conditions. Records of changes in the diameter of all trees in six permanent plots over the past 7 decades were evaluated to depict patterns in stand development and structure (leaf area, stem density, and aboveground biomass). Long-term data were obtained from those Douglas-fir dominated stands for which the disturbance history, climate, and successional development are known. Simulations of forest development under different temperature scenarios were analyzed to suggest how Pacific Northwest forest ecosystems might respond to future changes in climate. Simulations are useful in studies of response of the Northwest forests to climate change because of the long life of trees and the possibility of delays in response of the forest. The delays might be expected to be longer in the Northwest conifer forests than the eastern deciduous forests because the trees can live up to twice as long. Together these approaches provide an understanding of the role that climate may have in past and future patterns of coniferous forest development.

Methods

Climate data

Long-term climate data from three stations in Oregon were used to document historical climate conditions of the Wind River and Cascade Head sites from which stand development data were obtained (Fig. 1). The climate of Wind River was represented by records of monthly mean temperature and precipitation from Cascade Locks Experimental Station (Bradley et al. 1985). Monthly data are available for temperature from 1891 to 1954 and for precipitation from 1879 to 1954. In addition, data concerning monthly mean precipitation and mean, minimum, and maximum temperature were obtained from the Historical Climatology

TABLE 1. Comparison of average climate data

	Cascade Head	Wind River
Elevation, m (ft)	49.1 (161)	396 (1299)
Temperature, °C (°F)		
Annual	10.3 (50.5)	8.7 (47.8)
January	5.3 (41.5)	0.0 (32.0)
January min	2.2 (36.0)	−3.7 (25.3)
July	15.3 (59.5)	17.5 (63.5)
July max	20.3 (69.6)	26.9 (80.5)
Precipitation, cm (in.)		
Annual	250 (98.3)	252 (99.5)
June–August	16 (6.4)	11 (4.6)
Annual snowfall		233 (91.7)

Network (Quinlan et al. 1986) for the Hood River Experiment Station and for the town of Newport. These data cover the period 1891 to 1984 for temperature and 1884 to 1984 for precipitation. The Hood River Station is southwest of Wind River and lower in elevation. Newport is almost directly south of Cascade Head and of a similar elevation.

The climate of the two study sites is broadly representative of the Pacific Northwest with cool summers and mild, wet winters (Table 1). The two sites differ, however, in the degree of maritime influence. Cascade Head is located 8 km from the Pacific Ocean in the coastal Sitka Spruce zone (Franklin and Dyrness 1973). Wind River is located in the Western Hemlock zone in the interior of the Cascade Range adjacent to the Columbia River. Consequently, conditions are considerably more moderate at Cascade Head than at Wind River, with less variability in annual temperature and higher summer and total precipitation. Substantial snowfall occurs at Wind River, whereas it is nearly absent at Cascade Head.

The choice of the climate data used in the study was determined by the desire to have the longest record possible that was most representative of the locations. The climate information collected at Cascade Head and Wind River were not used because they cover only a few decades. Although climate division data generally correlate better with tree growth than do station data (Blasing et al. 1981), the division data were not appropriate to use in this study because both Cascade Head and Wind River are near the geographic margins of their climate divisions and have unusual climate conditions compared with the entire division.

The climate data were analyzed to determine if there have been patterns in temperature or precipitation changes over time and to find the relations between seasonal climate conditions. Linear regressions of mean, minimum, and maximum temperature and of mean precipitation over time were calculated to ascertain if there has been a significant trend (as indicated by a significant Student's t-value). Correlations by season of average temperature and precipitation were performed to determine if relationships exist between seasonal climatic patterns. We were particularly concerned about correlations between temperature and precipitation, since we varied only temperature in the model runs discussed below. In the correlation analyses, winter includes the months of January, February, and March, when the highest rainfall occurs; spring includes April, May, and June; summer includes July, August, and September, which is warm and generally dry; and fall includes October, November, and December.

Long-term forest records

Long-term forest records were obtained from two locales: Cascade Head Experimental Forest along the Oregon coast and Wind River Experimental Forest in the southern Washington Cascade Range (Fig. 1). Long-term permanent sample plots exist in Douglas-fir dominated stands that regenerated following catastrophic wildfires about 1845; the stands have had little subsequent disturbance. Records of forest growth and mortality cover-

ing 48 to 74 years were obtained from three 0.4-ha plots at both locations.

The environment and productivity of the two locales differ. Productivity at Cascade Head is high (class II for Douglas-fir) as measured by the forest site index (height of dominant trees at 100 years) (McArdle 1982). The Wind River location has moderate to low productivity (forest site indexes III to IV +).

Soils at the two locations are derived from different parent materials. The Cascade Head soils are developed in tuffaceous silt, sand, and clay stones of sedimentary origin with occasional intrusions of underlying basalt; typical textures are silt loam and silty clay loam. Soils at Wind River are developed in tephra mixed with colluvium derived from andesitic bedrock; typical textures are sandy loam and loamy sand. Soils are moderately acid (pH 4.5 to 5.5) at both locations, but levels of organic matter and soil nutrients, especially nitrogen, are higher at Cascade Head than Wind River.

