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POTENTIAL RESPONSE OF PACIFIC NORTHWESTERN FORESTS TO CLIMATIC CHANGE, EFFECTS OF STAND AGE AND INITIAL COMPOSITION

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Abstract. We used an individual-based forest simulator (a gap model) to assess the potential effects of anthropogenic climatic change on conifer forests of the Pacific Northwestern United States. Steady-state simulations suggested that forest zones could be shifted on the order of 500–1000 m in elevation, which could lead to the local extirpation of some high-altitude species. For low-elevation sites, species which currently are more abundant hundreds of kilometers to the south would be favored under greenhouse scenarios. Simulations of transient responses suggested that forest stands could show complex responses depending on initial species composition, stand age and canopy development, and the magnitude and duration of climatic warming. Assumptions about species response to temperature, which are crucial to the model's behaviors, were evaluated using data on species temperature limits inferred from regional distributions. The high level of within-species variability in these data, and other confounding factors influencing species distributions, argue against over-interpreting simulations. We suggest how we might resolve critical uncertainties with further research.

1. Introduction

The specter of anthropogenic climatic change has marshalled a great deal of research on ecosystem response to climate and on feedbacks between atmospheric and biospheric processes (Houghton *et al.*, 1990). Ecosystem attributes of concern include biodiversity (Peters and Darling, 1985), productivity and nutrient cycling (Agren *et al.*, 1991), as well as carbon and water balances which in turn could affect climate (Melillo *et al.*, 1990). Most assessments of climate-change effects have used steady-state methods (*e.g.*, Emanuel *et al.*, 1985). While this approach may be appropriate for global-scale concerns, for many ecosystems transient responses are of greater interest because of potentially complex interactions mediated by initial conditions and system-level feedbacks.

Forest gap models (Shugart and West, 1980) have been used frequently to

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examine the potential response of forests to climatic change (Solomon, 1986; Pastor and Post, 1988; Dale and Franklin, 1989; Overpeck *et al.*, 1990; Botkin and Nisbet, 1992). Although they are not without limitations (Urban, *in review*), gap models are appealing tools for modeling climate-change effects because they can simulate complex transient dynamics as well as steady-state conditions. For North American forests under the current suite of climate-change scenarios, gap models predict responses corresponding to northward migrations on the order of perhaps hundreds of kilometers.

Here we develop a specific case study, conifer forests of the Pacific Northwestern United States, to examine the range of complex responses that forests might exhibit due to initial species composition and age structure. Simulations suggest that stands in the same locale might show qualitatively different transient response depending on age and composition. We use data on regional species distribution to examine issues that might confound climate-change assessments, and identify scaling problems related to local and regional variability that undermine these efforts. Finally, we offer suggestions on how these issues might be resolved with further research.

2. Methods

2.1. *The Study Area*

Our primary study site within the Pacific Northwestern (PNW) region is the H. J. Andrews Experimental Forest, a 6400-ha watershed on the western slope of the Cascade Range (44° N, 122° W). The site ranges from 425–1620 m elevation, and topographic position (elevation, slope, and aspect) is an important control on vegetation pattern (Franklin and Dyrness, 1973; Zobel *et al.*, 1976; Hawk *et al.*, 1982). The region has mild, wet winters and dry summers. Low-elevation forests are dominated by Douglas-fir, western hemlock, and western redcedar (scientific names are in Table I). At elevations above 1050 m cold temperatures and winter snowpack are associated with a distinct change in forest composition: these upper elevations support a mixture of true firs (especially silver fir) and mountain hemlock.

2.1.1. *Regional Environmental Field*

A climatological database was collated from 320 meteorological stations west of the Cascade crest in California, Oregon, and Washington. These data were used to compute regressions to predict mean monthly temperatures based on site latitude, elevation, and distance from the coast. The regressions showed the expected pattern: the coastal influence resulted in warmer winters and cooler summers than at inland sites, and the overall lapse rate with elevation was slightly less than the standard (dry) adiabatic rate. All regressions were highly significant ($p < 0.01$) and accounted for 58–91% of the variance. Regressions were typically most predictive

TABLE I: Parameter estimates for Pacific Northwestern tree species used in simulations[1]

Species	A_{max}	D_{max}	H_{max}	G	L	M	$DD_{min, max}$	
Abies amabilis (Pacific silver fir)	600	200	75	180	1	2	118	1815
Abies concolor (white fir)	600	225	70	190	2	4	348	1828
Abies grandis (grand fir)	600	225	70	190	2	4	545	2193
Abies lasiocarpa (subalpine fir)	300	80	40	150	2	1	58	764
Abies procera (noble fir)	600	75	85	200	4	3	442	1408
Acer macrophyllum (big-leaf maple)	300	250	40	100	2	2	478	2361
Alnus rubra (red alder)	100	150	40	225	4	2	400	3080
Arbutus menziesii (Pacific madrone)	200	150	25	60	2	5	205	2643
Castanopsis chrysophylla (chinkapin)	300	100	40	160	2	5	876	2585
Calocedrus decurrens (incense cedar)	550	250	60	175	3	4	456	2388
Chamaecyparis lawsoniana (Port-orford-cedar)	600	350	60	150	2	1	325	1941
C. nootkatensis (Alaska-cedar)	3500	300	40	80	2	1	85	925
Lithocarpus densiflora (tanoak)	300	140	70	160	2	4	461	2952
Picea engelmannii (Engelman spruce)	600	200	55	100	2	2	375	1126
Picea sitchensis (Sitka spruce)	750	400	90	210	2	1	161	1938
Pinus contorta (lodgepole pine)	500	200	30	100	5	5	587	1054
Pinus jeffreyi (Jeffrey pine)	700	200	60	175	4	5	555	2149
Pinus lambertiana (sugar pine)	600	300	75	150	3	4	516	2312
Pinus monticola (western white pine)	600	200	75	190	3	3	176	1104
Pinus ponderosa (ponderosa pine)	700	200	75	175	4	5	600	2320
Populus trichocarpa (black cottonwood)	250	200	45	200	5	2	548	2012
Pseudotsuga menziesii (Douglas-fir)	1100	425	85	190	4	4	441	2012
Quercus garryana (Oregon white oak)	500	225	25	65	3	5	530	2430
Thuja plicata (western redcedar)	1500	350	60	150	2	3	292	2032
Tsuga heterophylla (western hemlock)	500	225	80	190	1	3	311	2030
Tsuga mertensiana (mountain hemlock)	800	225	35	90	1	3	183	1027

