

# Response of high-elevation forests in the Olympic Mountains to climatic change

A. Nana Zolbrod and David L. Peterson

**Abstract:** The gap model ZELIG was used to examine the effects of increased temperature (2°C) and altered precipitation on high-elevation ecosystems of the Olympic Mountains, Washington, U.S.A. Changes in tree species distribution and abundance, as well as stand biomass, were examined on north and south aspects in the dry northeast (NE) and wet southwest (SW) regions of the Olympics for (i) warmer, (ii) warmer and 20% wetter, and (iii) warmer and 20% drier climatic-change scenarios. Dominant tree species shift upwards 300–600 m in elevation in the SW, with subalpine meadows and *Tsuga mertensiana* (Bong.) Carr. forests being replaced by *Abies amabilis* (Dougl.) Forbes forests at higher elevations and *A. amabilis* forests being replaced by *Tsuga heterophylla* (Raf.) Sarg. forests at lower elevations. In the NE, drought-tolerant species become dominant approximately 200 m lower than present, with *A. lasiocarpa* dominating the north aspect and *Pinus contorta* Dougl. ex Loud. the south aspect. Biomass increases in the SW and generally decreases in the NE, depending on aspect and precipitation regime. This study suggests that species and site-specific responses at mesoscale (e.g., wet vs. dry climatic regime) and microscale (e.g., north vs. south aspect) resolutions must be characterized to quantify the variation in potential effects of climatic change on forest vegetation in mountainous regions.

**Résumé :** Le modèle d'ouverture ZELIG a été utilisé pour examiner les effets d'une température plus élevée (2°C) et d'une modification des précipitations sur les écosystèmes de haute altitude, dans les monts Olympic de l'État de Washington, aux États-Unis. On a examiné les changements dans la répartition et l'abondance des espèces arborescentes, ainsi que la biomasse du peuplement, sur les expositions nord et sud, dans les régions nord-est (N.-E.) sèches et sud-ouest (S.-O.) humides des monts Olympic, pour trois scénarios de changements climatiques : (i) plus chaud, (ii) plus chaud et 20% plus humide et (iii) plus chaud et 20% plus sec. Dans le S.-O., les espèces d'arbres dominants migraient vers le haut de 300 à 600 m d'altitude, alors que les prairies subalpines et les forêts de *Tsuga mertensiana* (Bong.) Carr. étaient remplacées, aux altitudes supérieures, par les forêts d'*Abies amabilis* (Dougl.) Forbes; les forêts d'*A. amabilis* étant remplacées, aux altitudes plus basses, par les forêts de *Tsuga heterophylla* (Raf.) Sarg. Dans le N.-E., les espèces tolérantes à la sécheresse devenaient dominantes à environ 200 m plus bas que leur site actuel, avec l'*A. lasiocarpa* dominant sur l'exposition nord et le *Pinus contorta* Dougl. ex Loud. sur l'exposition sud. La biomasse s'est accrue dans le S.-O. et a généralement diminué dans le N.-E. selon l'exposition et le régime des précipitations. Cette étude suggère que les espèces et les réactions spécifiques à un site à moyenne échelle (p. ex., régime climatique sec versus régime climatique humide) et à petite échelle (p. ex., exposition nord versus exposition sud) doivent être caractérisées afin de pouvoir quantifier la variation des effets potentiels du changement climatique sur la végétation forestière dans les régions montagneuses.

[Traduit par la Rédaction]

## Introduction

Increased levels of greenhouse gases in the earth's atmosphere in the past century have led to much speculation about the potential effects on climatic regimes and vegetation patterns. With a doubling of CO<sub>2</sub> levels, general circulation models predict that global mean temperature may rise 1.0–3.5°C within the next 100 years (Schlesinger and Mitchell 1987; Schneider 1989; Houghton et al. 1990; Mitchell et

al. 1995; Watson et al. 1996). Altered climatic regimes will undoubtedly lead to changes in distribution of individual species and plant species assemblages (Mitchell et al. 1990). These changes should be detectable in the subalpine zone of mountain ecosystems (Hansen-Bristow et al. 1988; Stevens and Fox 1991), where species are at their limit of competitive ability or their tolerance to environmental conditions (low temperature, snowpack duration, low soil moisture, and wind at some sites) (Wardle 1974; Tranquillini 1979; Hadley and Smith 1986; Cui and Smith 1991; Innes 1991; Slatyer and Noble 1992; Villalba et al. 1994; Weisberg and Baker 1995a, 1995b; Hessl et al. 1996; Peterson 1998) and where small changes in physical environmental conditions may shift competitive interactions between species (Körner 1989, 1994; Körner et al. 1991; Rochefort et al. 1994; Harte and Shaw 1995; Harte et al. 1995).

Subalpine tree growth and establishment in the Pacific Northwest region of North America (primarily British Columbia (Canada), Washington and Oregon (U.S.A.)) are

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affected by total and seasonal distribution of precipitation. Spatiotemporal patterns of growth and establishment are generally limited by accumulation of winter snowpack and timing of snowmelt (Brink 1959; Franklin et al. 1971; Canaday and Fonda 1974; Peterson and Peterson 1994; Woodward et al. 1995; Ettl and Peterson 1995a, 1995b; Rochefort and Peterson 1996; Peterson 1998), and by low temperature and low soil moisture (at some locations) during the growing season (Little et al. 1994; Ettl and Peterson 1995a, 1995b; Woodward et al. 1995). Indeed, widespread tree establishment has been occurring in snow-dominated subalpine meadows of the Pacific Northwest during the past century (Brink 1959; Fonda and Bliss 1969; Franklin et al. 1971; Heikkinen 1984; Magee and Antos 1992; Rochefort et al. 1994; Woodward et al. 1995; Rochefort and Peterson 1996; Miller and Halpern 1998; Peterson 1998). This establishment may be related partly to warmer air temperatures since the 1890s following the end of the Little Ice Age (Heikkinen 1984). However, on a subregional scale, periods of tree establishment are associated with specific long-term precipitation trends and the amelioration of limiting factors. High-snowfall sites have high regeneration during periods of lower than average winter precipitation (ca. 1900–1950), and low-snowfall sites have high regeneration during periods of higher than average winter precipitation (ca. 1950–1990) (Agee and Smith 1984; Woodward et al. 1995).

Modeling can be used to simulate vegetation responses to climatic change at a number of different spatial scales, from the individual tree to the biome (reviewed in Ågren et al. 1991; Dale and Rauscher 1994; Neilson 1992, 1995). Gap-replacement models, which examine the competitive dynamics of tree species, have been used to predict vegetation response to climatic change in various forest types (Davis and Botkin 1985; Solomon 1986; Pastor and Post 1988; Dale and Franklin 1989; Urban and Shugart 1989; Overpeck et al. 1990; Botkin and Nisbet 1992; Urban et al. 1993). Most gap models are derived from JABOWA (Botkin et al. 1972) and FORET (Shugart and West 1977) and simulate individual tree establishment, growth, and mortality within canopy gaps in a model plot. Species-specific deterministic responses to environmental parameters, primarily the annual sum of growing degree-days, soil moisture levels, and light availability (Urban 1993) and stochastic subroutines for seedling establishment, dispersal, maximum growth rates, and mortality are important components of gap models. A number of small-scale gap-replacement model plots can be combined within a grid to simulate stand-level dynamics in response to climatic change, as in ZELIG (Urban 1993), allowing for the effects of interplot shading and for spatial variation. Gap models can also be adapted to respond to continuous variations in climatic regimes (Urban et al. 1993).

The Olympic Mountains of northwestern Washington are characterized by a diversity of climates and subalpine forest vegetation within a relatively small area. Limited empirical data suggest that these vegetation types may be particularly susceptible to a rapidly changing climate (Brubaker 1988; Peterson 1991, 1998). In the Pacific Northwest, gap models have been used to predict forest response to climatic change

primarily at low elevations (Dale and Franklin 1989; Keane et al. 1990; Franklin et al. 1992; Urban et al. 1993), but no studies have focused on high-elevation forests nor has there been any modeling of potential climate-induced changes in forest composition and tree species distribution in the Olympic Mountains.

