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## Assessing the past and future distribution and productivity of ponderosa pine in the Pacific Northwest using a process model, 3-PG

Nicholas C. Coops<sup>a,\*</sup>, Richard H. Waring<sup>b</sup>, Beverly E. Law<sup>c</sup>

<sup>a</sup> CSIRO Forestry and Forest Products, Private Bag 10, Clayton South 3169, Vic., Australia

<sup>b</sup> College of Forestry, 326 Richardson Hall, Oregon State University, Corvallis, OR 97331, USA

<sup>c</sup> College of Forestry/College of Oceanic and Atmospheric Sciences, 328 Richardson Hall, Oregon State University, Corvallis, OR 97331, USA

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### Abstract

Climate variability at decadal scales influences not only the growth of widely distributed species such as *Pinus ponderosa*, but also can have an effect on the timing and severity of fire and insect outbreaks that may alter species distributions. In this paper, we present a spatial modelling technique to assess the influence of climatic variability on the annual productivity of *P. ponderosa* in the Pacific Northwest (PNW) of North America over the past 100 years and infer how a sustained change in climate might alter the geographic distribution of this species across defined ecotones. Field observations were used to establish criteria for *P. ponderosa* dominance including: (1) maximum summer leaf area index (LAI), ranges between 1.5 and 2.5; (2) 80% of available soil water is depleted during summer months; and (3) soil water will return to full capacity at least once during the year. Where these three criteria were not met, eventual replacement of *P. ponderosa* would be predicted. We utilized a simple physiological model, Physiological Principles for Predicting Growth (3-PG) to predict annual variation in LAI from climatic data provided by the Oregon Climate Service over the period from 1900 to 2000 and from broad scale 0.5°-spatial resolution future climate projections produced by the Hadley Climate Center, UK. From these simulations we produced a series of maps that display predicted shifts of zones where ponderosa pine might be expected to contract or expand its range if modeled climatic conditions at annual and decadal intervals were sustained. From the historical simulations, the most favorable year for pine dominance was 1958 and the least favorable, 1924. The most favorable decade was in the 1900s and the least favorable in the 1930s. The future predictions indicate a reduction in the current range of the *P. ponderosa* type along the western Cascade Range however, an increase along the east side and inland PNW. The model predicts that pine dominance should increase between 5 and 10% over the next century, mainly in inland Oregon, Idaho, and Washington.

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**Keywords:** Ecosystem and process models; Limiting factors; Climate change; Hadley; VEMAP-2; Process models

\* Corresponding author. Present address: Department of Forest Resource Management, 2424 Main Mall, University of British Columbia, Vancouver, Canada V6T 1Z4. Tel.: +1 604 822 6452; fax: +1 604 822 9106.

E-mail address: [Nicholas.coops@ubc.ca](mailto:Nicholas.coops@ubc.ca) (N.C. Coops).

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## 1. Introduction

Changes in historical and future climate are likely to alter the structure of both natural and managed plant communities, which has implications to biodiversity, carbon sequestration, and the exchange of greenhouse gases. In much of the western portion of the United States, natural vegetation is highly responsive to slight changes in precipitation. Small, progressive changes in the annual water balance can result in replacement of forests by shrublands, grasslands, or desert vegetation. Even within a region with extensive forest cover, such as the Pacific Northwest US, ecotones exist where currently widely distributed and valued forest types could be replaced by less productive, less valued species. In this regard, we investigate the growth response of the widely distributed ponderosa pine forest type (*Pinus ponderosa* Doug. ex Loud.).

Ponderosa pine represents a major forest type in the PNW region (Fig. 1) of the United States; it occurs in nearly pure stands in a 15–30 km wide band along the eastern flanks of the Cascade Mountains in Oregon and Washington where annual precipitation is generally between 300 and 800 mm. Historically, ground fires at 8–20 year intervals maintained the *P. ponderosa* forest type free of other potential competing conifers. On more moist sites, however, *P. ponderosa* occurs in a mixture with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.), and other conifers (Franklin and Dyrness, 1973). On more arid sites, juniper (*Juniperus occidentalis* Hook.) and/or sagebrush (*Purshia tridentata* (Pursh) D.C.) replace ponderosa pine as drought becomes more severe and fires more frequent (Franklin and Dyrness, 1973).

Today, the *P. ponderosa* type occupies an extensive range, larger than that of any other related species in

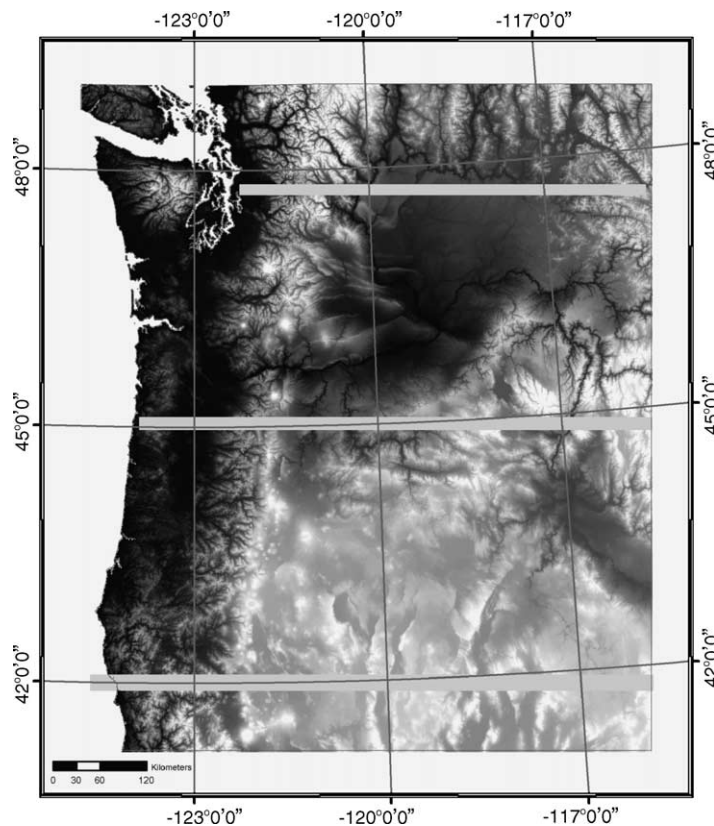


Fig. 1. Extent of Pacific Northwest study area displayed with a Digital Elevation Model (DEM) and three transect locations at 42°, 45°, and 48°N).

North America. Yet it maintains an ecologically precarious position in the PNW, constrained to the east by more arid conditions that favor juniper woodlands, to the west by mountains with more moderate precipitation that favors a mixture of other conifers, and by elevation where heavy snow loads can damage pine branches (Waring et al., 1975). Because of a century of fire suppression, encroachment of fir into more fire-resistant pine has occurred on the western edge of the distribution. Ponderosa pine, along with Douglas-fir, has served as a basis for evaluating growth potential across a wide range of forests in the western United States (e.g., Waring et al., 2002). The ecological distributions of these two species and their relations with other forest types are therefore well described (Franklin and Dyrness, 1973). The relative importance of various environmental factors on the growth and distribution of ponderosa pine has also been quantified in some parts of its range, although measurements were restricted to less than a decade (see special issue on “The ponderosa pine ecosystem and environmental stress: past, present, and future” published in *Tree Physiology*, volume 21, 2001).