[1] Parameters are: A_{max}, maximum age (yr); D_{max}, maximum diameter (cm); H_{max}, maximum height (m); G, growth rate scaling constant; L, shade tolerance class (1 = very tolerant); M, relative drought tolerance (1 = very drought intolerant); $DD_{min, max}$, minimum and maximum degree-days

(had highest R^2) in the winter months and least predictive in the summer. A more localized set of regressions were used to predict monthly precipitation (provided by R. Neilson, U.S. EPA, Corvallis). These regressions were general to the western slope of the Cascade Range near 44° N latitude, and predicted a slight increase in precipitation with elevation.

These predicted data should be interpreted as an 'idealized' climate, in that the regressions do not resolve such important features as slope aspect effects or cold-air drainage. We realize that more sophisticated approaches are available for this purpose (*e.g.*, Running *et al.*, 1987), but we feel our approach was consistent with the spatial resolution and precision of available meteorological data. The shortcomings in our approach reflect a bias in the location of meteorological stations that is probably general to mountainous terrain: stations tend to be located on accessible sites, hence there are few high-elevation sites and existing sites are often on sites with biased microclimate (especially cold-air drainage). Moreover, we predicted lapse rates only for the western slope of the Cascades; inclusion of the eastern slope would have degraded predictions because of very different air mass conditions. Thus, our regressions provided useful estimates of monthly temperatures and precipitation for most sites within the general study area, but interpretation should be tempered by an appreciation of the scope and resolution of the data.

The regressed climate data were used as input for the forest gap model, which uses monthly temperature and precipitation to compute a temperature index and an index of soil moisture availability. These indices, computed for the range of sites represented within the study area, yielded an 'environmental field' of parameters to drive the forest model.

2.2. *Forest Gap Model*

The forest model used in this study was ZELIG (Urban, 1990), a recent reformulation of the basic JABOWA (Botkin *et al.*, 1972a, b) and FORET (Shugart 1984) models. Although gap models have been applied to a variety of forests and differ on some details, they all share the same basic structure and logic (reviewed in Shugart, 1984; Urban and Shugart, 1992).

Gap models simulate individual trees on a small model plot defined to correspond to the zone of influence of a canopy-dominant tree. The models use simple formulations to simulate demographic processes and environmental responses. As in most gap models, diameter growth in ZELIG is deterministic and defined by current size relative to a species-specific maximum. Species responses to light, soil moisture, soil fertility, and temperature are described by scaling functions that reduce tree performance under suboptimal conditions. The demographic processes of establishment and mortality are partly stochastic, so stand-level dynamics are estimated by aggregating the behaviors of a large number of model plots.

For applications concerned with climate change, a few model assumptions and algorithms are of particular importance. 'Climate' is defined in terms of air temperature and available soil moisture. Temperature is indexed as a growing-season heat sum (degree-days), which influences tree growth directly via a parabolic scaling function. Temperature also determines potential evapotranspiration (PET), and thus affects soil moisture. The soil water balance is simulated with a Thornthwaite estimate of PET (Thornthwaite and Mather, 1957) and a single-layer soil (Pastor and Post, 1986). Trees respond to soil water deficit by reducing their performance as a species-specific maximum drought tolerance is approached. Trees do not influence either temperature or available soil moisture; thus, climate is an extrinsic driver in the model.

2.2.1. *Species Parameters*

The regional climate regressions were used to estimate degree-days limits for tree species, given their minimum and maximum elevations at particular locations (latitude and distance from coast). Minimum and maximum elevations provided maximum and minimum degree-day estimates for each site. For most species, data from

5–20 locations were available. For our applications, we used locations within a *ca* 5° latitude zone encompassing Andrews Forest, from which we used the extreme degree-day values (*i.e.*, the lowest minimum heat sum and warmest maximum). Thus, these provided a local but generous estimate of these parameters. Our intention was to minimize the confounding effects of subspecific variation in species responses without being unduly site-specific in our choice of parameters (we return to this issue in section 4.2.).

Other species parameters (Table I) were estimated from a regional autecological review (Minore, 1979), other published summaries (Waring and Franklin, 1979), a gap model previously implemented for these forests (Dale and Hemstrom, 1984), and archived data from reference stands at Andrews. Tree growth rates were calibrated to empirical growth records from the study area.

2.3. *Simulations*

2.3.1. *Baseline Forests*

To represent the entire Andrews study area and beyond, we simulated the environmental field for the study area. In Monte-Carlo fashion, 1000 model plots were simulated using a uniform-random distribution of degree-day and soil moisture indices to represent the field, that is, all possible climate conditions within our database. The soil fertility parameter was set to a generous 15 Mg ha^{-1} yr^{-1}, forcing the model to emphasize climate effects. This version of the model does not simulate feedbacks between climate and nutrient cycling (*cf* Pastor and Post, 1988); our emphasis is on the implications of age structure and initial species composition under transient climatic change.

Simulations were run to steady-state (750 yr), and plot-level output from the model was processed to provide stand-level summaries in terms of the input parameters (degree-days and soil moisture). We should emphasize that our intent here was not to reproduce the fine-scale details of forests throughout the PNW region. Instead, the exercise of 'mapping' forests within the parametric field provided a rapid and graphic summary of how the model performed under a wide range of climatic conditions. This, in turn, indicated parametric domains where the model did not perform well (in terms of present-day forests), and so tempered our interpretations of climate-change scenarios.