In this study, we explore the potential effects of increased temperature and altered precipitation on tree species distribution and forest stand composition in the subalpine and upper montane zones of the Olympic Mountains, using the gap-replacement model ZELIG (Urban 1993). Empirical data on current vegetation distribution and forest composition were integrated with results from recent studies (Soll 1994; Ettl and Peterson 1995a, 1995b; Woodward et al. 1995; Woodward 1998; Prichard et al., unpublished data<sup>3</sup>) and autecological information (Minore 1979; Henderson et al. 1989) to calibrate the model and predict future vegetation changes. We emphasize potential changes on north and south aspects in two regions of the Olympic Mountains with distinct precipitation regimes, the low-precipitation northeast and the high-precipitation southwest.

## Methods

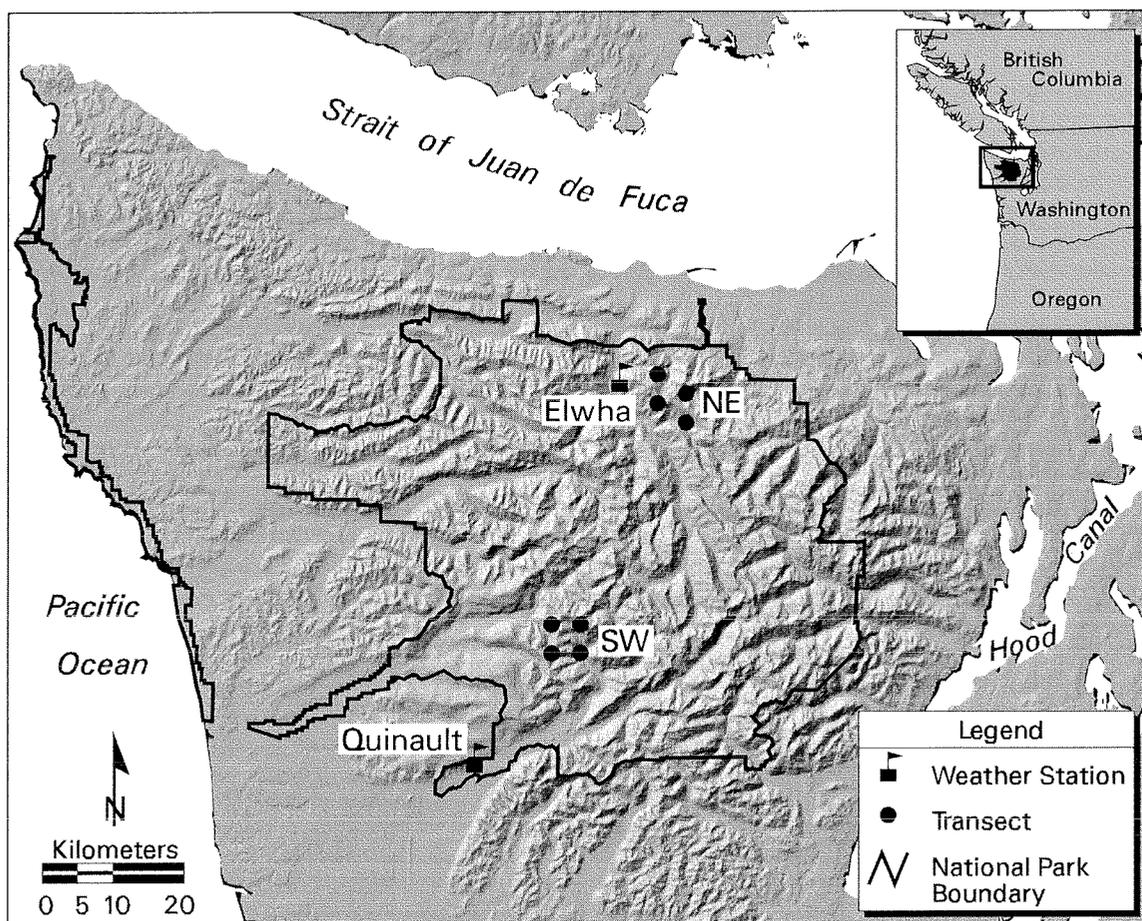
### Study area

The Olympic Mountains are located on the Olympic Peninsula in the northwestern corner of Washington state (Fig. 1). The region is characterized by steep mountains extending from sea level to 2400 m, with most ridgetop elevations ranging from 1200 to 1600 m. The climate consists of cool, wet winters and mild, dry summers with prevailing winter winds from the southwest carrying moisture off the Pacific Ocean. The mountains create a sharp precipitation gradient between the wet, southwestern (SW) region (~500 cm/year at ridgetops) of the Peninsula and the dry, northeastern (NE) region (~100 cm/year at ridgetops) (Phillips and Donaldson 1972 (estimates based on the use of physiographic relationships to extrapolate data from long-term, low-elevation weather stations; Henderson et al. 1989; Buckingham et al. 1995). Over 60% of annual precipitation is deposited as snow (Belsky and del Moral 1982), which influences the timing of snowmelt and the length of the growing season (Fonda and Bliss 1969; Kuramoto and Bliss 1970; Canaday and Fonda 1974). At the Quinault Ranger Station (Olympic National Park, 50 m elevation), the weather station closest to the SW transects in this study, January mean temperature is 3.3°C, and total precipitation is 52.3 cm; August mean temperature is 17.2°C, and total precipitation is 7.6 cm. At the Elwha Ranger Station, (100 m elevation), the weather station closest to the NE transects in this study, January mean temperature is 2.2°C and total precipitation is 22.4 cm; August mean temperature is 16.9°C, and total precipitation is 2.7 cm (U.S. National Climatic Data Center, Asheville, N.C.).

In the wetter SW region, subalpine meadows are heath–shrub communities dominated by *Phyllodoce empetriformis* (Sw.) D. Don (pink mountain-heather) and *Vaccinium* L. (huckleberry) species (Kuramoto and Bliss 1970), subalpine forests are dominated by *Tsuga mertensiana* (Bong.) Carr. (mountain hemlock) and the mid-slope montane forests are dominated by *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) (Franklin and Dyrness 1988; Henderson et al. 1989, Buckingham et al. 1995). In the drier NE region, meadows are more variable and include heath–shrub communities on wetter north aspects, grass–forb communities dominated by *Festuca idahoensis* Elmer (Idaho fescue) on drier south aspects and

<sup>3</sup>Prichard, S.J., Peterson, D.L., and Hammer, R.D. Soil carbon distribution in subalpine ecosystems of the Olympic Mountains.

**Fig. 1.** Map of study transects in the northeastern (NE) and southwestern (SW) Olympic Mountains on the Olympic Peninsula, Washington. Locations of Olympic National Park, weather stations (ranger stations), and study transects are shown.



cushion plant communities dominated by *Phlox diffusa* Benth. (spreading phlox) and *Lupinus lepidus* Dougl. (prairie lupine) at the highest elevations (Kuramoto and Bliss 1970; Belsky and del Moral 1982; Buckingham et al. 1995). Subalpine forests in this region are dominated by *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir) and *Pinus contorta* Dougl. var. *latifolia* Engelm. (lodgepole pine) on drier sites, and montane forests are generally absent, with transition directly to forests dominated by *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) on north aspects and by *P. menziesii* on south aspects (Fonda and Bliss 1969). The subalpine meadow – forest ecotone is abrupt and related to microclimate and topography, while the subalpine–montane forest ecotone is more gradual.