Ecologically- and physiologically-based models have been applied to predict forest growth potential under historical and current climatic conditions and these predictions have been extended to incorporate possible future climatic scenarios (Bachelet et al., 2001; Coops and Waring, 2001a). Recently, process models have been employed to estimate annual variation in growth over decades into the past and future (Hunt et al., 1991; Coops and Waring, 2001a). We sought the opportunity to extend the application of process models to evaluate a past and future century of climatic variation and to display the results spatially to reflect conditions that should have increased or decreased the production of the ponderosa pine type in the past or will do so in the future.

To accomplish these objectives, we used field-based observations from a range of *P. ponderosa* datasets to define the extent of drought and the range of LAI typical for the ponderosa pine type, similar to the rule-based approach described by Neilson et al. (1992). We then employed a simple (Physiological Principles for Predicting Growth (3-PG)) physiological model to generate estimates of LAI and water use over the previous and current century and display these results spatially in terms of the potential area that favored

or disfavored the dominance of the ponderosa pine type.

## 2. Methods

To meet our stated objectives, we needed to acquire climatic data from 1900 to 2100 in a form appropriate to drive a process model and at a spatial resolution sufficient to discriminate variable growth responses where the ponderosa pine type currently dominates. In this section, we describe the data sets, their transformations, and use in the 3-PG process model.

### 2.1. DAYMET fine scale spatial climate coverages (1980–1997)

As a spatial base we obtained eighteen years (1980–1997) of averaged mean monthly data for precipitation, minimum and maximum temperature, frost occurrence, and short wave radiation from the DAYMET US climatological database (Thornton et al., 1997; Thornton and Running, 1999) for the PNW (<http://www.daymet.org>). At 1 km, these layers were at a sufficiently fine spatial resolution for model predictions.

### 2.2. Climatic data (1900–1995)

The National Climatic Data Center (NCDC) separates its point source long-term weather data summaries into defined eco-regions within the United States. The Oregon Climate Service (OCS) provided us with point source summarized monthly precipitation (mm) and temperature records (°C) averaged within those eco-regions that fall within state boundaries for the period from 1900 to 1995 (<http://www.ocs.orst.edu>). To provide estimates of mean monthly daytime vapor pressure deficits ( $D$ ) required for modeling, we assumed that the saturated vapor pressure (SVP) of the atmosphere is equivalent to that at the minimum average monthly temperature, that the maximum deficit represents the difference in SVP between mean monthly temperature extremes, and that the monthly mean daytime  $D$  was set at 0.67 of the latter value, based on meteorological measurements at a ponderosa pine AmeriFlux site (Waring, 2000).

To generate monthly estimates of meteorological variables at 1-km spatial resolution for the period from 1900 to 2000, we took long-term monthly weather data acquired for the eco-region most representative of the current *P. ponderosa* distribution in central Oregon, and established a relationship between each set of averaged monthly temperature and precipitation with the DAYMET 1 km resolution data for 18 years, 1980–1997. The long-term records lacked information on temperature extremes necessary to derive additional meteorological variables required to run the process models (described below). We therefore used the short-term DAYMET estimates of the frequency of subfreezing days each month, and monthly estimates of short-wave radiation continually over the 1900–1995 period (Running et al., 1987; Waring, 2000). From eddy-flux covariance analyses at intensively monitored pine forests in Oregon we had evidence that summertime transpiration rates were essentially constant at 2 mm/day over a fair range in day-time  $D$  (Law et al., 2000b), that the frequency of frost is high only during months when mean temperatures are suboptimal for photosynthesis, and that short-wave radiation does not vary significantly annually, even in years when precipitation ranged from <200 to 800 mm (Law et al., 2001b). We, thus, justify our substitution of these three meteorological variables from the averaged monthly values attained from the DAYMET data set into the long-term climatic data set. Any change in simulated growth of *P. ponderosa* over a century, therefore, reflects only seasonal variation in precipitation and suboptimal temperatures.

### 2.3. Climatic data (1995–2100)

The future climate estimates utilized in this study were developed by the vegetation-ecosystem modeling and analysis project (VEMAP) in conjunction with the Hadley Center (HADCM2) (Mitchell et al., 1995; Johns et al., 1997) whose goals include development of a common data set for driving models and specifically include a high-resolution topographically adjusted climate history and future projections on a  $0.5^\circ$  geographic grid. Phase 2 (transient dynamics) of the program projected transient forcing functions across the USA (Kittel et al., 1997; Schimel et al., 2000).

The VEMAP-2 dataset, developed with the Hadley Center, provides monthly estimates from 1994 to 2100

of minimum and maximum temperature ( $^\circ\text{C}$ ), precipitation (mm), vapor pressure (mbar), and solar radiation ( $\text{MJ m}^{-2} \text{ day}^{-1}$ ) (Mitchell et al., 1995; Johns et al., 1997). These data are available via Climate Impacts LINK Project, Climatic Research Unit, University of East Anglia. To downscale the Hadley climate forcing scenarios to 1-km spatial resolution, we again compared the  $0.5^\circ$  ( $\sim 50 \text{ km} \times 50 \text{ km}$ ) dataset to  $1 \text{ km}^2$  resolution DAYMET climate data (Thornton et al., 1997; Thornton and Running, 1999). To convert the Hadley climate forcing scenario, we utilized a residual correction approach. For each month, we determined the difference between estimates made at the two different scales at a series of intersections on a user-defined grid. From these differences, a spline surface was generated that smoothly interpolated the residual at a predefined spatial resolution. Specifically the approach involves five steps; first, the monthly 1 km 18 year average DAYMET surfaces were smoothed using a simple local average to simulate 50-km spatial resolution coverages (12 for each climate variable). A point coverage of each grid center of the  $0.5^\circ$  VEMAP-2 coverage was then developed and climate data for each variable for each month from 1995 to 2100 were extracted. Using the same point coverage, the 50 km smoothed DAYMET monthly values for each variable were also extracted and a residual surface at 1-km spatial resolution was then fitted (using a spline function) to the points to create a 1 km surface of differences between the VEMAP-2 monthly predictions and the long-term 1 km DAYMET values. Finally, the residual surface was then subtracted from the relevant DAYMET 1 km surfaces for each month 1995–2100 for each variable.

### 2.4. 3-PG model description

Landsberg and Waring (1997) developed a physiologically based forest growth model called 3-PG based on a number of established biophysical relationships and constants. The model simplifies application because it requires only a few parameters that can be derived from literature or from field measurements. The monthly time step of the model requires average daily short-wave incoming radiation for each month, daily mean vapor pressure deficits ( $D$ ), temperature extremes, total monthly precipitation, and estimates of soil water storage capacity and soil fertility (Fig. 2).