The three plots near the Cascade Head Experimental Station are dominated by 140-year-old Douglas-fir, which established following the 141, 640-ha Nestucca fire in 1845 (Morris 1934; Munger 1944). Plot 14 has a slight slope and much blowdown particularly in the north corner. Ground cover is dominated by swordfern (Polystichum munitum (Kaulf.) Presl) and oxalis (Oxalis oregana Nutt.). The Douglas-fir range in size from 49 to 115 cm diameter at breast height (dbh). Plot 41 has some large western hemlocks (Tsuga heterophylla (Raf.) Sarg.), but it is composed mostly of large Douglas-fir (50–85 cm). Ground cover is predominantly mosses. Some blowdown has occurred in recent years. The trees in plot 42 are mainly Douglas-fir (42–87 cm dbh) with a few western hemlocks. The ground cover is about 80% devils club (Oplopanax horridum (Smith) Miq.) and swordfern. There are a few standing dead Douglas-fir.

The three Wind River Experiment Station plots are dominated by Douglas-fir. Plots 4 and 90 have a 5% slope to the west and to the northwest, respectively. The ground cover of these two plots consists of vine maple (Acer circinatum Pursh), broadleaf maple (A. macrophyllum Pursh), dogwood (Cornus canadensis L.), Oregon grape (Berberis nervosa Pursh), and some ferns (about 20% ground cover). Plot 5 is on a very steep slope (from 100 to 115% east). Ground cover is about 80% Oregon grape and vine maple.

The Wind River plots have suffered damage from recurrent windstorms and ice storms and bark beetle (Dendroctonus pseudotsugae Hopkins) attacks (Williamson 1963). Between 1952 and 1956, an area adjacent to plot 5 was clear-cut, including five trees (approximately 0.021-ha) on the plot.

The USDA Forest Service has maintained long-term records on stand structure of the six plots. The Wind River measurement plots 4 and 5 were established in 1914 by J.V. Hoffman, and plot 90 was established in 1939 by W. Peterson. The Cascase Head plot 35 was established in 1935, and plots 41 and 42 were first measured in 1940. The plots were established by tagging trees larger than 5 cm dbh and by recording species and dbh. The dbh, height, and crown condition or mortality of each tree on the plots have been recorded at approximately 5-year intervals.

We calculated leaf area and aboveground stemwood and foliage biomass for each tree using published allometric equations (see Dale and Hemstrom 1984 using the equations in Gholz et al. 1979 and Binkley 1983). To calculate leaf area index for each plot, the leaf areas of all trees on the plot are added, and the sum is divided by the area of the plot. Total aboveground biomass per hectare is obtained by summing the calculated stemwood and foliage biomass of all trees on a plot and dividing by the area of the plot.

Model of forest development

The CLIMACS model of forest development (Dale and Hemstrom 1984; Dale et al. 1986) projects the effect that temperature variation can have on patterns of forest development and structure. CLIMACS simulates tree growth and stand development for sites in the Pacific Northwest. The regeneration, growth, and death of each tree on a 0.2-ha plot is simulated as affected by prevailing light,
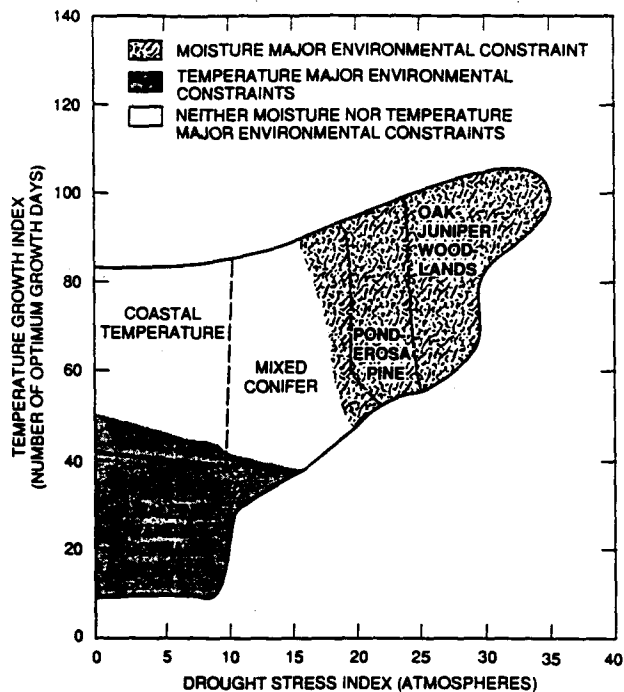
FIG. 2. Distribution of the major forest zones within an environmental field based on plant moisture stress (PMS) and temperature growth index (TGI) (from Franklin and Dyrness 1973).

temperature, moisture, and nutrient conditions. New trees appear in the model plot at a size between 10 and 15 cm dbh. Thus, the model year is not equal to the age of the previously cleared plot. The CLIMACS code is derived from JABOWA (Botkin et al. 1972) and FORET (Shugart and West 1977; Shugart 1984).