2.3.2. *Climate Change Scenarios*

We used climate-change scenarios simulated as steady-state 2 ×: 1 × CO_2 experiments with general circulation models (GCM's). The GCM runs (provided by U.S. EPA-Corvallis) were by Goddard Institute of Space Studies (GISS; Hansen *et al.*, 1983) and Oregon State University (OSU; Schlesinger and Zhao, 1989), which represented the most extreme and most conservative scenarios for the PNW region as simulated by GCM's available to us (after Smith and Tirpak, 1989). The scenarios predict a moderate to substantial warming in temperature (1–5 °C per month), and a slight increase in precipitation with no change in seasonality. The GISS model predicts an increase in mean annual temperature of about 5 °C with a 23% increase in annual precipitation, while the OSU scenario predicts roughly a 2 °C warming with little change in precipitation.

2.3.3. *Transient Responses*

Given the size (age) structure of forests, transient responses to a changing climate can be quite complex (Davis and Botkin, 1985; Solomon, 1986). We designed a series of simulations to explore the range of transient responses for PNW forests.

Transient scenarios were organized using a factorial combination of initial degree-days (*i.e.*, elevation), magnitude and duration of change, and stand age. Warming was implemented as a linear 'ramp' in degree-days, specified by initial and ending values and the years over which the warming occurred. Stand age at which the transient began was specified as year 0 (no trees present), 200 (mature trees), or 500 (mixed ages). An initial degree-day value of 1300 represented the baseline condition at 1000 m elevation in Andrews, which are sites dominated by Douglas-fir and western hemlock. A 600 degree-day warming corresponded to the OSU greenhouse scenario, and a 1200 degree-day warming was predicted by the GISS model. For a site at 1500 m elevation, the baseline was 750 degree-days, and the OSU and GISS warmings were 500 and 1000 degree-days, respectively. Transients occurred over 50, 100, or 200 yr duration. Thus, there were 2 elevations, 2 magnitudes of warming, 3 transient durations, and 3 stand ages: a total of 36 possible cases in the factorial design. We considered only a sample of these cases. For comparison, reference forests were simulated with random climate with means and standard deviations corresponding to the baseline cases.

All simulations were of 50 model plots and output was aggregated to represent a 5-ha stand. Forest stature was represented in terms of total above-ground woody biomass. A composition index (CI) was defined as the weighted sum of relative woody biomass of each species multiplied by the mode of its degree-day curve. This index has a value equal to the degree-day driver if the forest tracks the driver in time. Thus, by comparing CI to the degree-day driver, we could assess lags in compositional response to the transient climate.

3. Results

3.1. *Baseline Forests*

Within the environmental field, the Andrew Forest represents a gradient from cold, wet high-elevation sites, to warm and seasonally droughty low-elevation sites. We computed contour plots of above-ground woody biomass and basal area of dominant species, so that forest stature and composition could be predicted for any site in the environmental field, given its degree-day and soil moisture indices. Attributes of the predicted forest were available as 'look up' values for all possible sites within the study area, within the resolution of our climate database.

These simulations adequately reproduce stand biomass (Figure 1) and species composition (Figure 2) for mid- to high-elevation forests at H. J. Andrews: the forests are dominated by Douglas-fir, western hemlock, and western redcedar. Lower-elevation forests are not well simulated by this parameterization of the model. For these sites, the model predicts forests dominated by incense-cedar, tanoak, and golden chinkapin, which are present but not dominant at Andrews; these species reach their greatest importance farther south. We did not attempt to verify our simulated environmental field in precise quantitative terms, but instead judged our results relative to qualitative summaries (*e.g.*, Zobel *et al.*, 1976; Hawk *et al.*, 1982). Still, Figures 1 and 2 are useful in indicating the parametric domains wherein model predictions are suspect, as we discuss below. We believe that the transient responses simulated by the model are useful and informative despite the model's bias at low elevations, but the compositional details of model predictions should not be overinterpreted. We emphasize mid- to high-elevation sites for the transient scenarios.

3.2. *Steady-State Responses to Climate Change*

Steady-state climate-change scenarios were straightforward translations of sites within the environmental field. Thus, given climate data predicted for a site, its new

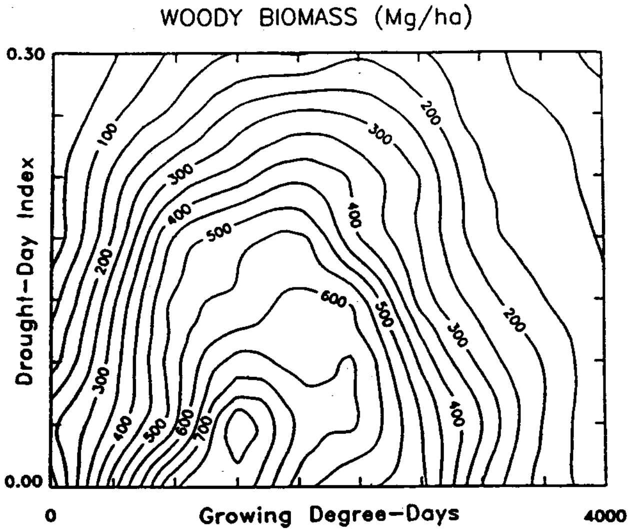


Fig. 1. Above-ground woody biomass (Mg/ha) simulated at steady state, as a function of growing degree-days and soil moisture. Model output from 1000 plots was contoured over the environmental field.