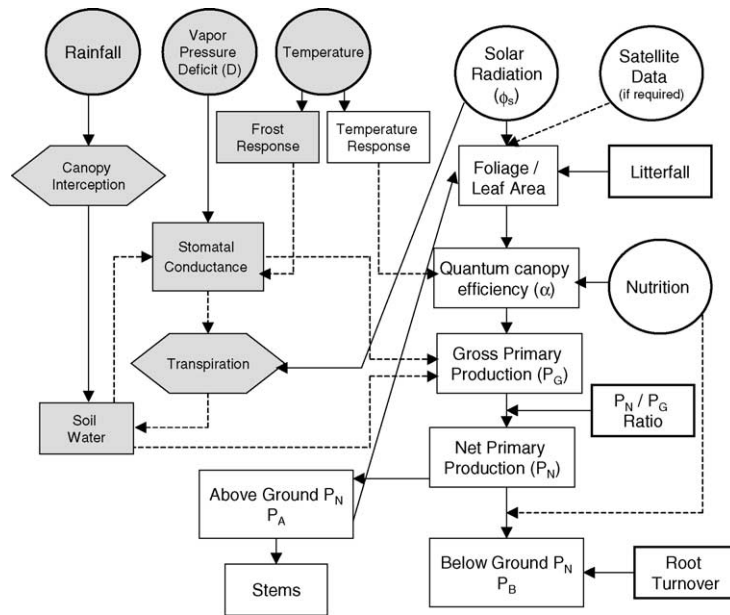


Fig. 2. Structure of the 3-PG model showing driving variables (circles) and how they affect processes controlling growth and the site water balance.

Absorbed photosynthetically active radiation (APAR) is estimated from global solar radiation and LAI; the utilized portion (APAR<sub>u</sub>) is calculated by reducing APAR by an amount determined by a series of modifiers that take values between 0 (system ‘shut-down’) and 1 (no constraint) to limit gas exchange via canopy stomatal conductance (Landsberg and Waring, 1997). The modifiers include: (a) high averaged day-time *D*; (b) the frequency of subfreezing conditions, and (c) soil drought. Limitations on APAR<sub>u</sub> are imposed each month by the modifier with the lowest value. Drought limitations are imposed as a function of soil texture when the total monthly precipitation and soil water supply is significantly less than transpiration estimated with the Penman–Monteith equation. Gross primary production (PG) is calculated by multiplying APAR<sub>u</sub> by a canopy quantum efficiency coefficient ( $\alpha$ ), with a maximum value set by the soil fertility ranking and reduced monthly when mean temperatures are suboptimal for photosynthesis and growth. A major simplification in the 3-PG model is that it does not require detailed calculation of respiration from knowledge of root turnover, but rather assumes that autotrophic respiration ( $R_a$ ) and total net primary production ( $P_N$ ) in temperate forests are

approximately fixed fractions (0.53 and 0.47, S.E. =  $\pm 0.04$ ) of  $P_G$  (Landsberg and Waring, 1997; Waring et al., 1998; Law et al., 2000a). The model partitions  $P_N$  into root and aboveground biomass. The fraction of total  $P_N$  allocated to root growth increases from 0.25 to 0.6 as the ratio APAR<sub>u</sub>/APAR decreases from 1.0 to 0.2. Under more favorable climatic conditions, the fraction of photosynthate allocated to roots increases with infertility of the soil (Landsberg and Waring, 1997).

All ecosystem models are simplified versions of reality. The choice of which process based model to utilize is dependent upon their input and output parameters, minimum spatial and temporal units of operation, maximum spatial extent and time period of application (Nightingale et al., 2004). In addition, the scale at which the model operates (leaf-tree, plot-stand, regional, and ecosystem levels) is also critical, with model complexity generally decreasing as the time-step and spatial extent of model operation increases (Nightingale et al., 2004). Given the limited amount of climatic data available over the last century and projections into the next, as well as the large spatial scale at which we are operating, we believe a monthly time step, stand-level, process based model is an appropriate

choice for our analysis. Within this specification a number of process-based models exist (see Nightingale et al., 2004 Fig. 1 for details; HYBRID (Friend et al., 1997), FOREST-BGC (Running and Coughlan, 1988), BIOME-BGC (Running and Hunt, 1993) amongst others). However, three features that together distinguish 3-PG from all other process-based models (some share one feature) include (Landsberg, 2003):

- The simplifying assumption that respiration is a fixed fraction of gross photosynthesis (Waring et al., 1998; Gifford, 2003). This simplification removes the difficulty in predicting belowground growth, protein turnover rates, and separating carbon dioxide generated by microbial activity.
- Detailed forestry inventory variables are readily predicted by the 3-PG model (such as standing volume) and indirectly support its simplifying assumptions. Confidence in the 3-PG structure and function is gained as it accurately predicts measured change in LAI, litterfall, stocking density, basal area, and mean tree diameters, in addition to annual growth in managed and unmanaged stands (Landsberg et al., 2003).
- Provides a satellite mode (3-PGS, Coops et al., 1998) that allows spatial predictions and direct comparisons with currently observed satellite-derived estimates of LAI and site index to the capacity of land to grow a specific tree species.

### 2.5. Modeling LAI and water stress

Products of the 3-PG model include predictions of LAI and plant water stress. In 3-PG, LAI is determined from predicted foliage mass and knowledge of specific leaf area ( $\text{m}^2 \text{kg}^{-1}$ , see Table 1). The model calculates a soil water balance as the difference between total monthly transpiration, residual soil water supply, and monthly precipitation. The model is initialized with soil water content equal to half of the maximum available water ( $\theta$ , mm) in the rooting zone, where  $\theta$  is dependent on the water holding characteristics of the soil and rooting depth of the trees (Landsberg and Waring, 1997). The moisture ratio ( $r\theta$ ) for the stand is calculated as  $r\theta = (\text{current soil water content} + \text{water balance})/\text{available water}$ . The water balance in any month will be reduced from that in the previous month if transpiration exceeds precipitation and vice versa. If the numerator of the expression for  $r\theta$  exceeds  $\theta$ , it is set to  $\theta$ ; i.e., the excess

water is assumed to have run off or drained out of the system. If it is negative,  $r\theta = 0$  (Landsberg and Waring, 1997).

### 2.6. Parameterization of 3-PG for *P. ponderosa*

Law et al. (2000a) undertook an evaluation of the 3-PG and PnET-II (Aber et al., 1995) models to examine their abilities to estimate gross photosynthesis and net primary production of *P. ponderosa*. They defined a number of parameters required for the 3-PG model (presented in Table 1) and conducted a sensitivity analysis of selected variables. They concluded that variations in soil fertility ranking resulted in <1% change in annual gross photosynthesis as fertility makes little difference in the harsh climate when *P. ponderosa* dominates; in most months, other environmental factors more strongly limit photosynthesis and carbon allocation (Law et al., 2000a).