CLIMACS has characteristics that differ from those of other stand development models: tree height growth is related to temperature and moisture conditions, the foliage biomass to diameter relationship is based on species-specific regression equations (Gholz et al. 1979), and five mortality classes and five shade tolerance classes are defined. Parameter values in CLIMACS for the 21 Pacific Northwest tree species are based on 36 published studies (see Dale and Hemstrom 1984). The model has not been calibrated for the sites to which it is applied in this study. The model was validated by including windthrows, fires, insect outbreaks, and clear-cuts in the model and by examining projections compared with known conditions on the Olympic Peninsula (Dale et al. 1986) and in western Oregon (Hemstrom and Adams 1982).

The model uses well-established physiological indices as site-specific driving variables to relate temperature and soil moisture conditions to tree growth: temperature growth index (TGI) (Cleary and Waring 1969) and plant moisture stress (PMS) (Waring and Cleary 1967) (Fig. 2). Previous studies indicate that the prime limitations of carbon accumulation for Douglas-fir, the dominant species in the forests of the Pacific Northwest, result from frost, low soil temperature, or moisture stress (Emmingham and Waring 1977). The distribution of Douglas-fir is more dependent upon temperature than soil moisture for wetter sites in the Pacific Northwest (0 < PMS < 10).

TGI is the number of optimum growing days during a season and is based on a temperature summation formula that weighs temperatures by their effect on productivity of seedlings of Douglas-fir (Cleary and Waring 1969). The first growing day occurs when the snow melts (i.e., when water is available to the roots) or when the average night temperature stays above 5°C for more than a week. The TGI accumulation ends with the first hard freeze in the fall, which occurs toward the end of September for sites in the Pacific Northwest. With a doubling of CO_2, Oregon is projected to have a mean annual temperature increase of 3 to 4°C (Gibbs

and Hoffman 1987). This temperature increase will add about 10 more growing days to the season or increase TGI from 80 to 90 days.

PMS is the predawn negative xylem pressure measured near the end of the growing season (Waring and Cleary 1967). PMS is an excellent indicator of the severity of the seasonal drought conditions on the site because (i) predawn xylem water potential reflects the soil water deprivation experienced by the tree and (ii) soils are drier at the end of the summer in the Pacific Northwest owing to seasonal rainfall patterns.

The CLIMACS model was used to assess the sensitivity of projected forest development to changes in temperature. The model was initiated at stand age 140 by using the conditions of the Cascade Head plots. The model was run with current climate conditions of the Cascade Head Experiment Station and conditions under predicted climate warming (TGI = 90 days). The driving variables were obtained from Emmingham and Waring (1977), who reported a minimum PMS for Cascade Head of 5 to 6 atm (1 atm = 101 kPa) and a TGI of 80 days.

Results

Trends in climate over recent decades

The first step of this research was evaluating the potential influence of recent climate trends on forest growth and development. There are three parts to this analysis: determining trends in climate, examining recent trends in forest development, and evaluating how climate trends relate to patterns of forest development.

The analyses of long-term climate data show that western Oregon has experienced few climate trends except for temperature during the month of September (Table 2). However, there is no consistent trend. For example, at the Hood River station, the monthly mean temperature does not have a slope significantly different from zero, but the slope of the minimum temperature is negative and the slope of the maximum temperature is positive. September is the time of most significant moisture stress for the trees in the Pacific Northwest, since maximum soil moisture depletion occurs at the end of the summer period of low rainfall. Thus, higher September temperatures could intensify the effects of drought stress. There are few changes in recent decades in precipitation, but Hood River has had an increase in August precipitation, and Newport has experienced an increase in rainfall in December. The lack of apparent climate trends made it impossible to relate climate to patterns of forest development.

For the purposes of the simulation, it was important to verify that temperature and precipitation are acting independently (because we separate them in the model scenarios). There are few correlations between seasonal temperatures and precipitation (Table 3), indicating that for western Oregon, these climatic variables are independent. Correlations are significant between the summer mean temperature and temperature averages for most seasons and sites considered. Warmer summer temperatures occur in years that have warmer temperatures during the other seasons.