The Olympic Mountains have limited potential for large-scale dispersal of plant species, because the mountain range is essentially isolated from other mainland areas by intervening water and low-elevation areas (Buckingham et al. 1995; Peterson et al. 1997). Changes in distribution and abundance of plant species must occur within the existing populations and communities of the Olympics, and species ranges will probably remain within the Olympics providing that the magnitude of climatic change is not extreme. Species adjustments to an altered climate are expected to be mainly altitudinal or between aspects.

#### Vegetation sampling

Vegetation structure and composition were sampled along elevational gradients in the NE and SW regions of Olympic National Park to provide an empirical data base to calibrate the gap

model. Human disturbance in this area has been minimal, and forests have never been harvested or otherwise manipulated. Field sampling was conducted on study transects located on two paired north and south aspects in the NE and SW regions for a total of eight transects (Fig. 1). Paired transects were selected after reconnaissance of potential study areas throughout the NE and SW Olympic Mountains, and transects were subjectively judged to be similar to each other in terms of the distribution and abundance of dominant tree species within each particular region and aspect. Each transect spanned an elevational range with similar aspect and slope, from subalpine meadows near the ridgetops through subalpine forest to the upper montane forest (transects ranged from 650 to 1600 m linear distance). Distance between plots was roughly equidistant within transects, with some variation to exclude major topographic features such as cliffs and streams.

Dominant tree species are defined as those with the greatest basal area in the sampling area. Tree species, diameter at breast height (DBH, 137 cm above ground level), and height for all trees greater than 1 cm DBH were recorded in eight plots of 15 × 15 m located along each transect, for a total of 64 sampling plots. Elevation, aspect, and slope for each plot were also recorded. We cored two to five trees per plot with an increment borer to determine approximate stand age. Basal area per hectare was calculated for each species in each plot to determine relative species rank.

#### Model structure and parameterization

We used the individual-based gap-replacement model ZELIG (Urban 1993), which is a reformulation of the basic JABOWA

**Table 1.** Elevation and climate for plots along transects used in climatic-change simulations for northeastern (NE) and southwestern (SW) regions, and north (N) and south (S) aspects.

Plot	Elevation (m)	January temperature (°C)	August temperature (°C)	Annual precipitation (cm)
NE-N1	1900	-4.6	10.3	109.8
NE-N2	1820	-4.3	10.6	106.0
NE-N3	1790	-4.2	10.7	104.8
NE-N4	1760	-4.0	10.7	103.4
NE-N5	1715	-3.9	11.0	101.7
NE-N6	1660	-3.7	11.2	99.1
NE-N7	1600	-3.5	11.4	96.5
NE-N8	1540	-3.2	11.6	94.0
NE-S1	1950	-4.8	10.1	114.1
NE-S2	1890	-4.5	10.3	111.9
NE-S3	1825	-4.3	10.6	109.0
NE-S4	1775	-4.1	10.7	106.8
NE-S5	1730	-3.9	10.9	104.8
NE-S6	1670	-3.7	11.1	102.3
NE-S7	1610	-3.5	11.3	99.6
NE-S8	1480	-3.0	11.8	94.2
SW-N1	1340	-0.2	11.2	533.3
SW-N2	1325	-0.2	11.2	531.2
SW-N3	1290	0.0	11.4	526.0
SW-N4	1260	0.1	11.5	521.7
SW-N5	1225	0.2	11.6	516.6
SW-N6	1195	0.3	11.7	512.2
SW-N7	1150	0.5	11.9	505.6
SW-N8	1125	0.6	12.0	502.0
SW-S1	1525	-0.9	10.5	560.4
SW-S2	1480	-0.7	10.7	553.8
SW-S3	1410	-0.5	10.9	543.6
SW-S4	1365	-0.3	11.1	537.0
SW-S5	1305	-0.1	11.3	528.2
SW-S6	1250	0.1	11.5	520.2
SW-S7	1180	0.4	11.8	510.0
SW-S8	1160	0.4	11.8	507.1

**Note:** January and August temperatures are mean monthly estimates; annual precipitation is estimated total.

(Botkin et al. 1972) and FORET models (Shugart 1984). The model has already been parameterized for some tree species of the Pacific Northwest (Urban et al. 1993). To calibrate the model for transects in the Olympic Mountains, each sampling plot was parameterized as a model input plot by determining or estimating current climate (Table 1), solar radiation, and soil characteristics.

Average monthly temperature and total precipitation for each plot were estimated by regressing differences in temperature and precipitation along an elevational range of weather stations on the west slope of the Cascade Mountains, Washington (Enumclaw, Longmire, Paradise, Snoqualmie Pass, and Stevens Pass weather stations; U.S. National Climatic Data Center data), because there are no long-term data for high-elevation sites in the Olympic Mountains. These regression models were adjusted for the Olympic Mountains using weather data from low-elevation sites at the Elwha Ranger Station and Quinault Ranger Station (Olympic National Park) (Fig. 1). Precipitation estimates were adjusted with data from Deer Park in the NE Olympics (Belsky and del Moral 1982) and the USDA Natural Resources Conservation Service

map, which has isolines of predicted annual precipitation associated with elevation.

Available soil moisture in ZELIG is calculated from monthly precipitation, monthly solar radiation, soil texture, and soil depth. Monthly potential solar radiation values for Olympic National Park were obtained for each transect (R. Hoffman, unpublished data) and were reduced by 40% to account for the effects of cloud cover and calculate surface solar radiation (Geiger 1950, Barry 1992). Soil field capacity and wilting point were estimated for the coarse to gravelly sandy loam soils found at high-elevation sites in the Olympic Mountains (Woodward 1998; Prichard et al. unpublished data<sup>3</sup>). Soil depth of 80 cm was used for all plots based on data from 36 soil profiles at high-elevation sites in the Olympics in the same vicinity as our vegetation plots (Prichard et al. unpublished data<sup>3</sup>). Soils are modeled as eight layers of 10 cm each for calculations of soil moisture availability.

ZELIG simulates a grid of interactive model plots defined to correspond to the zone of influence of a canopy-dominant tree (Urban et al. 1993). Plot size was set at 15 × 15 m, equivalent to the largest canopy area of dominant trees on the study transects. We ran simulations under current climate for the estimated stand age based on tree cores, rounded up to the nearest 50-year mark. Plots that are currently meadow were run for 200 years. Stand age in the NE ranged from 100 to 400 years, with a median age of 150 years. In the SW, all forest plots were run for 600 years, rounded up from the oldest core obtained (a 586-year old *T. mertensiana*). It was assumed that seed sources would be locally available for all species contained on the model plots. Some species (e.g., *A. lasiocarpa*) can produce new ramets through vegetative propagation by branches (layering), but there are no demographic data on which to base the contribution of this propagation to long-term population dynamics.

ZELIG requires quantification of the following for each tree species: maximum age, DBH, height, growing degree-day minima and maxima, shade tolerance, and drought tolerance (Urban et al. 1993). These species parameters were quantified for tree species in the Olympic Mountains using our field data and data from the literature (Table 2) (Minore 1979; Henderson et al. 1989; Urban et al. 1993), except for growing degree-day values, which are described below. The age of the largest tree from each vegetation plot was used to parameterize age in the model plots, and the model was run to that age under current climate to create a model stand that was the starting point for climatic-change scenarios. Tree-height data from the vegetation plots were used to parameterize maximum tree height for each species. Relationships between DBH and height and between age and growth were derived from our field data and other studies in the Pacific Northwest (Ettl and Peterson 1995a, 1995b; Garman et al. 1995; J.A. Henderson, unpublished data).

Determining minimum and maximum degree-day values for each species is critical in using ZELIG to accurately reproduce the composition at each elevation and the transitions between species dominance along each transect. Growing degree-days are accumulated above a baseline temperature of 5.56°C (Urban 1993) and decrease with increasing elevation. Minimum degree-day values determine the upper-elevation limit of a species and the relationship between temperature and potential growth rate. In older gap models, the growth versus degree-day curve is a concave-down parabola, where the growth factor is maximal at the midpoint of a species degree-day distribution, and growth decreases to 0 at the minimum and maximum degree-day values (lower elevation limit). For our high-elevation sites, however, it was more realistic to assume that any increase in degree-days beyond the midpoint would not limit growth, so we used maximum degree-day values to determine the midpoint of a species distribution (D.L. Urban, personal communication).