## 3. Modeling approach

### 3.1. Rule-based definition of ponderosa pine range

The importance of the *P. ponderosa* pine type in the PNW has resulted in a large number of studies that define how various environmental factors affect pine growth and distribution. Field observations of *P. ponderosa* document that across the Deschutes National Forest in east-central Oregon, soil drought is minimal through winter months when soil water supply is at capacity. In the spring, as temperature and radiation increases, and precipitation decreases, monthly water use by the vegetation draws down soil water supply, reaching the minimum available at the end of summer. This characteristic of the pine type with near full winter water storage and a minimum, but not exhausted water supply, in summer is typical (Irvine and Law, 2002) and has been previously documented by Running (1994) who found greater than 50% available soil water exhausted at pine sites in late summer as evidence by correspondence between measured predawn water potentials and simulated water balance with FOREST BGC. In contrast, the juniper woodland type experiences predawn water potentials less than  $-2.0 \text{ MPa}$  by July (indicative of extreme drought) whereas the mixed conifer type does not

Table 1  
3-PG Model functions and parameters used for ponderosa pine (after Law et al., 2000a)

| Variable  | Name         | Units              | Value  |
|---|--------------|--------------------|--------|
| <b>Allometric relationships and partitioning</b>          |              |                    |        |
| Foliage: stem partitioning ratio @ $D = 2$ cm             | pFS2         | –                  | 1.2745 |
| Foliage: stem partitioning ratio @ $D = 20$ cm            | pFS20        | –                  | 0.5132 |
| Constant in the stem mass vs. diameter relationship       | StemConst    | –                  | 0.0046 |
| Power in the stem mass vs. diameter relationship          | StemPower    | –                  | 2.97   |
| Maximum fraction of NPP to roots                          | pRx          | –                  | 0.8    |
| Minimum fraction of NPP to roots                          | pRn          | –                  | 0.25   |
| <b>Temperature modifier (fT)</b>                          |              |                    |        |
| Minimum temperature for growth                            | Tmin         | °C                 | –2     |
| Optimum temperature for growth                            | Topt         | °C                 | 20     |
| Maximum temperature for growth                            | Tmax         | °C                 | 40     |
| <b>Frost modifier (fFRost)</b>                            |              |                    |        |
| Days production lost per frost day                        | kF           | Days               | 1      |
| <b>Litterfall and root turnover</b>                       |              |                    |        |
| Maximum litterfall rate                                   | gammaFx      | 1/month            | 0.021  |
| Litterfall rate at $t = 0$                                | gammaF0      | 1/month            | 0.001  |
| Age at which litterfall rate has median value             | tgammaF      | Month              | 36     |
| Average monthly root turnover rate                        | Rtturn       | 1/month            | 0.04   |
| <b>Conductance</b>  |              |                    |        |
| Maximum canopy conductance                                | MaxCond      | M/s                | 0.02   |
| Maximum stomatal conductance                              | StomCond     | M/s                | 0.005  |
| Defines stomatal response to VPD                          | CoeffCond    | 1/kPa              | 0.05   |
| Canopy boundary layer conductance                         | BLcond       | M/s                | 0.14   |
| <b>Fertility effects</b>                                  |              |                    |        |
| Soil fertility rank (0–1)                                 |              | –                  | 0.4    |
| Value of 'm' when FR = 0                                  | m0           | –                  | 0      |
| Value of 'fNutr' when FR = 0                              | fN0          | –                  | 1      |
| <b>Soil water modifier (fSW)</b>                          |              |                    |        |
| Soil water holding capacity                               |              | mm                 | 170    |
| Moisture ratio deficit for $f_q = 0.5$                    | SWconst      | –                  | 0.7    |
| Power of moisture ratio deficit                           | SWpower      | –                  | 9      |
| <b>Stem numbers</b>                                       |              |                    |        |
| Initial   | Initial      | trees/ha           | 1000   |
| Max. stem mass per tree @ 1000 trees/hectare              | wSx1000      | kg/tree            | 300    |
| <b>Age modifier (fAge)</b>                                |              |                    |        |
| Maximum stand age used in age modifier                    | MaxAge       | years              | 400    |
| Power of relative age in function for fAge                | nAge         | –                  | 4      |
| Relative age to give fAge = 0.5                           | rAge         | –                  | 0.95   |
| <b>Canopy structure and processes</b>                     |              |                    |        |
| Specific leaf area at age 0                               | SLA0         | m <sup>2</sup> /kg | 4.2    |
| Specific leaf area for mature leaves                      | SLA1         | m <sup>2</sup> /kg | 4.2    |
| Age at which specific leaf area = (SLA0 + SLA1)/2         | tSLA         | years              | 2.5    |
| Extinction coefficient for absorption of PAR by canopy    | k            | –                  | 0.5    |
| Age at canopy cover                                       | fullCanAge   | years              | 0      |
| Proportion of intercepted rainfall evaporated from canopy | Interception | –                  | 0.1    |
| Canopy quantum efficiency                                 | alpha        | molC/molPAR        | 0.045  |
| <b>Branch and bark fraction (fracBB)</b>                  |              |                    |        |
| Branch and bark fraction at age 0                         | fracBB0      | –                  | 0.15   |
| Branch and bark fraction for mature stands                | fracBB1      | –                  | 0.15   |
| Age at which fracBB = (fracBB0 + fracBB1)/2               | tBB          | years              | 1.5    |
| <b>Various</b>  |              |                    |        |
| Ratio NPP/GPP   | Y            | –                  | 0.47   |
| Basic density   | Density      | t/m <sup>3</sup>   | 0.4    |

experience drought stress  $<-1.5$  MPa in late summer (Waring, 1969).

The LAI of forests containing *P. ponderosa* ranged from about 1 to 3 (one-sided leaf area, mean 2.0) (Van Tuyl et al., submitted for publication) with the lowest values associated with regenerating or thinned stands of pine and the highest values associated with a mixture with Douglas-fir and coniferous species (Law et al., 2001a; Law et al., 2001c). Across Oregon, maximum LAI varies from  $>10$  in coastal rain forests to less than 1 in juniper woodland (Runyon et al., 1994).

Based on these field observations we derived a series of rules to interpret the suitability of the environment for the dominance of *P. ponderosa*. Specifically, an environment was deemed suitable if it met all of the following criteria: (i) available soil water supply is not exhausted below 20% of capacity; (ii) precipitation recharges soil water storage sometime during the year; and (iii) maximum summer LAI is between 1.5 and 2.5.

Using these rules we spatially defined areas with changing growth potential for the *P. ponderosa* type. These distributions were summarized at annual and decadal intervals to provide an indication of potential variation in the range of the species over the last and current century. Like other studies (Swetnam and Betancourt, 1998; Ogle et al., 2000), our research focuses on decadal and regional scales for a number of reasons, generally the minimum generation times of most of the forest that dominate in the Pacific Northwest is greater than 10 year, therefore, this is the minimal time span to observe general population movements. Secondly, to capture climate behavior on decadal scales (15–30-year period), which has been well demonstrated from instrumental data (Swetnam and Betancourt, 1998; Cayan and Webb, 1992) and as observed by Swetnam and Betancourt (1998) local and shorter time frames have dominated empirical and experimental work in ecology, as well as resource management, while regional and historical perspectives have had less of a priority.

We selected three narrow longitudinal transects at 42°, 45°, and 48°N to illustrate in more detail, the geographic implications of our analyses. In addition, we reference predictions to published range maps of *P. ponderosa* (Little, 1971), which in central Oregon closely match Current Vegetation Survey (<http://www.fs.fed.us/r6/survey>) records (Fig. 3).