Trends in forest development observed over recent decades

Trends in stem density, leaf area, and biomass are similar for plots at Cascade Head and Wind River, although there are differences between the two sites (Fig. 3). In general, there are more trees, greater leaf area, and greater biomass at Cascade Head than at Wind River. This difference probably reflects the site differences and milder climate at the

TABLE 2. The values of the Student's t-statistic for testing the hypothesis that the slope equals zero (indicating if there was a trend in the climate variables over time)

| | Hood River | | | | Newport | | | | Cascade Locks | |
| | Mean precipitation | Temperature | | | Mean precipitation | Temperature | | | Mean precipitation | Mean temperature |
		Mean	Min	Max		Mean	Min	Max		
Jan.	0.65	0.28	0.13	0.83	0.99	0.48	0.47	0.40	0.15	0.70
Feb.	1.19	0.28	0.13	0.84	0.23	0.48	0.47	0.40	0.31	0.53
Mar.	0.78	1.20	1.03	1.04	0.94	0.47	0.39	0.43	0.72	0.69
Apr.	1.15	1.21	0.76	1.05	0.31	1.55	1.32	1.39	1.58	0.84
May	1.22	0.03	0.05	0.52	1.49	0.93	0.81	0.70	0.21	0.13
June	0.72	0.94	0.78	0.57	0.67	0.14	0.17	0.44	0.09	1.34
Jul.	0.11	0.99	0.82	0.64	0.91	0.44	0.47	0.27	0.84	0.68
Aug.	2.76a	0.27	0.30	0.12	1.42	1.69	0.83	1.60	0.36	0.26
Sept.	1.46	1.25	2.31b	2.79c	0.42	2.29d	0.84	2.45e	1.20	2.59f
Oct.	0.24	1.28	3.48g	0.80	1.42	0.88	1.90	0.44	0.01	1.04
Nov.	0.42	0.45	1.31	0.48	0.34	1.16	1.73	0.27	0.31	0.50
Dec.	1.06	0.81	0.11	1.78	2.34h	1.51	1.40	1.31	0.20	0.49

NOTE: Linear regressions of climate variables (x) were calculated using the model $x = a + b\,(year)$. All values of t followed by a letter are significant at $p < 0.05$. The value of the slope (b) for each significant relationship was $a = 0.01$, $b = -0.002$, $c = 0.001$, $d = 0.0009$, $e = 0.002$, $f = -0.4$, $g = -0.001$, and $h = 0.1$.

TABLE 3. Correlations between seasonal temperature and precipitation

| | Site | Temperature | | | | Precipitation | | | |
		Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Temperature									
Winter	Hood River	1.0	0.73***	0.50***	0.43***	0.01	0.19*	0.14	0.02
	Newport	1.0	0.85***	0.41***	−0.03	0.02	0.03	0.02	0.06
	Cascade Locks	1.0	0.45***	0.09	0.03	−0.19	0.08	0.23*	−0.02
Spring	Hood River		1.0	0.85***	0.56***	−0.01	−0.04	0.10	−0.06
	Newport		1.0	0.80***	0.35***	0.02	0.04	0.03	0.01
	Cascade Locks		1.0	0.33***	0.02	−0.20	−0.15	0.08	−0.13
Summer	Hood River			1.0	0.58**	−0.01	−0.09	0.16*	−0.02
	Newport			1.0	0.69***	0.02	0.04	0.03	0.01
	Cascade Locks			1.0	0.22*	−0.02	−0.01	0.02	−0.06
Fall	Hood River				1.0	0.03	−0.02	0.18*	−0.02
	Newport				1.0	0.03	0.05	0.03	0.02
	Cascade Locks				1.0	−0.29*	−0.07	0.01	−0.17
Precipitation									
Winter	Hood River					1.0	0.01	0.17*	0.06
	Newport					1.0	0.87***	0.50***	0.11
	Cascade Locks					1.0	0.06	0.01	−0.01
Spring	Hood River						1.0	0.16	0.14
	Newport						1.0	0.78***	0.43***
	Cascade Locks						1.0	0.11	0.23*
Summer	Hood River							1.0	−0.09
	Newport							1.0	0.71***
	Cascade Locks							1.0	0.19**

*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

lower elevation site (Table 1) since the sites are similar in their species composition, stand age, and history. The differences are what one would expect between high and low productivity sites (McArdle 1982).

The number of stems has the typical decline as the stand age increases (Fig. 3) (McArdle 1982; Long and Turner 1975; Harcombe 1986). As the stands mature, stem density declines from a high of 150 to 200 stems/ha to a low of about 80 to 130 stems/ha. The stands have entered the stem exclusion stage (Oliver 1981) when recruitment is infrequent yet some mortality occurs. There is overlap between the stem density data for the two sites even though the monitoring of the Cascade Head plots began later than at Wind River. This overlap suggests that for plots 41 and 42, the earlier stem density may be similar to that of the Wind River plots.