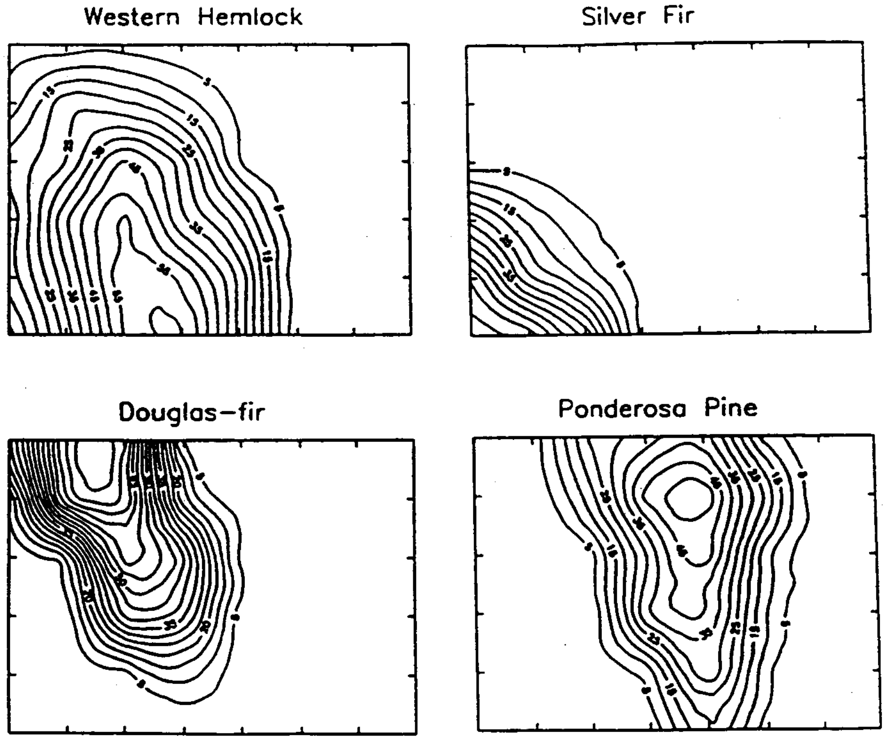


Fig. 2. Basal area (m^2/ha) of tree species which dominate selected domains of the environmental field (data contoured as in Figure 1).

degree-day and soil moisture indices associated the site with a forest that was already simulated as part of the environmental field.

Climate-change scenarios resulted in substantial translations of the elevation gradient representing the Andrews site (Figure 3). Temperature changes were more important than changes in precipitation; while the soil moisture index increased slightly under climate change (soils became drier), forests were still generally not moisture-limited. The conservative OSU scenario shifted the gradient the equivalent of *ca* 500 m in elevation; that is, a 1500-m site under the OSU scenario would correspond to a baseline site at 1000 m. The GISS scenario predicted that a site at 1500 m elevation would correspond to a baseline site at about 500 m. Importantly, both climate-change scenarios exceeded our species database for at least some sites. Species included in the model span temperatures to *ca* 3000 degree-days; Douglas-fir and western hemlock occur at temperatures less than 2500 degree-days. Moreover, both scenarios push the forests into parametric domains where model performance is suspect (*i.e.*, more than *ca* 2000 degree-days); the GISS scenario is mostly within this domain of uncertainty and should be interpreted with caution.

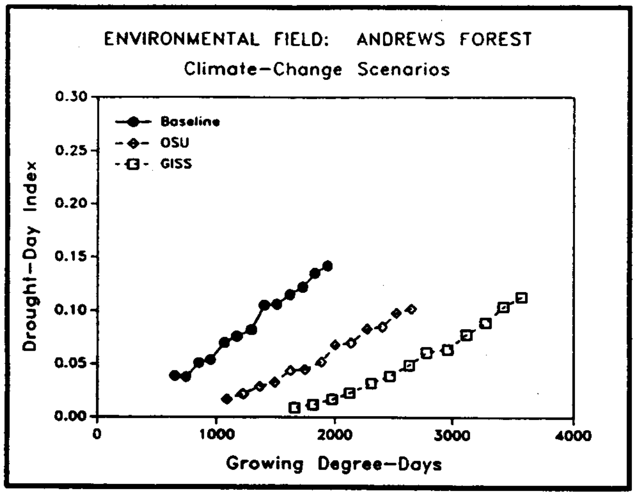
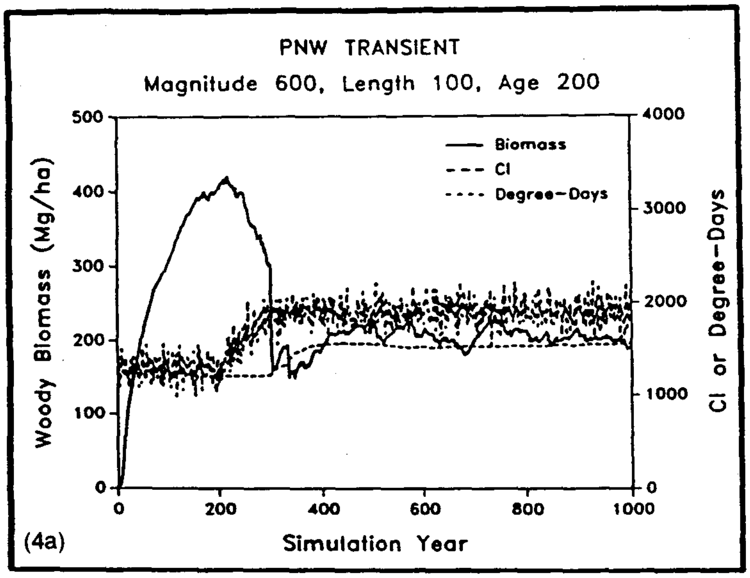


Fig. 3. H. J. Andrews Forest as a gradient within the environmental field, under current climate and two climate-change scenarios. The species database used in the model has a domain of less than 3000 degree-days.