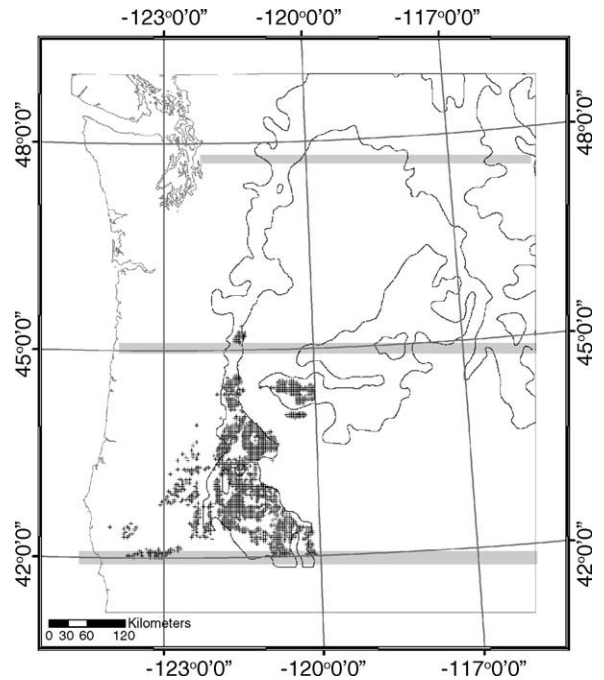


Fig. 3. Geographic range of *P. ponderosa* in Oregon and Washington (from Little, 1971) and locations of current vegetation system (CVS) plots with occurrence of *P. ponderosa* recorded in Oregon (includes subspecies that extend to west of the Cascade Mountains).

#### 4. Results

The decadal averages indicate that there is significant variation among years in historical climatic record. Fig. 4a shows the mean annual rainfall over the PNW from 1900 to 2100 from historical observations and as projected by the Hadley Center (Mitchell et al., 1995; Johns et al., 1997) for VEMAP-2. Fig. 4b shows the decadal variation in annual rainfall compared to a long-term mean. In particular, the 1920–1930s period shows lower than average mean monthly rainfall. Similarly, for years in the 1950s, there is evidence of drier and hotter climates. By contrast, the 1940s and years in the 1980s were periods with high rainfall. The future climate scenarios indicate the current decade will be one of the driest on record followed by a number of decades of average rainfall with an above average increase in rainfall at the turn of the next century.

At each monthly time step from 1900 to 2100, monthly LAI and soil water stress were predicted in ad-

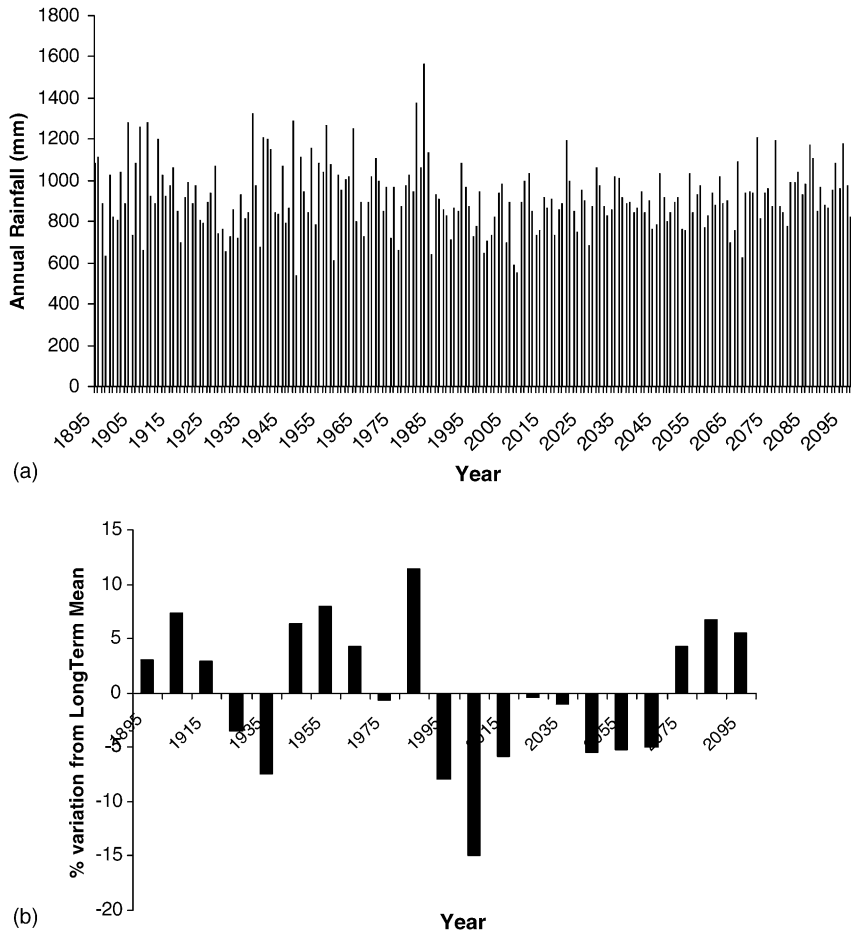


Fig. 4. (a) Mean annual rainfall (in mm) 1900–2100 and (b) variation from mean decadal rainfall (in %) 1900–2100.

dition to conventional estimates of stand growth. Using the three rules established from field observations, summer LAI and the annual pattern of soil water stress was assessed for each pixel to predict year-by-year potential shifts in the distribution of *P. ponderosa*. Fig. 5a–f indicates areas favorable for the expansion of *P. ponderosa* (black: very favorable, white: unfavorable) averaged for each decade from 1900 to 2100. The geographic distribution of *P. ponderosa* from Little (1971) is shown for reference in the figures. There is considerable variation observed in the predicted suitability of the climate for *P. ponderosa* dominance, particularly at the beginning and end of the century. A simple geographic query indicates the year with the highest and lowest count of cells suitable for *P. ponderosa* is 1958

and 1924, respectively (Fig. 6). The poorest year for *P. ponderosa* growth and range expansion corresponds to the significant drought periods in the 1930s.

Fig. 7 shows the cumulative implications of climatic variation over the previous and current century by combining predicted yearly *P. ponderosa* distribution into two single layers with black representing the most favorable locations and white the least suitable environments for *P. ponderosa*.

To examine changes in potential distribution of *P. ponderosa* throughout the previous and current century three longitudinal transects were analyzed in detail at 42°, 45° and 48°N latitudes (Fig. 1). The first, in the south of the PNW at 42°N, passes near the Oregon, Californian border, east from the Pacific Ocean across

the Siskiyou Mountains with highly variable and complex topography and species distributions, to Klamath Lake. The transect extends on to Goose Lake and Trident Peak. The transect ends approximately 700 km

inland from the ocean in the Santa Rosa Mountains at the junction of the Oregon, California, and Idaho borders. The second transect at 45°N crosses Oregon along a similar line to the OTTER transect (Peterson