The differences between plots in the number of stems contribute to the differences in calculated leaf area and biomass, although the pattern of decline in stem density does not explain the observed patterns in leaf area and biomass. The trends in leaf area and biomass are partially attributable to the fact that these stands are still maturing (Kira and Shidei 1967). As the stem density declines, a few trees are able to
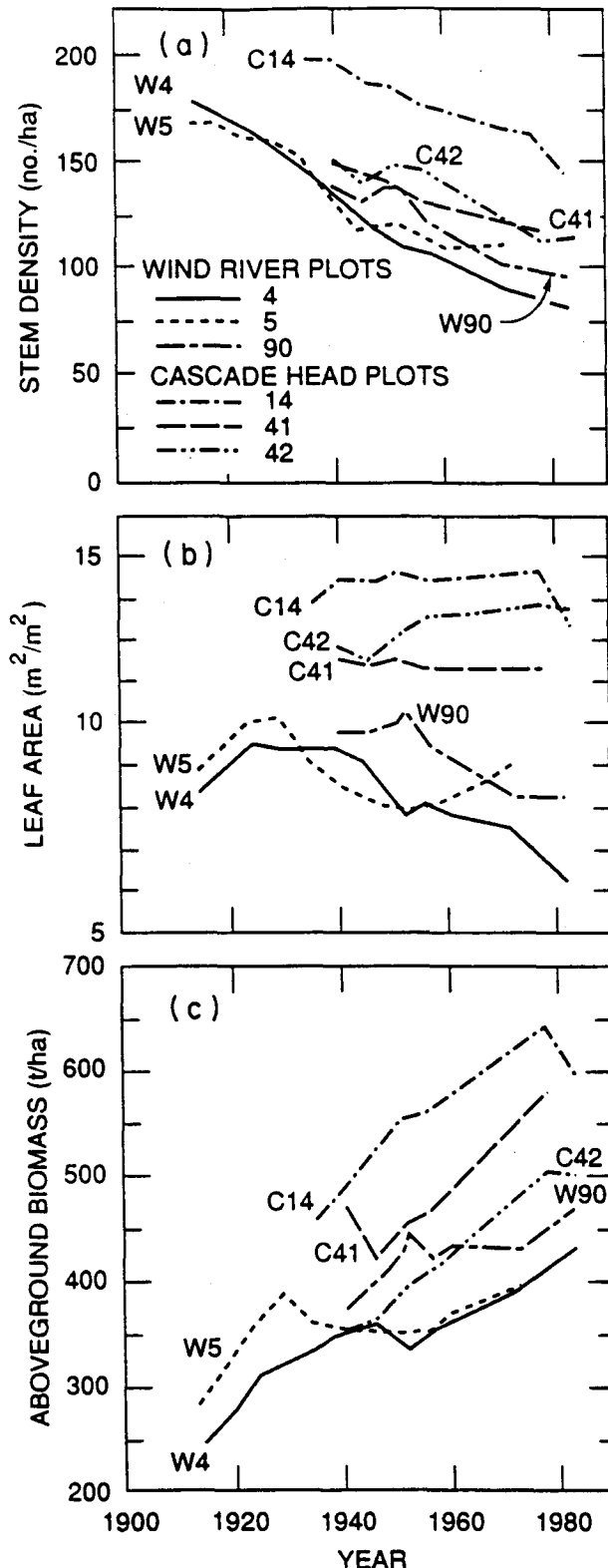
FIG. 3. Values for (*a*) stem density, (*b*) leaf area, and (*c*) aboveground biomass over time for trees on plots at the Cascade Head and Wind River Experimental Stations.

survive and grow very large. As these trees grow, they contribute a greater amount of leaf area to the stand. Thus, the decline in density and the increase in the leaf area per tree combine to cause a stabilization of the leaf area in the plot. The stand biomass continues to increase as the individual trees grow. By 1945, the stands were about 100 years old, and the trees are still in the exponential phase of biomass

increase. At some point, there should be a leveling of the biomass curve (Kira and Shidei 1967).

The size structure pattern partially explains the changes in stand structural characteristics over time. A major shift in the density–diameter distribution has occurred over 60 years of stand development (e.g., see Fig. 4). This shift occurred primarily between stand ages 70 and 90. Many of the intermediate-sized trees died, and the larger trees grew even larger with the reduced competition.

The shift in size distribution for the Wind River plots corresponds to a bark beetle outbreak in the stands (Williamson 1963). Bark beetles have been active in the Wind River plots since 1924 and have tended to attack and kill intermediate-sized trees (Fig. 4). Because beetles generally kill the intermediate-sized and stressed trees (Graham and Knight 1965; Waring and Pitman 1983), they probably do not change the future size distribution pattern of the stand. This suggestion is supported by the observation that, even without bark beetles, the stands at Cascade Head eventually had a size distribution typical of that observed in the later years in plot 5 with many large trees and a few small trees. Therefore, the presence of beetles does not necessarily change the expected forest structure, although it could change the successional dynamics by removing stressed trees before they would have died naturally. The timing of tree death is an important consideration for assessing the impacts of CO_2-induced climate change because of the possibility that temperature changes may affect the probability of beetle outbreaks. Temperature does affect the emergence time and seasonal activity times of the beetles as well as limits their geographic distribution both locally and regionally (Graham and Knight 1965). Also, beetle outbreaks are generally associated with periods of drought. Thus, climate shifts could alter the pattern of outbreak of pest insects such as bark beetles.