ZELIG calculates the average fraction of rain versus snow and the maximum snowpack depth for a given plot and climate. Snow

**Table 2.** Selected parameters for species used in model simulations, including maximum age, maximum DBH, maximum height, minimum and maximum growing degree-days (GDD), and relative shade and drought tolerances (5 is most tolerant and 1 least).

Species	Maximum age (years)	Maximum DBH (cm)	Maximum height (m)	GDD minimum	GDD maximum	Shade tolerance	Drought tolerance
<i>Abies amabilis</i>	700	225	60	296	1925	5	1
<i>Abies lasiocarpa</i> <sup>a</sup>	400	100	32	294	734	4	3
<i>Acer macrophyllum</i> Pursh <sup>b</sup>	300	250	30	678	3741	4	2
<i>Alnus rubra</i> Bong. <sup>b</sup>	100	150	36	600	3680	1	2
<i>Chamaecyparis nootkatensis</i>	1000	250	35	299	1915	3	2
<i>Pinus contorta</i> <sup>a</sup>	250	100	19	276	1054	1	5
<i>Pinus monticola</i> Dougl. <sup>a</sup>	600	200	58	297	1004	2	3
<i>Picea sitchensis</i> (Bong.) Carr. <sup>b</sup>	750	350	57	561	3638	4	1
<i>Pseudotsuga menziesii</i>	800	325	68	340	3761	1	4
<i>Thuja plicata</i> Donn.	1500	300	53	528	3681	4	2
<i>Tsuga heterophylla</i>	900	275	57	329	3680	5	2
<i>Tsuga mertensiana</i>	900	225	38	295	761	5	1

<sup>a</sup>Species used in simulations for NE region only.

<sup>b</sup>Species used in simulations for SW region only.

begins to be accumulated when monthly average temperature is below 5°C, and the fraction of precipitation as snow increases linearly from 0% at that temperature to 100% by -2°C (Barry 1992), giving an average percentage of 60–70% of annual precipitation as snow for the simulated plots. Snowmelt is a function of degree-days when the average monthly temperature is greater than 0°C; the rate of this function is based on empirical data from the Olympic Mountains in the same vicinity as our vegetation plots (Woodward 1998). Regeneration does not occur in the model if the snow-free season does not exceed 100 days in a given year (Soll 1994).

The model was run with current climate for each plot to its estimated stand age to obtain starting estimates of the number of trees, species, diameters, and biomass for each model plot. The initial composition reflected two major transitions in dominant vegetation type in the raw data: between subalpine meadow and forest, and between subalpine tree species (*A. lasiocarpa*, *T. mertensiana*) and montane species (*P. menziesii*, *A. amabilis*), with elevation differences of <300 m and temperature range of <2°C (Table 1).

### Climatic-change simulations

We used an increase of 2°C in average monthly temperature as a potential climatic-change scenario for the Pacific Northwest (e.g., Mitchell et al. 1995). Three climatic-change scenarios were simulated for 1000 years, with each set of climatic conditions beginning at the start of the simulations: a 2°C increase in temperature combined with (i) no change in annual precipitation (warmer), (ii) a 20% precipitation increase (warmer-wetter), and (iii) a 20% precipitation decrease (warmer-drier). The temperature and precipitation scenarios were selected as conservative possibilities, based on regionalized inferences from four general circulation models (Joint Institute for the Study of the Atmosphere and the Oceans 1999). There is greater certainty about future temperature increases than about the direction, magnitude, and seasonality of precipitation.

The warmer scenario represents an increase of ~300 growing degree-days in the NE region and ~500 degree-days in the SW. Warmer-drier simulations have a slightly larger increase (~50) in growing degree-days and warmer-wetter simulations have a slightly smaller increase than the warmer scenario. Differences in degree-days between NE and SW and among the scenarios are caused by different levels of snow and the delay of the accumulation of degree-days until snowpack has melted.

ZELIG requires that a different random-number seed be entered for each model run. Climatic parameters (monthly temperature and precipitation) are entered in the model with a mean and standard deviation. The random-number seed is used to vary climate each

year around the mean, and the variable climate results in slightly different regeneration, growth, and stand characteristics each year. The minimum number of runs (five) necessary to reduce standard deviation in model output to an acceptable level (less than 20% of the mean) was determined in a pilot study, in which the mean and standard deviation in basal area and biomass were calculated sequentially for 1 to 20 model runs.

Climatic-change simulations used the N and S transects with the largest range in elevation from each region (NE-N, NE-S, SW-N, and SW-S) for a total of 32 plots. Each plot along these transects was also simulated for 1000 years using no change in climate as a control. The output from the five simulations was averaged to give mean changes in stand woody biomass and species basal area for each scenario. If a simulation result had no trees, the plot was assumed to be meadow. The predicted changes in vegetation patterns were evaluated for each scenario by NE and SW subregion, elevation, and aspect.

### Results and discussion

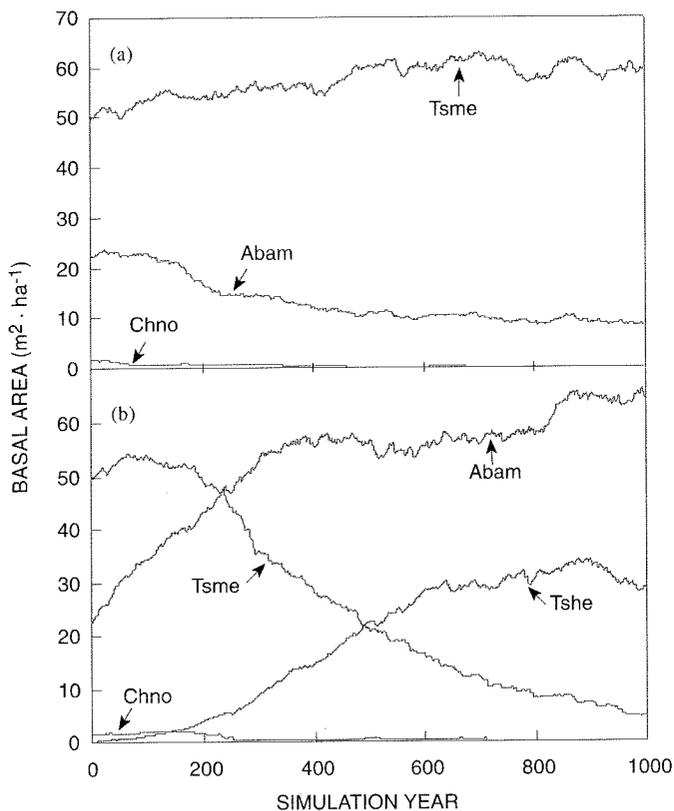
Model output for simulated transitions between species dominance generally occur within 50 m of the elevation observed in the field, and species basal area is similar to actual values from sample plots (Zolbrod 1995) and other studies in the Olympic Mountains (Ettl and Peterson 1995b). This model output was used as the initial stand condition for climatic-change simulations.

Model simulations with no change in climate, which were run for 1000 years, generally show little change from initial species composition or biomass. The meadow plots in these simulations gain little or no tree basal area or biomass, while the forest plots have stable basal area and species dominance (Fig. 2). Therefore, the results discussed hereafter are the effects of changing climatic parameters, not fluctuations in tree species composition or biomass caused by stochastic elements or random variation in the model.