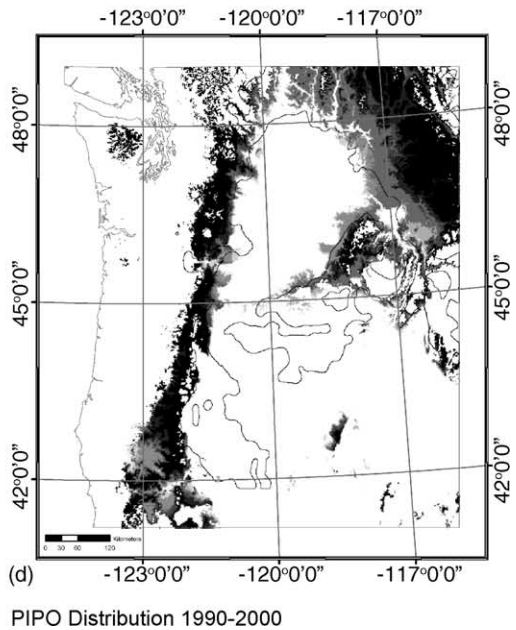
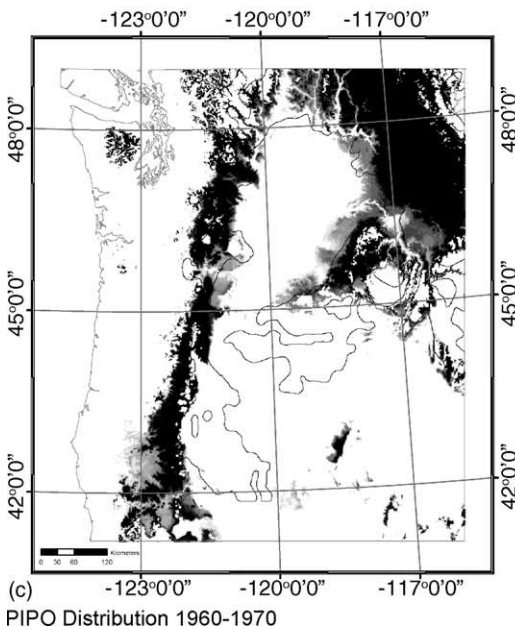
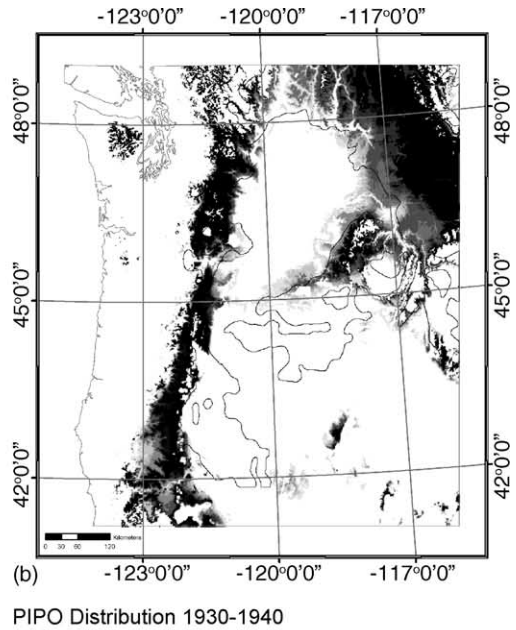
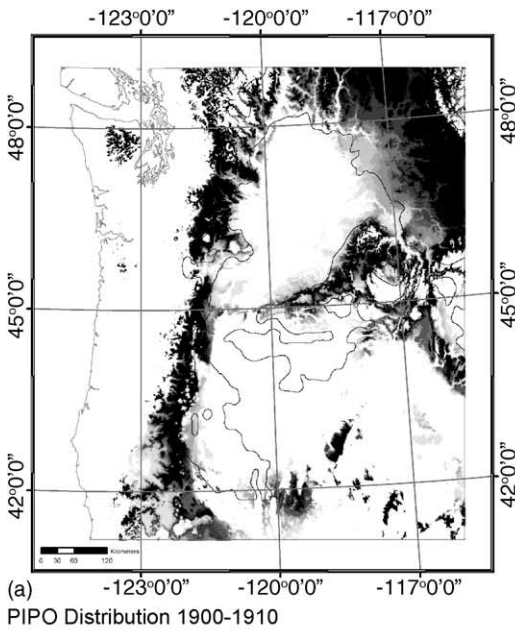


Fig. 5. Predicted potential shifts in distribution of *P. ponderosa* averaged over each decade from 1900 to 2100 if those climatic conditions were to persist. The current range of the species east of the crest of Cascade Mountains is outlined (from Little, 1971, see Fig. 3).

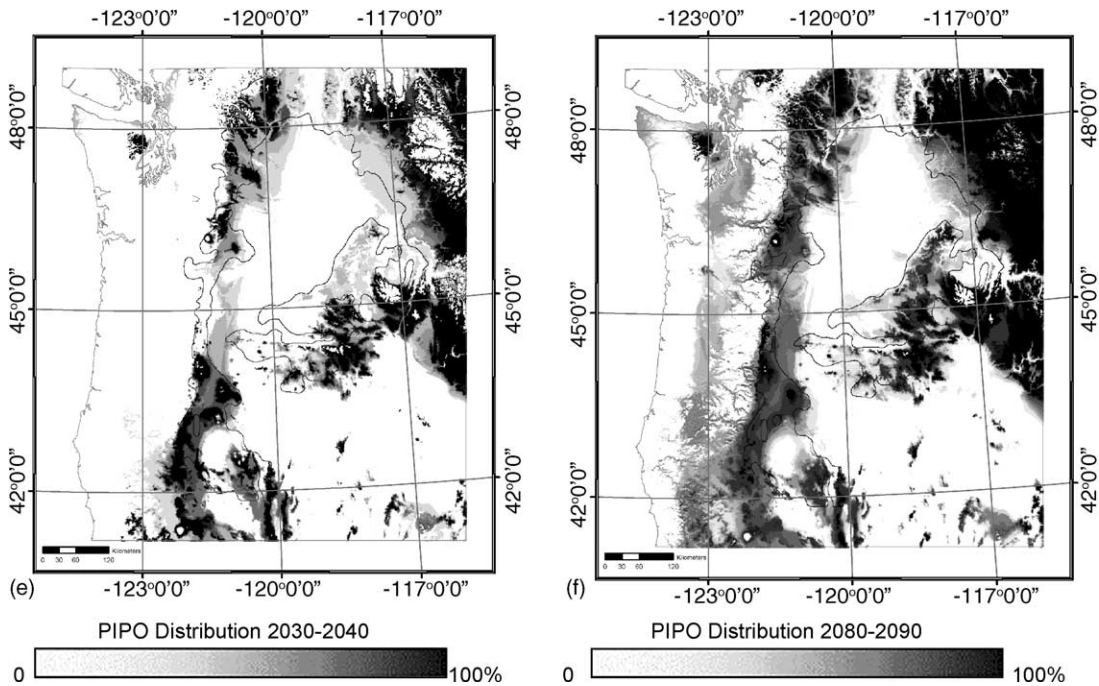


Fig. 5. (Continued).

and Waring, 1994) proceeding from the Pacific Ocean, across both the Coast and the Cascade Mountain ranges passing through Salem. The transect extends through the AmeriFlux pine sites, John Day River, the township of Fossil, and terminates near McCall, Idaho. The third transect at 48°N extends inland at Puget Sound and Seattle, passing through Mt. Stuart in further inland north of Spokane. It continues into Idaho and ends south of Libby, Montana.

We provide a graphic picture of the dynamic changes in environmental conditions over seven selected decades from 1900 to 2100 that might favor or disfavor dominance of ponderosa pine along each transect. Where the gray scale darkens and its duration persists in Fig. 8, ponderosa pine is predicted to maintain sustained dominance. Where the gray scale lightens, other species are likely to dominate. Fig. 8a indicates that along the southern most transect, 100–200 km inland, the *P. ponderosa* type should, as is evident, be well represented over the past century. In the future, with predicted changes in climate, the pine type is predicted to broaden its distribution and to occur between 80 and 400 km inland and also to occupy lower el-

evation sites than in the past century. In the eastern Siskiyou Mountains, 350 km inland, conditions are predicted to improve for the pine, increasing LAI from 1.5 to 2.0 in the decade 2080–2090. Areas further inland in Oregon and Idaho are predicted to remain too arid to support *P. ponderosa*. Along the middle transect, our analysis predicts major changes in the distribution of *P. ponderosa* over the current century (Fig. 8b). In response to moister conditions, we predict high LAI in the Coast and Cascade Mountains with the likely consequence that Douglas-fir (*P. menziesii*), western hemlock (*Tsuga heterophylla*), grand fir (*A. grandis*), and white fir (*Abies concolor*) will replace ponderosa pine. In contrast, on the eastern side of the Cascade Mountains, we predict expansion of the ponderosa pine 400–600 km inland.