Projected forest development

The model simulations using the current temperature conditions of western Oregon project a coniferous forest typical of the Pacific Northwest dominated by Douglas-fir that succeeds to a forest dominated by western hemlock (Fig. 5). Small western hemlock, silver fir (*Abies amabilis* Dougl. ex Forbes), and western red cedar (*Thuja plicata* Donn) are present on the stand throughout the 500-year projection. Neither the western red cedar nor the silver fir attains over 15 cm dbh. At about stand age 340, the hemlocks become large enough to dominate the forest.

The model simulations with predicted temperature warming also project a forest dominated by Douglas-fir that succeeds to dominance by western hemlock (Fig. 6). In contrast to the projection under current temperatures, grand fir (*Abies grandis* (Dougl.) Forbes) becomes a codominant species and is lost from the stand at about stand age 620. Thus, a major effect of the temperature changes is a shift in importance of codominant species. Grand fir is typical of areas in Oregon with a mild climate (Franklin and Dyrness 1973) and is better adapted to warmer temperatures than is silver fir (Minore 1979). Thus, the species shift from silver fir to grand fir is a reasonable projection.

The simulated temperature changes affected stem density and leaf area, but not total aboveground biomass (Fig. 7). The projected biomass under current climate conditions corresponds to measured stand biomass, which remains stable
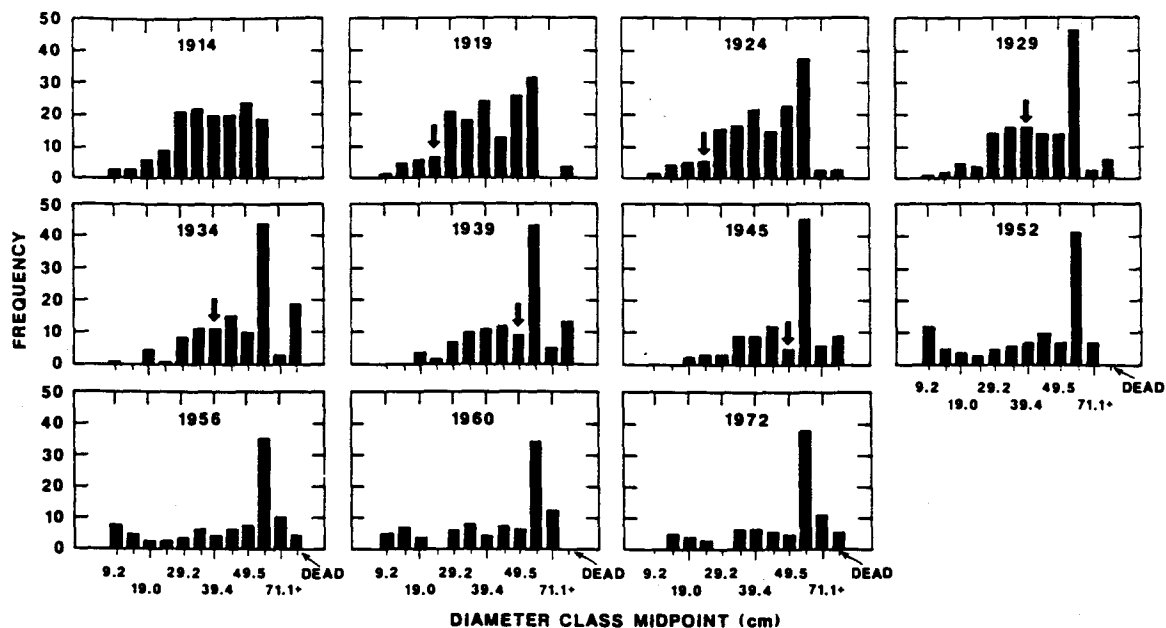
FIG. 4. Density–diameter distributions for 11 periods from 1914 to 1972 for plot 5 at the Wind River Experimental Station. The arrows indicate the diameter class that sustained the heaviest mortality due to bark beetles. Five trees were logged between 1952 and 1956.
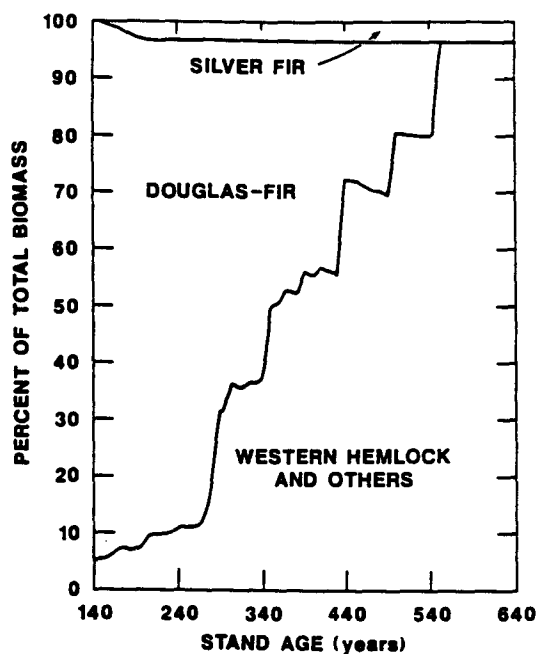