#### Effects of increased temperature on tree establishment in meadows

In all transects, trees establish in the subalpine meadows in the warmer climatic scenario, continuing the pattern of tree establishment documented for the 20th century (Agee

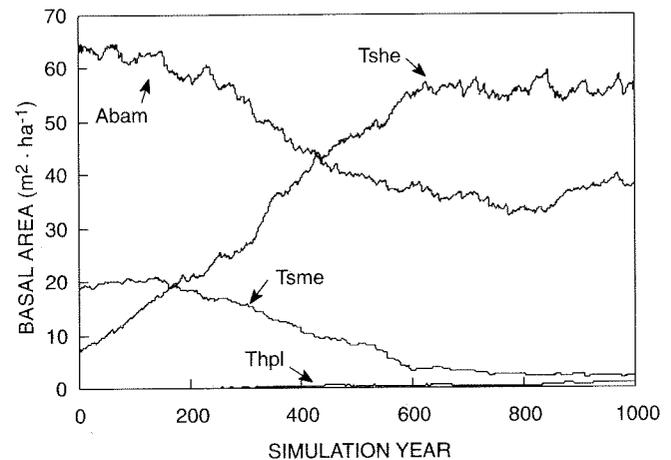
**Fig. 2.** Tree species basal area change for plot SW-N2 for scenarios with (a) no change in climate and (b) warmer climate. Lines represent mean basal area from five simulations. Abam, *Abies amabilis*; Chno, *Chamaecyparis nootkatensis*; Tshe, *Tsuga heterophylla*; Tsme, *T. mertensiana*.



and Smith 1984; Rochefort et al. 1994; Woodward et al. 1995; Rochefort and Peterson 1996; Miller and Halpern 1998; Peterson 1998). Tree establishment in the meadows is related to two factors associated with the increase in temperature: (i) the increase in growing degree-days and (ii) the increased duration of growing season resulting from less accumulation of snowpack and more rapid snowmelt. In the NE region, the high-elevation meadows on both N and S aspects are dominated by *Pinus contorta* stands in 150–200 years (Table 3). In the SW region, the subalpine meadows are dominated by stands of large *A. amabilis* with *T. heterophylla* and *T. mertensiana* subdominant in about 200 years.

The establishment of forest in the SW matches predictions for a warmer climate in a high precipitation regime (Franklin et al. 1971; Little et al. 1994; Woodward et al. 1995; Rochefort and Peterson 1996). However, the establishment of forest in the NE meadows is contrary to predictions that warmer summers would increase evapotranspiration and drought during the growing season, thereby increasing moisture stress in seedlings and reducing regeneration (Little et al. 1994; Soll 1994; Woodward et al. 1995). The earlier initiation of growing season when more precipitation is available may enable seedlings to withstand low soil moisture in sum-

**Fig. 3.** Tree species basal area change for plot SW-N8 for a warmer climatic scenario (mean of five simulations). Abam, *Abies amabilis*; Thpl, *Thuja plicata*; Tshe, *Tsuga heterophylla*; Tsme, *T. mertensiana*.



mer, and extension of the growing season in the autumn may increase the probability of surviving through the winter.

Several factors not considered in the model could affect patterns of tree establishment in the subalpine meadows with a warmer climate. In the NE Olympics, seedling establishment and survival rates are low in most meadow types other than heath–shrub communities (Kuramoto and Bliss 1970; Agee and Smith 1984; Soll 1994; Rochefort and Peterson 1996); this competition may reduce actual establishment of forests in meadows in a warmer climate. Insufficient seed dispersal and availability could also reduce tree establishment in meadows (Franklin et al. 1971; Agee and Smith 1984; Little et al. 1994). In the NE, meadows located at the highest elevations are above treeline, and trees are much less likely to disperse seeds up-slope (Little et al. 1994). Fire disturbance may also limit establishment of forests and maintain subalpine meadows (Agee and Smith 1984; Little et al. 1994; Huff 1995), because the present distribution of subalpine meadows and forest in the Olympics is closely related to fire patterns (Fonda and Bliss 1969; Kuramoto and Bliss 1970; Buckingham et al. 1995).

#### Effects of increased temperature on tree species distribution

Increased temperature results in a greater change in the elevational distribution of dominant tree species in the SW region than the NE, because the distribution of species in the SW is limited primarily by temperature and snowpack duration (Fonda and Bliss 1969). On both N and S aspects in the SW, species presently dominant at lower elevations shift up in elevation without much change in stand composition. Montane forests dominated by *A. amabilis* are 300–400 m higher in elevation, with *A. amabilis* replacing *T. mertensiana* as the dominant species in 200–300 years, and *T. heterophylla* becoming the subdominant species in 400–500 years (Fig. 2b, Table 3). At the lower elevation plots, *T. heterophylla* becomes the dominant species in 500–600 years with *A. amabilis* still abundant, and *T. mertensiana* becomes a minor component of the forest stand in about 200 years (Fig. 3). The transition elevation between *A. amabilis*

**Table 3.** Basal area ( $\text{m}^2\text{-ha}^{-1}$ ) at 1000 years for dominant species in the warmer climatic simulations.

Plot	Abam	Abla	Pico	Psme	Tshe	Tsme
NE-N1	—	2.5 (+2.5)	27.1 (+26.3)	—	—	0.6 (+0.6)
NE-N2	—	18.3 (+5.9)	13.4 (+2.5)	—	—	—
NE-N3	—	0.1 (+0.1)	28.8 (+24.5)	—	—	—
NE-N4	—	27.5 (−4.9)	2.0 (−4.3)	—	—	0.0 (−3.1)
NE-N5	—	39.3 (+5.2)	—	—	1.3 (+1.3)	0.1 (−15.1)
NE-N6	—	37.7 (+10.3)	0.0 (−0.5)	—	1.8 (+1.8)	0.1 (−19.3)
NE-N7	0.0 (−10.2)	33.5 (+7.1)	0.0 (−0.3)	—	3.6 (+3.5)	0.0 (−20.5)
NE-N8	2.1 (−13.8)	3.3 (−7.2)	—	—	38.6 (+38.5)	0.7 (−35.7)
NE-S1	—	—	19.3 (+19.3)	—	—	—
NE-S2	—	—	20.3 (+18.4)	—	—	—
NE-S3	—	0.3 (−9.6)	22.9 (+19.2)	1.0 (+1.0)	—	—
NE-S4	—	0.2 (+0.2)	23.0 (+19.3)	1.9 (+1.9)	—	—
NE-S5	—	0.0 (−3.8)	23.6 (+4.3)	0.9 (+0.9)	—	—
NE-S6	—	0.0 (−8.0)	22.4 (+2.0)	2.2 (+2.2)	—	—
NE-S7	—	0.0 (−26.7)	23.3 (+8.6)	3.3 (+3.3)	—	—
NE-S8	—	6.4 (−32.1)	7.2 (+4.5)	20.9 (+19.8)	—	—
SW-N1	68.9 (+49.3)	—	—	—	29.8 (+29.8)	3.1 (−44.4)
SW-N2	65.1 (+19.4)	—	—	—	29.0 (+29.0)	4.5 (−37.1)
SW-N3	62.9 (+40.9)	—	—	—	38.4 (+38.2)	5.1 (−43.6)
SW-N4	51.2 (+19.4)	—	—	—	45.5 (+38.7)	3.2 (−37.1)
SW-N5	51.9 (+22.9)	—	—	—	44.4 (+39.8)	3.6 (−31.2)
SW-N6	40.8 (−1.5)	—	—	—	57.8 (+52.0)	4.2 (−24.4)
SW-N7	43.3 (−18.1)	—	—	—	51.0 (+46.0)	3.1 (−17.7)
SW-N8	38.5 (−25.0)	—	—	—	55.0 (+46.6)	2.2 (−16.1)
SW-S1	79.1 (+79.1)	—	—	—	11.5 (+11.5)	11.5 (+11.5)
SW-S2	75.4 (+75.4)	—	—	—	16.6 (+16.6)	8.9 (+8.9)
SW-S3	74.0 (+67.0)	—	—	—	24.0 (+24.0)	5.4 (−46.6)
SW-S4	80.1 (+70.3)	—	—	—	22.0 (+21.9)	3.5 (−50.2)
SW-S5	61.8 (+44.8)	—	—	—	35.3 (+33.5)	5.2 (−46.9)
SW-S6	52.9 (+33.3)	—	—	—	48.9 (+47.3)	4.7 (−44.3)
SW-S7	38.3 (−12.5)	—	—	—	57.0 (+52.0)	1.9 (−30.0)
SW-S8	37.5 (−17.4)	—	—	—	62.5 (+53.8)	2.2 (−15.6)