3.3. *Transient Responses to Climate Change*

Sites under baseline conditions at 1000 m elevation in Andrews were dominated by Douglas-fir and western hemlock. The simulated forest was perfectly adjusted to the climate: the composition index equalled the degree-day parameter. A 600-degree-day transient in a mature forest elicited a strong pulse of mortality and a rapid change in composition (Figure 4a). But this forest never adjusted back to the degree-day driver because the local species could not span the new temperature range (the warmest degree-day midpoint is roughly 1750 for the species included in these simulations). Consequently, trees could not grow adequately and stand biomass did not recover; site productivity was temperature-limited. At the same elevation, a transient that began in year 0 of the simulation did not show strong episodic mortality; composition adjusted as trees were replaced gradually (Figure 4b). Again, the forest did not recover fully because the warmer climate exceeds the temperature limits of the local species. When this same transient was applied to a forest in year 500, the canopy was removed in a single mortality episode and the forest was replaced with a new cohort of better-adapted species – though again, the new climate was warmer than the local species could track (Figure 4c). The similarity of the even-aged stand and the mixed-age case emphasizes the importance of the canopy layer in governing transient forest response.

A transient warming of greater magnitude (corresponding to the GISS scenario) killed the established forest, with a precipitous drop in biomass (Figure 4d). Composition was forced to the limits of the species pool and only a marginal forest was supported. In this case the climate was beyond the parametric domain of the model.



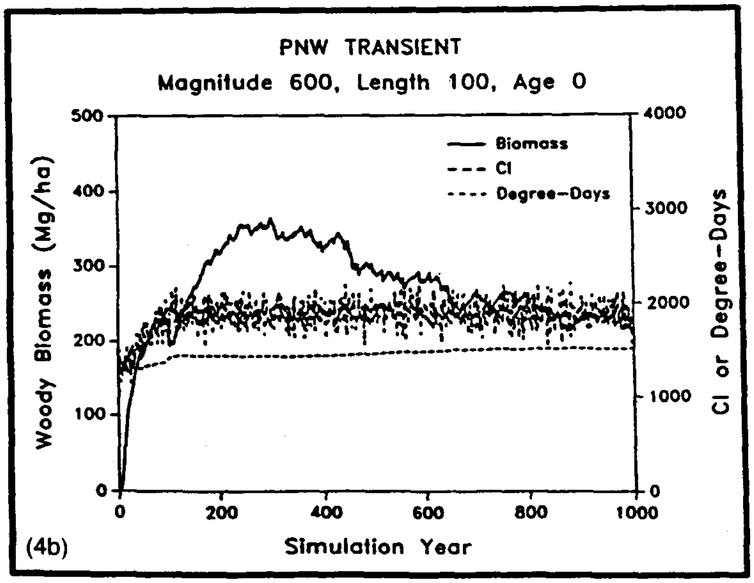
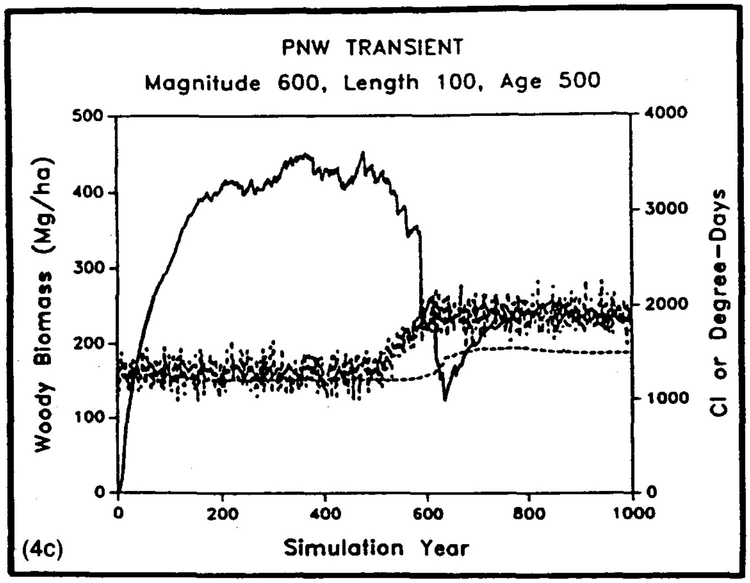


Fig. 4 (a) and (b). Transient responses of PNW forests at 1000 m elevation to climate change (see figure captions for details of transients).

The duration of the transient controlled the timing of the mortality episode. Relative to the initial case, a shorter transient induced mortality sooner while a longer transient deferred the episode (Figures 4e, 4f, *cf* 4a). The forest response