FIG. 5. Model projections of percent of total biomass over 500 years under current climate conditions. The model was initiated at year 140, using stand structure of the Cascade Head plots.
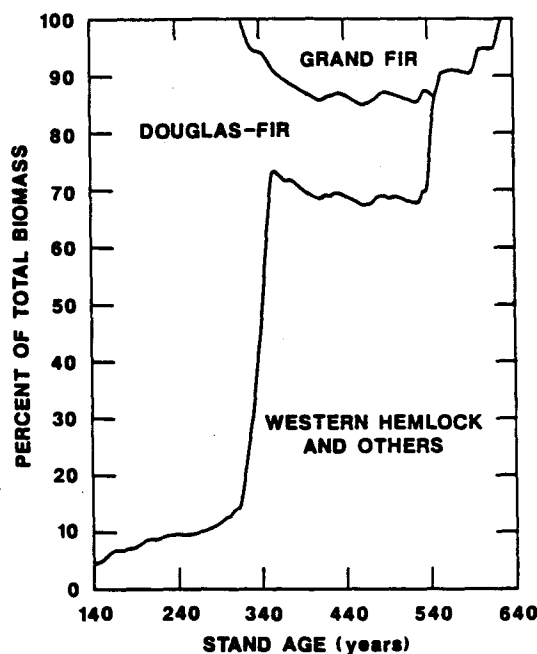

FIG. 6. Model projections of percent of total biomass over 500 years with climatic warming. The model was initiated at year 140 using stand structure of the Cascade Head plots.

for old-growth forests in the Cascade Range. With a temperature warming, there is a projected decrease in the total number of stems and greater variability in leaf area as compared with the projection under the current temperature conditions. The differences in stem density and leaf area can be explained by the shifts in species composition. When grand fir is a codominant, only a few individuals of that species occur on each plot. In contrast, many small silver fir are simulated to occur under current temperature conditions. The number and size distributon of the Douglas-fir and western hemlock are similar for the two scenarios. The fluctuations in leaf area with temperature warming are related to the abrupt transitions in species biomass (Fig. 6).

The biomass of Douglas-fir is replaced by that of a few large grand fir and western hemlock, and leaf area rises as those trees become larger and declines as the trees achieve dominance. When the large grand fir begin to die, leaf area again increases as more trees enter the subcanopy.

Discussion

The predicted climate shifts induced by increases in atmospheric CO_2 concentrations (Schlesinger and Mitchell 1987) far exceed temperature conditions that have been experienced in recent decades in western Oregon. There have been no apparent climate trends in western Oregon during the past
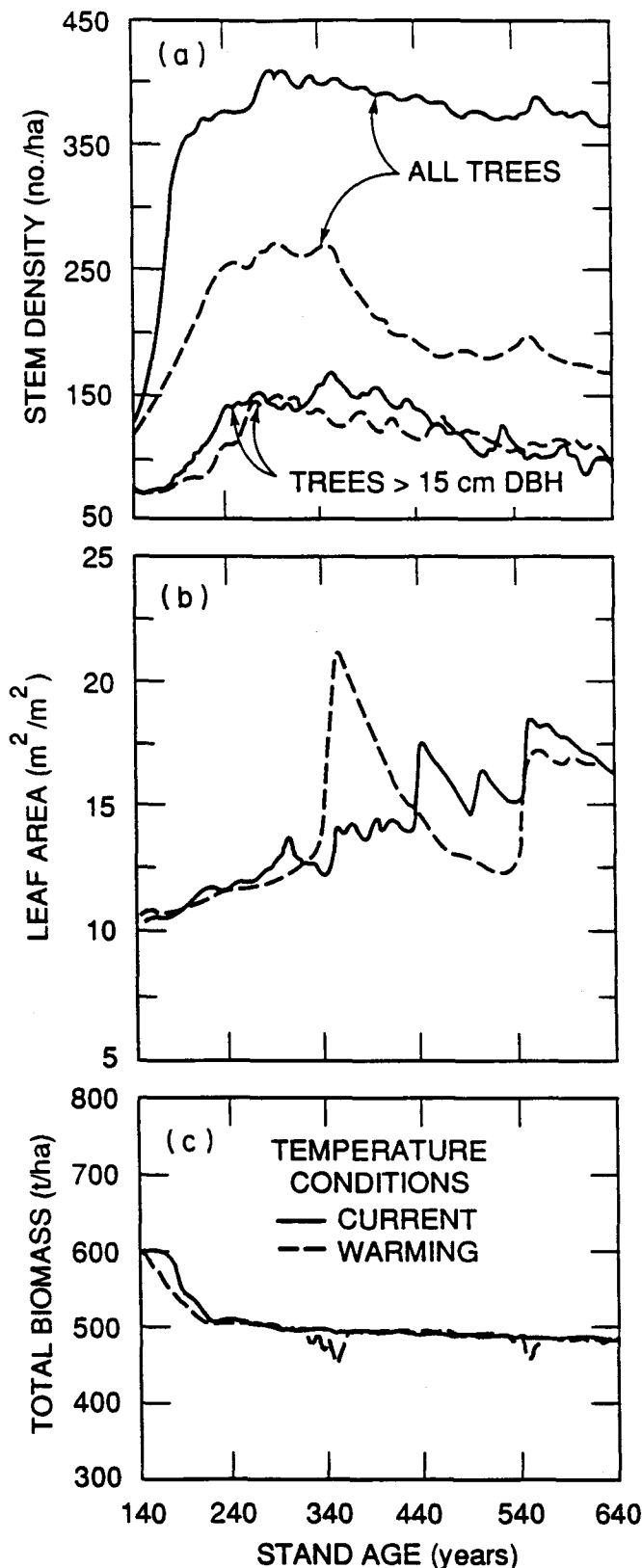
FIG. 7. Model projections of (a) stem density, (b) leaf area, and (c) total aboveground biomass over 500 years of stand development under two temperature scenarios for northwest Oregon.