**Note:** Difference from initial basal area values is shown in parentheses. Only species with basal area greater than  $20 \text{ m}^2\text{-ha}^{-1}$  in any plot in each transect are shown. Abam, *Abies amabilis*; Abla, *Abies lasiocarpa*; Pico, *Pinus contorta*; Psme, *Pseudotsuga menziesii*; Tshe, *Tsuga heterophylla*; Tsme, *Tsuga mertensiana*.

and *T. heterophylla* dominance with a warmer climate is approximately 1200 m, whereas this transition presently occurs at approximately 550 m (Fonda and Bliss 1969; Henderson et al. 1989). Paleoecological records show that *T. heterophylla* replaced *A. amabilis* and *T. mertensiana* forests during a warmer period with longer growing seasons in the 19th century on Mount Rainier in the Cascade Range of Washington (Dunwiddie 1986), which supports our prediction that *T. heterophylla* will move up in elevation in a warmer climate.

With increased temperature in the NE region, shifts occur in the distribution of individual species, but the dominant species are unchanged in many plots (Table 3). Lower elevation species do not dominate at higher elevations as they do in the SW, except for the establishment of *Pinus contorta* forests in the meadows. The initial vegetation distribution and the response to warmer climate are different between the N and S transects in this region.

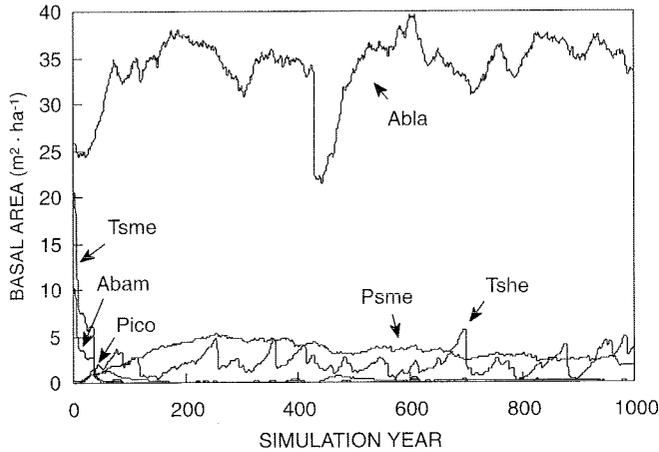
In the NE-N transect, *Abies lasiocarpa* continues to dominate at most plots except for the highest and lowest elevations. The dominance of *T. mertensiana* and *A. amabilis* at the mid- to low-elevation plots is reduced in about 50 years,

and *T. heterophylla* and *Pseudotsuga menziesii* become established as the subdominant species (Fig. 4). Species basal area fluctuates throughout the duration of the climatic-change simulations, but the new species composition generally stabilizes in 100–200 years.

The continued dominance of *A. lasiocarpa* with warming is supported by tree growth – climate correlations, which indicate that *A. lasiocarpa* at high-elevation, wetter sites grow faster during years with higher summer temperature (Ettl and Peterson 1995a, 1995b). It is also supported by paleoecological evidence showing increased dominance of *A. lasiocarpa* during the warmer climate of the Holocene optimum 8000–5000 years BP (McLachlan and Brubaker 1995; Brubaker and McLachlan 1996). The persistence of *A. lasiocarpa* is probably related to its tolerance of drought and shade, because the N transect has sufficient moisture for *A. lasiocarpa* to compete with the less shade tolerant *Pinus contorta* and *Pseudotsuga menziesii* but not enough moisture for the less drought tolerant species *A. amabilis*, *T. heterophylla* and *T. mertensiana*.

In the NE-S transect, there is generally little change in the midelevation forest stands, which continue to be dominated

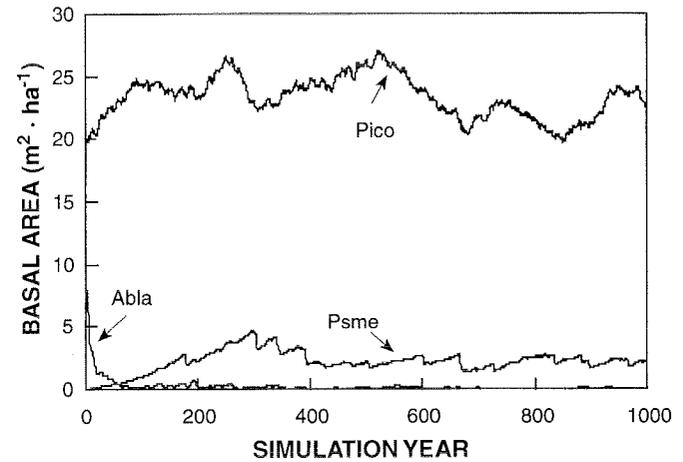
**Fig. 4.** Tree species basal area change for plot NE-N7 for a warmer climatic scenario (mean of five simulations). Abam, *Abies amabilis*; Abla, *A. lasiocarpa*; Pico, *Pinus contorta*; Psme, *Pseudotsuga menziesii*; Tshe, *Tsuga heterophylla*; Tsme, *T. mertensiana*.



**Table 4.** Biomass (Mg/ha) for each plot for initial conditions and each climatic-change scenario.

Plot	Initial	+2°C	+2°C, -20% precipitation	+2°C, +20% precipitation
NE-N1	2.5	136.3	126.2	145.7
NE-N2	107.7	168.2	140.4	217.4
NE-N3	11.6	137.2	139.0	136.1
NE-N4	250.6	202.2	106.9	233.1
NE-N5	352.0	275.2	234.5	323.7
NE-N6	401.6	272.9	229.2	295.3
NE-N7	429.8	273.9	246.6	351.9
NE-N8	711.1	644.3	448.5	619.8
NE-S1	0.2	88.8	86.2	95.0
NE-S2	4.5	102.3	93.5	118.1
NE-S3	62.5	111.8	103.5	134.6
NE-S4	9.5	121.2	100.8	142.3
NE-S5	85.8	112.5	118.4	140.3
NE-S6	108.9	118.8	109.8	170.3
NE-S7	193.5	128.7	148.3	190.5
NE-S8	282.6	253.6	178.1	319.0
SW-N1	727.2	1331.6	1447.5	1418.8
SW-N2	771.5	1292.1	1435.2	1386.4
SW-N3	1003.6	1514.1	1446.9	1404.7
SW-N4	1059.6	1428.8	1396.6	1496.1
SW-N5	1027.0	1425.4	1377.1	1475.3
SW-N6	1025.6	1624.7	1551.9	1443.2
SW-N7	1071.6	1431.9	1508.2	1590.8
SW-N8	1111.4	1403.5	1505.5	1428.8
SW-S1	0.0	1292.3	1257.5	1222.4
SW-S2	38.3	1289.5	1149.5	1293.0
SW-S3	785.5	1313.4	1328.6	1374.4
SW-S4	910.9	1354.1	1445.5	1349.8
SW-S5	1046.7	1415.2	1356.4	1427.7
SW-S6	980.7	1581.8	1485.8	1325.9
SW-S7	1093.3	1436.8	1450.0	1449.8
SW-S8	937.8	1602.8	1318.9	1477.3

**Fig. 5.** Tree species basal area change for plot NE-S6 for a warmer climatic scenario (mean of five simulations). Abla, *Abies lasiocarpa*, Pico, *Pinus contorta*, and Psme, *Pseudotsuga menziesii*.



by *P. contorta* (Table 3). Tree establishment and growth at these locations are limited by soil moisture and fire disturbance, as well as low temperature. At most of these plots, basal area of *A. lasiocarpa* decreases from initial values in the first 50 years of the simulations, and *Pseudotsuga menziesii* increases in basal area, but both species remain minor components of the forest stands (Fig. 5). However, at the lowest elevation plot, *Pseudotsuga menziesii* becomes dominant with basal area of 15–20 m<sup>2</sup>·ha<sup>-1</sup> by year 200, while *Pinus contorta* and *A. lasiocarpa* basal areas fluctuate between 0 and 15 m<sup>2</sup>·ha<sup>-1</sup> during the simulation.