Across the most northern transect (Fig. 8c), patterns are predicted to be similar to those at 45°N, over the next century with the simulations predicting an increase in LAI that would shift *P. ponderosa* from its current location at 100 km inland to a much broader distribution from 80 to 250 km, again at lower elevations than currently occupied. The Rockies along

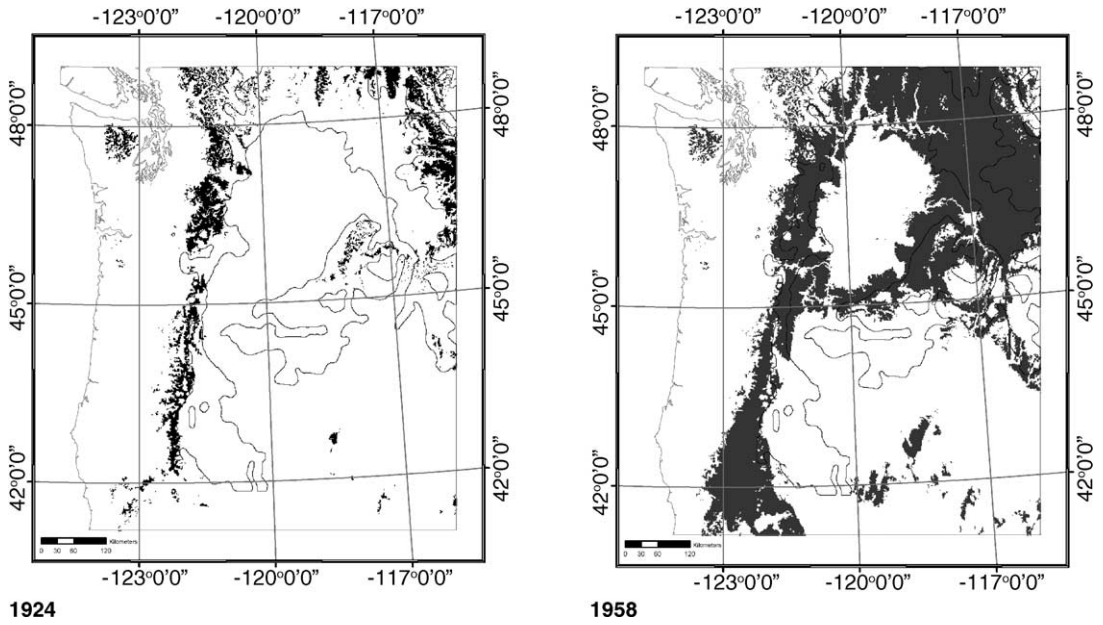


Fig. 6. During the last century the most favorable conditions (largest cell count in 3-PG simulations) for the expansion of ponderosa pine’s range occurred in 1958, whereas the least favorable conditions for range expansion by the species occurred in 1924.

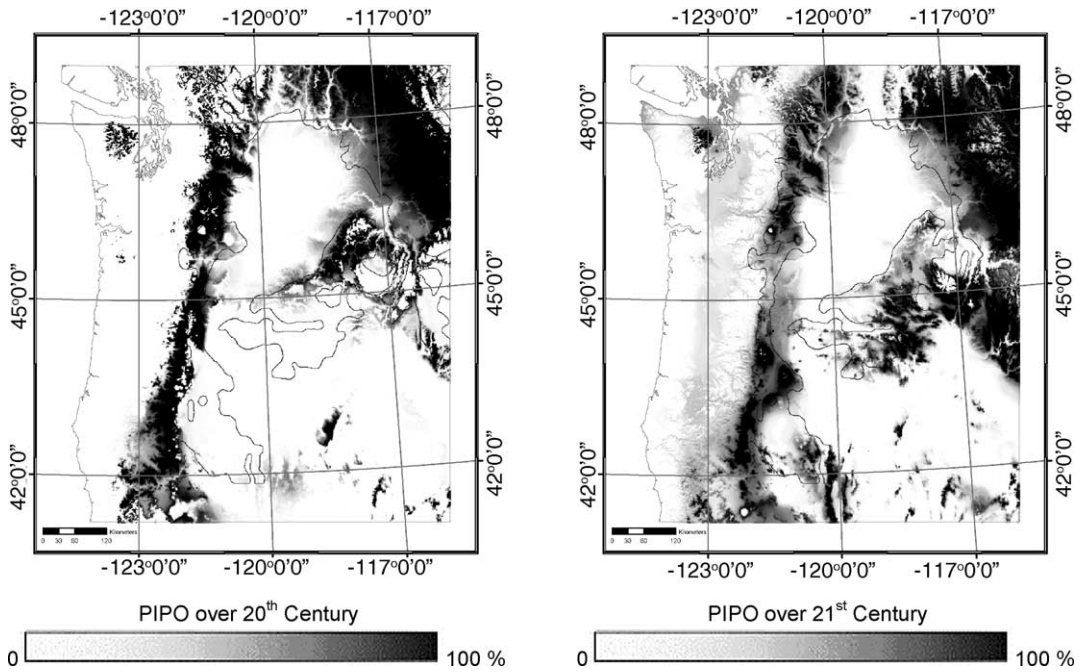


Fig. 7. Cumulative predictions of *P. ponderosa* distribution in eastern Oregon and Washington over the last and current century. Areas of black indicate where *P. ponderosa* would be expected to sustain dominance; areas in white indicate where other species should be more competitive.

the Canadian boarder have, and are predicted to sustain, conditions too cool for *P. ponderosa* to compete well with lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea en-*

*gelmannii*), leading to the absence of pine about 280 km inland but counter-balanced by a significant expansion of *P. ponderosa* from 300 to 500 km inland into Montana.