century. The observed Douglas-fir forest development over the past 100 years is typical of successional changes, with many trees becoming established in early years, followed by a stem exclusion stage during which biomass increases (Long and Turner 1975; Oliver 1981).

Differences in timing of shifts in density–diameter distributions can be explained by insect disturbances. Bark beetles have killed trees in some of the plots, but the resulting tree size distribution in those stands is similar to stands in which beetles have not killed trees. Changes in the intensity and frequency of such disturbances can be induced by climate changes and can have greater effects on stand structure and composition than are discussed here (Cwynar 1987; Turner et al. 1989).

The forest simulations indicate that predicted temperature changes will alter codominant species composition, stem density, and leaf area, but will not affect total carbon storage (assuming a linear relationship between biomass and carbon stored). The insensitivity of woody biomass production to temperature changes is an important aspect of the feedback between atmospheric CO_2 and climate changes, since as much as 70% of the organic carbon in warm-temperature evergreen forests is in woody tissue (Kira and Shidei 1967). The simulations suggest that increasing temperatures will have little direct effect on the total aboveground biomass in Pacific Northwest forests and thus are not likely to have a feedback effect upon atmospheric CO_2 levels.

These simulation results are in contrast to simulations of eastern deciduous forests, which predicted changes in total aboveground biomass as a result of climate change (Solomon 1986; Pastor and Post 1988). The differences may be due to the species diversity of the two areas. The Pacific Northwest is dominated by Douglas-fir in excess of 600 years of stand development (Franklin and DeBell 1988), and the predicted temperature changes were within the range that Douglas-fir was still able to maintain its dominance (Franklin and Dyrness 1973). In contrast, the eastern deciduous forests are composed of about 24 species. Initial warming produced a dieback of many of the dominant eastern deciduous species, particularly those with a narrow ecological amplitude (Solomon 1986). Species shifts that occur in the aftermath of temperature change induce changes in stand size structure and biomass.

There are differences in the treatment of nutrient cycling in CLIMACS and the version of the FORET model used by Pastor and Post (1988) that can affect stand structure projections. Both CLIMACS and the FORENA model used by Solomon (1986) have a single multiplier that accounts for nutrient limitations on tree growth rather a nutrient feedback cycle (Pastor and Post 1986). This simplistic treatment of nutrients and the lack of consideration of dead wood were the two major limitations of the CLIMACS model identified by Dale et al. (1986). Therefore, we ran the model with a much higher value for the nutrient multiplier as a test to evaluate if nutrient conditions were controlling the total predicted biomass. No differences were found between the values reported in Figs. 5, 6, or 7 and the simulations with a higher nutrient multiplier. Therefore, we surmise that nutrient conditions in the model formulations do not account for the differences in the projected biomass changes for the eastern deciduous and the coniferous Northwest forests.

The differences between the projected stand structure under climate warming for the coniferous and deciduous forest of North America emphasize the need to explore many scenarios of climate change. These scenarios should include a variety of biomes and physical conditions. The simulations reported in this paper do not predict forest responses

to changes in precipitation patterns or disturbance regimes that may occur with climate change (Franklin et al. 1989). However, increased fire frequency would favor the presence of grand fir (Franklin and Dyrness 1973) and reduce the projected long-term basal area of stands (Dale et al. 1984).

These simulations show that the sensitivity of stem density and leaf area to temperature increase can be explained by changes in species composition. This sensitivity suggests that temperature limits on species should be studied carefully, focusing on conditions under which a species cannot survive or when its competitive role is altered. For species that have their geographic distribution limited by moisture, similar attention must be given to soil type and moisture conditions.

Acknowledgements

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