The rate of change in species dominance is lower for the SW than the NE, probably because the stable canopy of mature trees creates shade and delays regeneration until there is substantial mortality of the dominant trees. Urban et al. (1993) also found a lag in response to warmer climate in Cascade Range forests because of canopy cover of dominant trees for medium-age stands. For a low-elevation site in the western Cascades of Oregon, Dale and Franklin (1989) found no change in the dominant species *Pseudotsuga menziesii* and *T. heterophylla* with a warmer climate but did find a change in codominant species.

Fire disturbance could play a role in the distribution of species, particularly along the NE-N transects. The NE-S transect is already dominated by *Pinus contorta*, which is often an early seral species following fire and would be favored in regeneration in the dry conditions found in the NE (Franklin and Dyrness 1988; Agee 1993). In the SW, while stand-replacement fires could occur with greater frequency, they are unlikely to cause major shifts in tree species distribution, although they may affect the rate of species change by removing the canopy (Franklin et al. 1992; Urban et al. 1993).

#### Effects of increased temperature on biomass

Average biomass levels generally decrease for forest stands in the NE, except where trees establish in meadows, and consistently increase in the SW (Table 4). In the NE, biomass on both N and S aspects increases 100–150 Mg/ha in high-elevation meadows where *Pinus contorta* and

*A. lasiocarpa* establish. However, biomass decreases 10–30% at the lower elevations because evapotranspiration increases and soil moisture decreases. Biomass changes within 200–250 years after the start of the simulations and then stabilizes. Species more commonly found at lower elevation, such as *T. heterophylla* and *Pseudotsuga menziesii*, may have potential for greater growth (Lassoie et al. 1985) but are not more productive than higher elevation species such as *A. lasiocarpa* if growth is limited by low soil moisture and temperature. Tree species at high elevations in the NE Olympics often have low conductance during summer, which reduces the potential for photosynthesis and growth and, thus, reduces accumulated biomass (Tranquillini 1979; Hadley and Smith 1986; Cui and Smith 1991).

The SW transects show biomass increases of 30–60% for all plots (Table 4). This increase in biomass is related to the longer growing season from the temperature increase, without the effects of lower soil moisture in reducing photosynthetic rates. Biomass levels in the SW stabilize in about 300 years after the climatic change is initiated. The slightly slower rate of biomass change may again be related to the slower change in species dominance resulting from the tolerance of mature trees to changing environmental conditions. Urban et al. (1993) predicted a decrease in biomass levels for mid- to high-elevation forests in the Cascade Range, because they did not include species that could potentially grow faster in a warmer climate. Dale and Franklin (1989) predicted stable biomass levels with warmer climate for low-elevation stands in the Cascades, which were probably not limited by low temperature, unlike higher elevation sites in the Olympics (Ettl and Peterson 1995a).

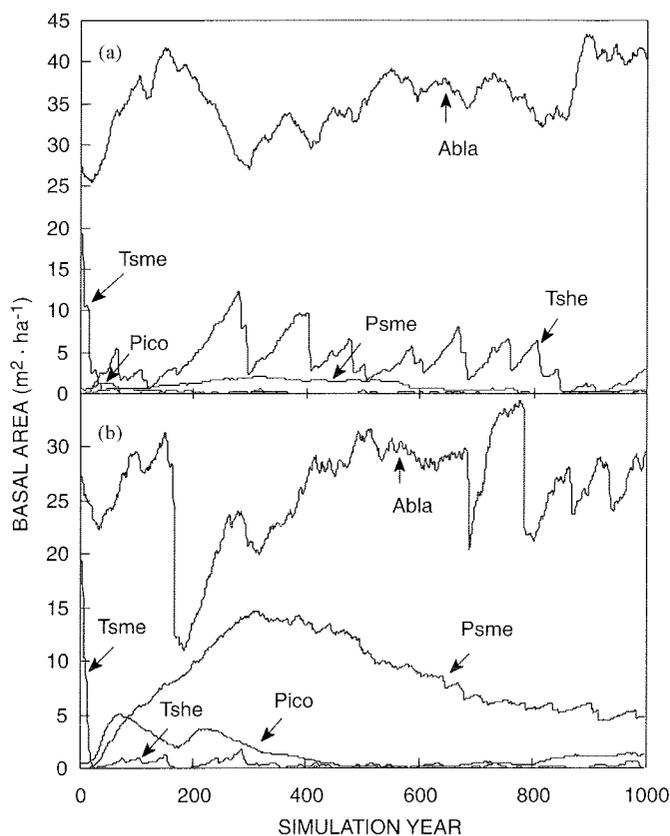
### Effects of altered precipitation

Different levels of precipitation coupled with increased temperature have little effect on the distribution of dominant species along the transects but do affect subdominant species composition and species basal area. Tree establishment in meadows occurs regardless of whether the climatic change is warmer–wetter or warmer–drier. The changes in species basal area (increase in the SW, decrease in the NE) in response to warmer temperatures with no change in precipitation are intermediate between the wetter and drier climatic-change scenarios for the SW but more variable for the NE. The difference in precipitation levels has a greater effect on species basal area levels in the NE than the SW, because small changes in precipitation can affect soil moisture, a highly limiting factor to growth and regeneration in the NE (Ettl and Peterson 1995a, 1995b; Woodward et al. 1995).

Altered precipitation causes the greatest relative change in species basal area on the NE-N transect. While the dominance of *A. lasiocarpa* is not affected by the precipitation regime, subdominant species differ on three of eight plots. Species with higher tolerance of low soil moisture (e.g., *Pseudotsuga menziesii*) (Table 2) have relatively higher basal area in the drier climatic scenario (Fig. 6). In addition, at the lower elevation plots previously dominated by *T. mertensiana* and *A. amabilis*, these species decline more rapidly in the drier scenario than in the wetter.

In the NE-S transect, there is no difference in dominant species between the wetter and drier scenarios and no difference in subdominant species rank except for NE-S8, where

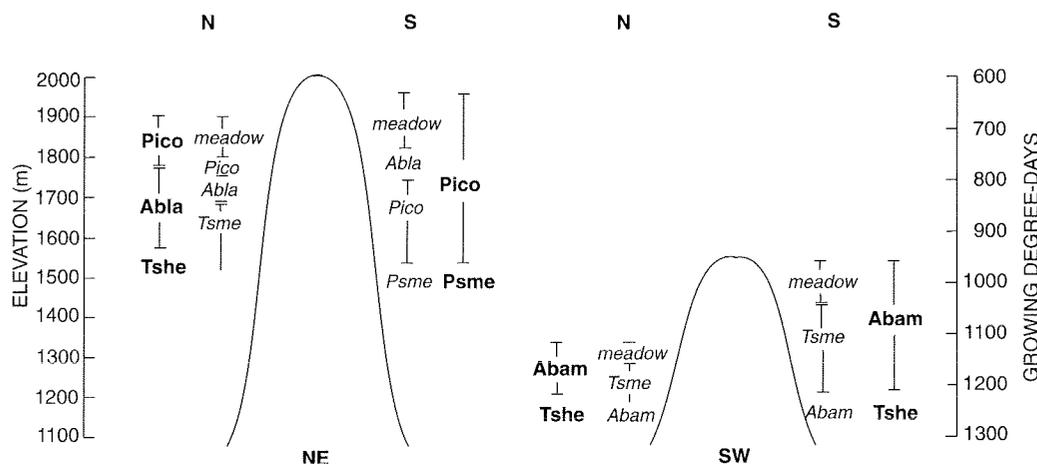
**Fig. 6.** Tree species basal area change for plot NE-N6 for a (a) warmer–wetter climatic scenario, and (b) warmer–drier climatic scenario (mean of five simulations). Abla, *Abies lasiocarpa*; Pico, *Pinus contorta*; Psme, *Pseudotsuga menziesii*; Tshe, *Tsuga heterophylla*; Tsme, *T. mertensiana*.