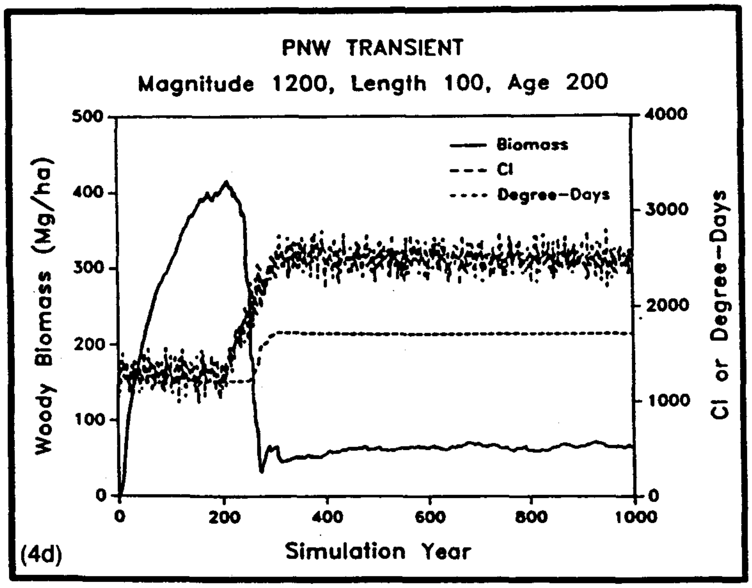
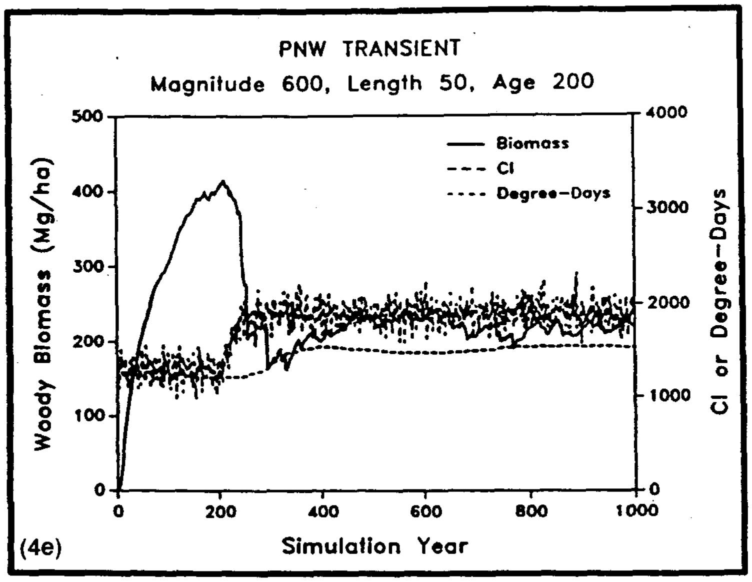


Fig. 4 (c) and (d). Transient responses of PNW forests at 1000 m elevation to climate change (see figure captions for details of transients).

was not triggered until the climate exceeded the temperature limits of the dominant trees growing on the site.

For the higher-elevation site, the baseline forest did not track its degree-day



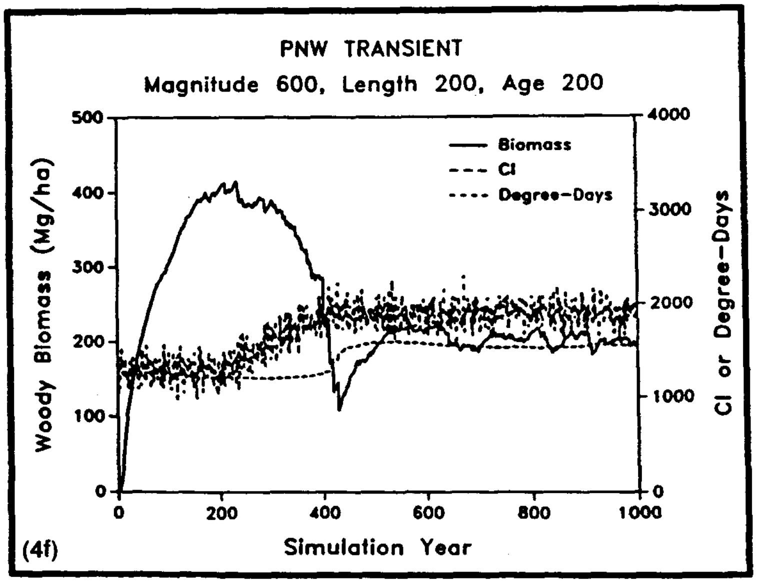


Fig. 4 (e) and (f). Transient responses of PNW forests at 1000 m elevation to climate change (see figure captions for details of transients).

driver: the site as somewhat cooler than the temperature mode of the dominant fir species, and so the composition index was greater than the degree-day driver. For a modest warming (500 degree-days), the site actually improved for these species, but a compositional shift then occurred because Douglas-fir and western hemlock were better competitors on the warmer site (Figure 5a). This replacement occurred gradually, and the forest adjusted to the warmer climate with only a small change in productivity. A more substantial warming (1000 degree-days) elicited a mortality episode and rapid replacement of the initial forest (Figure 5b). In this case the transition was from 'too cool' to 'too warm' and the forest could not adjust compositionally; forest productivity was also reduced.

4. Discussion

4.1. *PNW Forests and Climate Change*

The simulated forest corresponded adequately to forests in the study area, except at the lowest elevations simulated. On these sites, the model underpredicted the abundance of Douglas-fir and western hemlock and instead predicted a forest dominated by species whose importance is realized farther south on warmer sites. This error in the model reflects our uncertainty in estimating parameters for these species, for which limited local data were available – our parameter estimates probably reflect their performance farther south.

Steady-State Responses. Climate-change scenarios predicted within the environmental field are consistent with other regional assessments based on 'translating' current species distributions. When assessments are made relative to climate associated with the current distribution of PNW species, climate-change scenarios generally imply a translation equivalent to 500–1000 m elevation (hundreds of kilometers latitude), depending on the specific scenario (Franklin *et al.*, 1991). These translations, in turn, imply that current high-elevation firs would be displaced upslope; in many areas this displacement could be beyond the highest elevation of the Cascades and these species could be locally extirpated. Lower-elevation forests dominated by Douglas-fir and western hemlock would be predicted to expand their distributions upslope, while perhaps constricting their distributions somewhat at low elevations. In mountainous terrain, such a discplacement would imply a reduction in total area dominated by these forests. Both GCM scenarios simulated predict that low-elevation forests would suffer encroachment by species which are currently more abundant farther south (*e.g.*, incense-cedar, tanoak, and golden chinkapin). It might be supposed that climate-change scenarios might favor pine forests such as are found presently on the east slopes of the Cascades, but these are much drier forests and the climate-change scenarios do not predict a significant drying (GISS in fact predicts a wetter climate).

It should be noted that these scenarios are simple translations of present-day distributions; complexities of ecophysiological responses might lead to different responses (Bonan and Sirois, 1992), and other proximate factors governing species would also alter these predictions (Leverenz and Lev, 1987) (see also Urban, *in review*).