*Pseudotsuga menziesii* is dominant in both scenarios; *A. lasiocarpa* is second in the wetter scenario and *Pinus contorta* second in the drier. *Pinus contorta* has slightly higher basal area in the wetter scenario than in the drier scenario; there are slightly higher levels of the subdominant *A. lasiocarpa* than *Pseudotsuga menziesii*. These results match predictions that *A. lasiocarpa* may grow relatively faster in wetter conditions with a warmer climate (Ettl and Peterson 1995a). In this transect as well, the transition in species dominance from *A. lasiocarpa* to *Pinus contorta* and *Pseudotsuga menziesii* at the lowest elevation plots occurs more rapidly in the drier than the wetter scenario.

In the SW, there are few differences in species composition or abundance with different levels of precipitation. The main difference is that the rate of transition in species dominance occurs more rapidly in the drier climatic-change scenarios. For example, in SW-N3, *A. amabilis* basal area exceeds that of *T. mertensiana* in 150 years, and *T. heterophylla* basal area exceeds *T. mertensiana* in 250 years in the drier scenario. In the wetter scenario, *A. amabilis* basal area exceeds *T. mertensiana* in about 250 years, and *T. heterophylla* basal area exceeds *T. mertensiana* in 420 years. In the SW-S transect, both *A. amabilis* and *T. heterophylla* overtake *T. mertensiana* more rapidly at the higher elevations in drier

**Fig. 7.** Summary of dominant tree species distribution by region, aspect, elevation, and growing degree-days calculated by ZELIG for a warmer climatic scenario (bold) and actual sampled stands (italics). Abam, *Abies amabilis*; Abla, *A. lasiocarpa*; Pico, *Pinus contorta*; Psme, *Pseudotsuga menziesii*; Tshe, *Tsuga heterophylla*; Tsmc, *T. mertensiana*.



climatic-change simulations, and *T. heterophylla* overtakes both *T. mertensiana* and *A. amabilis* more rapidly at the lower elevations.

These differences in the rate and elevation of species transition are related to snowpack and growing-season length. There is less accumulation of snowpack in the drier scenario, and therefore, the growing season can begin earlier, favoring species such as *T. heterophylla* and *Thuja plicata* Donn. This relationship is corroborated by average annual climatic output for each scenario, which shows that growing season is shorter in the wetter scenario because of higher snowpack accumulation. Mean growing season length for the SW plots is 140 days and total snowfall is 216 cm in the warmer-wetter scenario, while growing season is 166 days and snowfall 145 cm in the warmer-drier scenario.

The largest differences in woody biomass between wetter and drier climatic-change simulations are in the NE region, where there is greater species response to different precipitation scenarios. For the NE-N transects, the wetter scenario results in a smaller biomass decrease at middle to lower elevation plots, and tree establishment in meadows at the highest elevations leads to increased biomass in both precipitation scenarios (Table 4). The NE-S plots maintain or increase biomass at most plots in the wetter scenario, while biomass decreases from present levels in the drier scenario for the lower elevation plots. There is no difference in rate of biomass change between wetter and drier climates, but the drier scenario generally has larger fluctuations in biomass levels during the course of the simulations. In the SW region, there is a trend of increased biomass with warmer climate in both N and S transects in about 300 years regardless of whether the climatic change is wetter or drier (Table 4).

## Conclusions

Response of high-elevation forests in the Olympic Mountains to large-scale climatic change depends on environmental factors at the mesoscale (e.g., wet vs. dry climatic regime due to orographic effects) and microscale (e.g., north vs. south aspect on the same landform). Regional precipitation

regimes play an important role in both the rate and type of predicted changes in tree species distribution (Fig. 7) and stand biomass levels in a warmer climate, and determine the importance of aspect on vegetation response. If temperature increases in the future, productivity of forest stands may increase in the SW region but decrease in the NE. Broad conclusions about vegetation response to a warmer climate in mountainous regions cannot be inferred from studying isolated areas (Beniston 1994; Peterson 1994; Beniston and Fox 1996; Peterson 1998). Areas with diverse topography must be examined systematically at a smaller spatial scale to infer larger scale changes (Peterson and Parker 1998).

Response of high-elevation forests in the Olympic Mountains to climatic change consists of changes in the distribution and abundance of individual species rather than translocation of intact communities, but again, this response varies by region (Fig. 7). In the SW region, tree species composition is relatively stable as these species shift upwards in elevation with a warmer climate. In the NE region, the warmer climatic simulations result in combinations of tree species that are currently uncommon. Paleocological studies confirm that species respond individually to climatic changes rather than as part of a static community of species (Davis 1981; Brubaker 1988; Delcourt and Delcourt 1991; Whitlock 1992; Schoonmaker 1998). Simply shifting a species or a broadly classified dominant vegetation type upward in elevation in response to increased temperature (e.g., Peters and Darling 1985) does not provide an adequate prediction of vegetation response.

Understanding the effects of changes in precipitation levels is also critical in quantifying potential vegetation changes, particularly where regeneration and growth are limited by duration of snowpack and soil moisture. Changes in precipitation levels coupled with increased temperature also result in region- (NE vs. SW) and aspect-specific (N vs. S) responses. In this study, altered precipitation produces greater differences in stand composition and structure in the low-precipitation NE region of the Olympics than in the SW.

Factors not incorporated in the current model or simulations could affect the predicted rate and extent of change in species distributions at high elevations because of a warmer

climate. Changes in the seasonal distribution of precipitation and temperature could have a large effect on vegetation, particularly if they affect patterns of snowpack accumulation, summer drought (Ettl and Peterson 1995b), or species phenology. Increased CO<sub>2</sub> concentration in the atmosphere could differentially affect growth rates of plant species (e.g., Körner 1994), and increased water-use efficiency of some species (e.g., Ward and Strain 1997) could alter competitive relationships, especially at drier sites. Fire could affect the rate and timing of vegetation response by removing current vegetation and "resetting" succession (Overpeck et al. 1990; Franklin et al. 1992; Neilson 1995; McKenzie et al. 1996; Lenihan and Neilson 1998) but would probably not affect forest and meadow ecosystem properties over sufficiently long time scales. Within the context of the ZELIG model, species composition, basal area, and biomass of a mature forest stand would not be greatly affected by an altered fire regime for long-term climatic-change scenarios, although stand characteristics would vary temporally during earlier successional stages.

Subalpine forests comprise a large proportion of the land area in parks and wilderness in the Pacific Northwest. Because dispersal and migration to other high-elevation sites is limited, altered forest composition and habitats may threaten the local survival of some species unless they are able to persist in refugia (Whitlock 1992; Peterson et al. 1993; Buckingham et al. 1995). While resource managers could use manipulative techniques (e.g., cutting trees) to modify these changes, it will be difficult to justify manipulation, because the general public may perceive such management activities as inappropriate. In any case, scientists and resource managers will need to work together to differentiate between the effects of "natural" ecological processes and human-induced, climatically driven processes on high-elevation forest ecosystems.

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