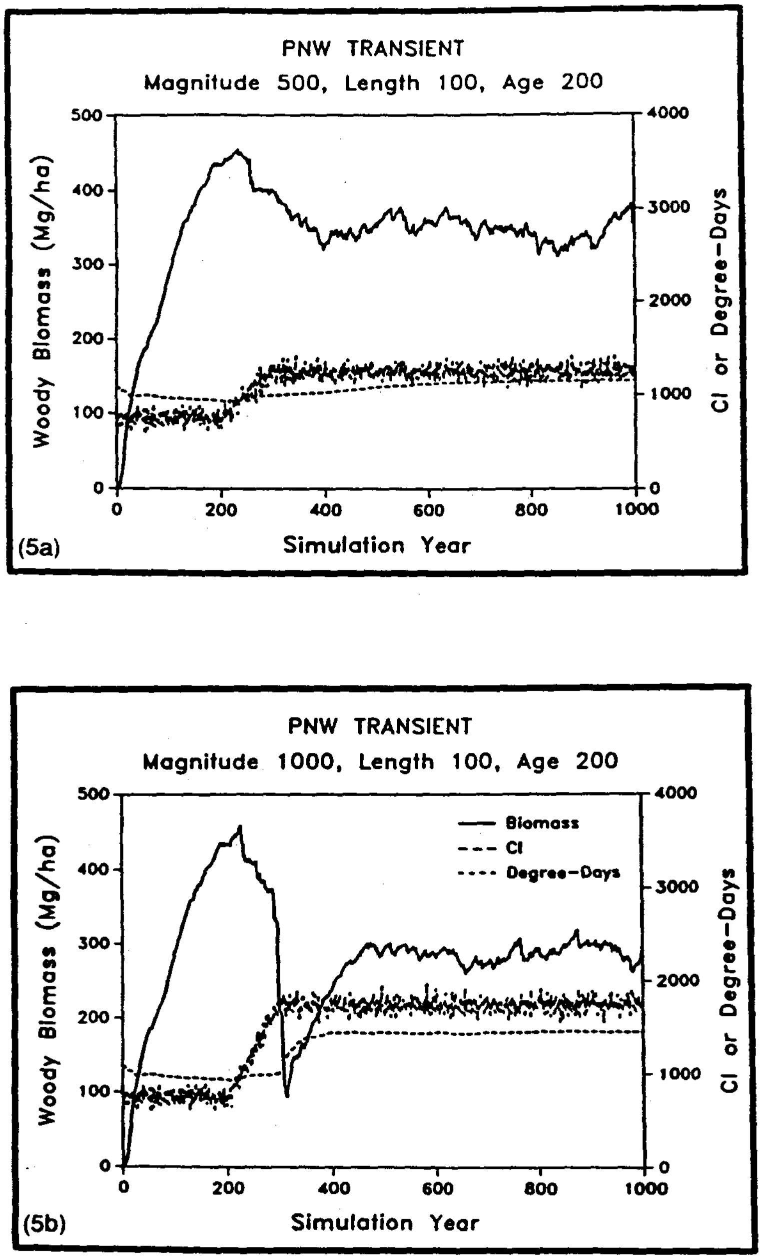


Fig. 5. Transient responses for PNW forests at 1500 m elevation (see figure captions for details).

Transient Responses. Forest age structure has an important effect on transient responses. Two aspects of age (actually size) structure contribute to this effect. Large (old) trees impart an inertia to forest response: rapid species replacement can occur only after the dominant canopy is removed; otherwise, replacement is gradual and mediated by competition. Size structure also affects mortality rates: very large (senescent) and very small (often suppressed) trees are more vulnerable than vigorous mid-size trees. Forests dominated by vigorously growing trees defer the transient response through their resilience to climatic stress. In some cases, canopy replacement may lag behind the changing climate by a few centuries.

Lagged responses can also be imparted by initial species composition – specifically, by the environmental tolerances of the dominant trees on a site. The 600 degree-day warming at 1000 m elevation was significant only because it exceeded the limits of Douglas-fir and hemlock dominating those sites (that is, that warming was sufficient to reach the extreme of their degree-day response curves). By contrast, a different threshold value would be significant for the higher-elevation site – specifically, a warming sufficient to reach the warm extreme of the degree-day curves for the firs which characterize those elevations.

The transient simulations emphasize that sites at various elevations within the same locale might begin to respond to a changing climate at different times, with lag times reflecting the temperature limits of species dominant at each elevation. At the same elevation (or for similar initial species composition), forest response would depend strongly on age structure, tree vigor, and canopy structure. Vigorous stands would respond later than senescent stands or those with multiple stressors. Stands with intact canopies would respond later than those with canopy openings that permitted rapid establishment of better-adapted species. Stands which suffered episodic loss of the canopy would be replaced more quickly than stands replaced via competitive interactions.

Finally, transient forest response would depend strongly on which species are present at a site. Urban *et al.* (1989) performed transient model experiments similar to those described here, but with a forest composed of hypothetical 'species' that completely and uniformly spanned all climatic conditions simulated. They found that transient responses were neatly predictable from initial stand conditions and the magnitude, duration, and timing of the transient. But when the local species pool does not perfectly span the range of anticipated climates (as seems to be the case in the PNW), transient responses are not so neatly predictable. For example, high-elevation species are apparently not well matched to their current distribution, which is cooler than their inferred temperature optima (see 4.2., below); this affected the timing and abruptness of forest response. Further, the climate predicted under GCM scenarios would be warmer than the optima of any species in the local pool; this was reflected in the failure of the simulated forests to adjust compositionally to the changing climate.

4.2. *Uncertainties and Confounding Factors*

Forest gap models are appealing tools for exploring climate-change scenarios because they attend the age structure and species-specific environmental responses that dictate the complexities of transient responses. Yet the models are far from perfect for these applications (Urban, *in review*). Within the model, forest response to climate change is determined by a rather small set of model assumptions and procedures for estimating parameters.

The temperature response in the model imparts a great deal of sensitivity to the model when temperatures approach the limits for a species. Temperature limits for PNW species are subject to three sources of uncertainty. Limits estimated from observed elevational limits are confounded by other biogeographic constraints: as one moves north along the coast, many species occur down to sea level; to the south, minimum temperatures for some species are artificially bounded by mountain tops. Similarly, other proximate factors may govern species distributions; upper elevation limits of some PNW species may be related to snow depth as well as temperature itself (Zobel *et al.*, 1976; Hawk *et al.*, 1982; Leverenz and Lev, 1987). Thus, temperature limits estimated from multiple locations are highly variable. Indeed, there is more *within*-species variability for some species than occurs *between* other species (Figure 6). This intraspecific variation likely includes genetic variation within the species (Lavender and Overton, 1972), a complexity not included in the model. Finally, inferring species tolerances from observed distribution can be confounded by competitive interactions that displace species from their physiological optima (Huston and Smith, 1987; Smith and Huston, 1989; Austin

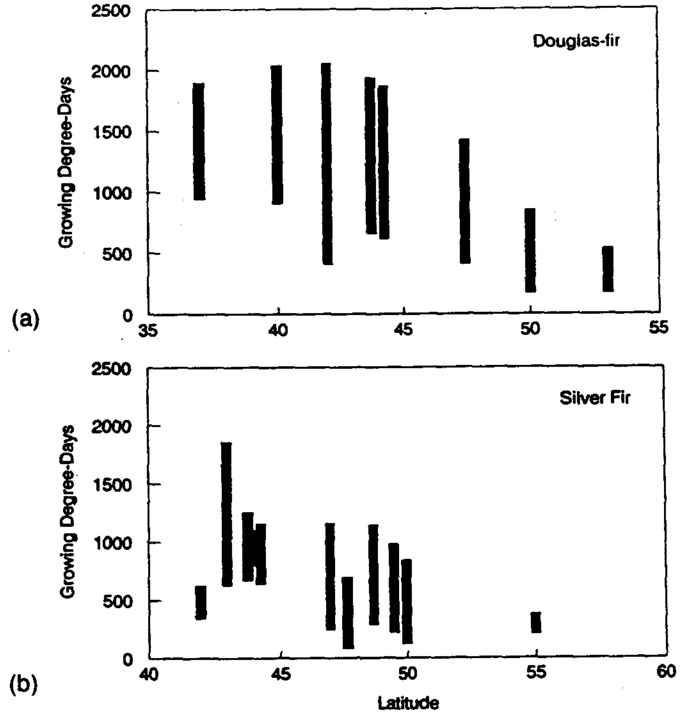


Fig. 6. Geographic variation in temperature limits of (a) Douglas-fir and (b) silver fir, as inferred from minimum and maximum elevations of occurrence.

and Smith, 1989). In our simulations for the PNW, competition with Douglas-fir and hemlock at lower elevations displaces the true firs to sites cooler than their optima. We used generous estimates of temperature limits to minimize the effects of these uncertainties. Regardless of the effectiveness of our attempt to mitigate current shortcomings in the temperature response, this remains an important area for model improvement (see also Graumlich, 1989; Overpeck *et al.*, 1990; Bonan and Sirois, 1992).

The high level of intraspecific variation in temperature limits as estimated from different locations implies that simulation results would differ somewhat if estimates from other locations were used. We used temperature limits from the vicinity of H. J. Andrews, which imply 'local' genetic variants. Thus, our simulations implicitly assme that there is no immigration of better-adapted variants (*i.e.*, from farther south) during the course of the simulations. The simulation results could vary considerably depending on alternative assumptions about the genetic heterogeneity of regional populations and species migration rates (Davis *et al.*, 1986; Urban, *in review*). Indeed, we encountered a frustrating corollary of this, which might be termed a 'local *versus* regional' modeling dilemma: a model calibrated to reproduce forests at a specific site cannot also simulate a broader range of regional forests, while a model calibrated to reproduce broad regional patterns does not simulate the details of forests at any given site very well. We believe this (usually unreported) problem in model calibration is a manifestation of local and regional heterogeneity in species, and this issue should be addressed directly in future studies.

Finally, climate-mediated disturbances could have important influences on the nature and timing of forest response to a changing climate (Solomon *et al.*, 1984; Overpeck *et al.*, 1990). Disturbances which remove the canopy would allow forests to adjust more quickly to changing climate than could forests with intact canopies. Franklin *et al.* (1991) have anticipated the importance of altered fire regimes in PNW forests, but we currently lack the means to make quantitative predictions about how a changing climate would affect the regional fire regime. There are models of forest response to fire (*e.g.*, Kercher and Axelrod, 1984; Keane *et al.*, 1990), but these models do not simulate climate effects on fire.

5. Conclusions

Age structure and initial species composition can have profound effects on the transient responses of forests to a changing climate, by influencing the timing of canopy replacement and whether this occurs gradually through competitive displacement or rapidly via synchronous mortality. Our results imply that stands in the same geographic locations, but differing in age or species composition, could show qualitatively different transient responses to a changing local climate. Some sites might appear to improve under climate change while other sites were degraded; some stands might show a response within decades while other stands might appear unchanged for centuries. Likewise, fine-scale heterogeneity due to edaphic variation or microclimate could effect profound local variation in forest response.

While we have identified several issues of uncertainty in our analyses, we believe that the qualitative effects of age structure and initial composition on transient responses are robust to these uncertainties. Better estimates of temperature and moisture responses, local and regional variation in species traits, and species migration rates would alter details of the simulated responses, and would improve confidence in our ability to predict forest response to a changing climate.

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