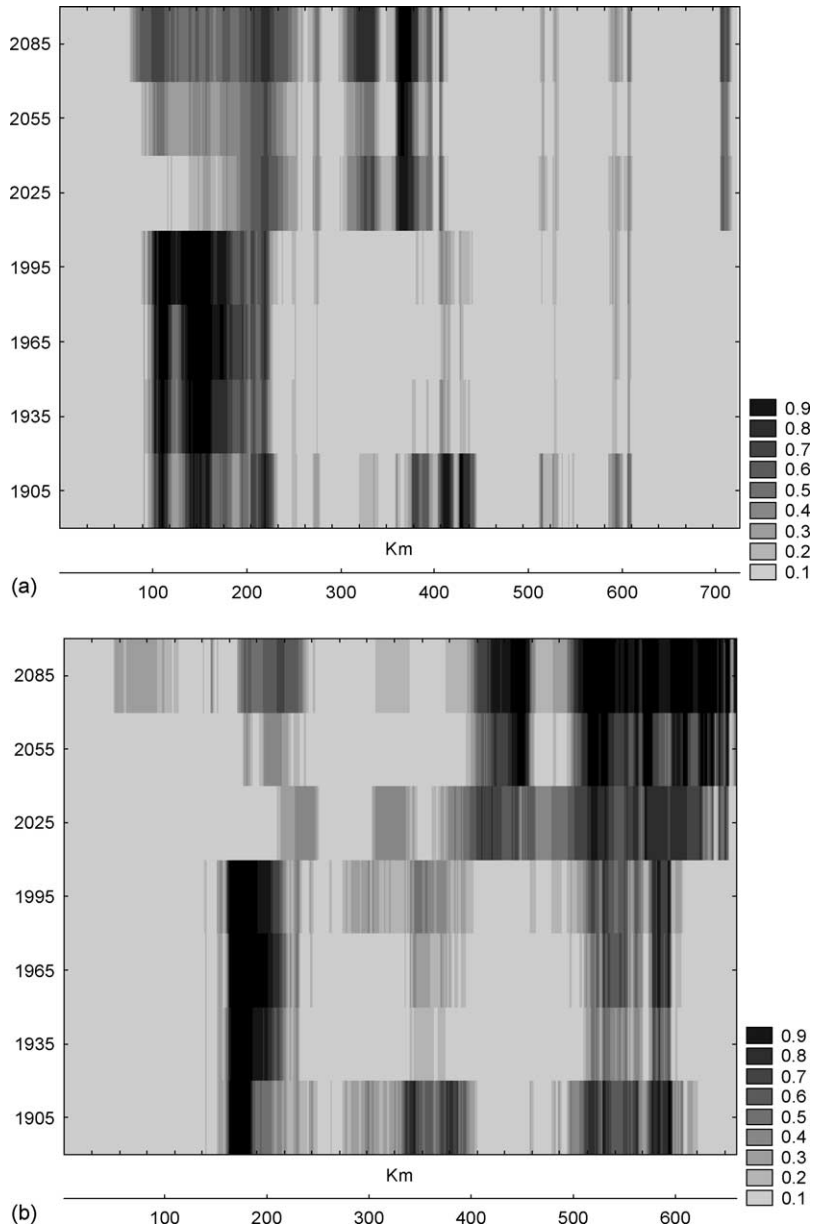


Fig. 8. (a) Longitudinal transect at 42°N of *P. ponderosa* potential dominance over seven decades (mid-year given on Y-axis). Gray scale indicates relative dominance, 0 = absence, 1 = dominance; (b) longitudinal transect at 45°N of *P. ponderosa* potential dominance over seven decades (mid-year given on Y-axis). Gray scale indicates relative dominance, 0 = absence, 1 = dominance; (c) longitudinal transect at 48°N of *P. ponderosa* potential dominance over seven decades (mid-year given on Y-axis). Gray scale indicates relative dominance, 0 = absence, 1 = dominance.

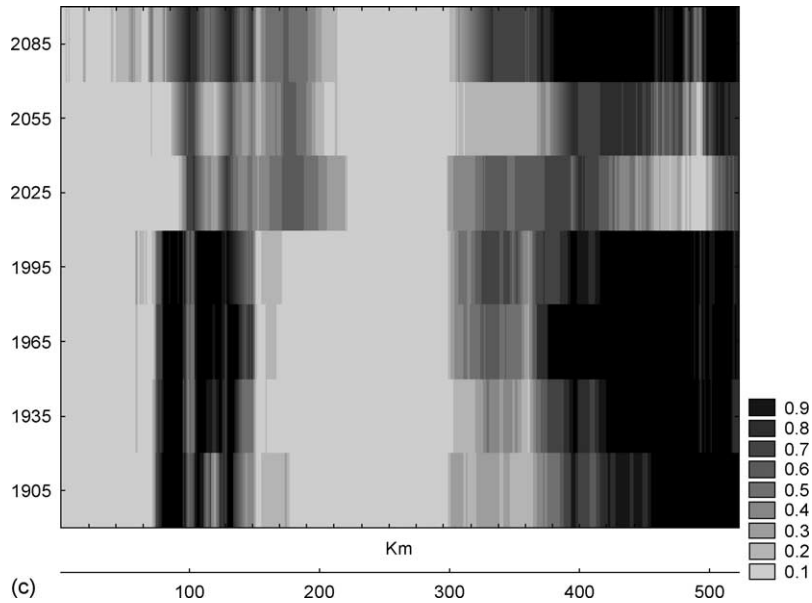


Fig. 8. (Continued).

Looking at the entire PNW, we illustrate in Fig. 9, predicted decadal changes in the fraction of the total area with conditions favorable for dominance of the pine type. The area potentially occupied by ponderosa pine would, according to our analysis, range from 25% in 1900 to a low of 18% of the total area in the 1930s. In the future, the pine type is predicted to extend its range to occupy from 35% of the total area at the turn of the century to a low of 15% of the total area in decade with mid-year 2035. These decadal trends are believed to

be consistent with the time required to demonstrate the likelihood of drought-induced death (by seedling and sapling mortality) or by subsequent disturbance events such as fire (Ogle et al., 2000).

### 5. Discussion

The three criteria for discriminating where the *P. ponderosa* type should dominate appear reasonable.

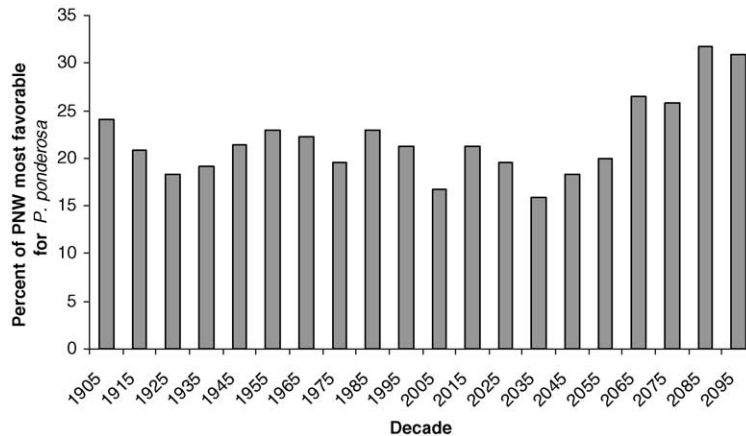


Fig. 9. Percentage of the PNW deemed suitable for *P. ponderosa* based on diagnostic criteria and simulations with 3-PG on the historical and future climatic sequence, summarized by decade.

These criteria clearly separate the ponderosa pine type from the more moist, mixed conifer type and the more arid, juniper woodlands. Fire frequency too increases with drought so that dominance of pine, juniper, sagebrush, and grass may vary from year to year but still exhibit general trends predicted by the process model. The mixed conifer type at canopy closure supports an LAI > 3.0 and does not experience drought sufficient to halt photosynthesis or growth, i.e., predawn water potentials remain above  $-1.5$  MPa (Coops and Waring, 2001b). The juniper woodland, on the other hand, does not compete well with ponderosa pine. Juniper woodlands support an LAI < 1.0 as a result of extended drought sufficient to halt photosynthesis and growth, i.e., predawn water potentials drop below  $-3.0$  MPa (Runyon et al., 1994; Law and Waring, 1994). The predicted distribution of areas favorable for *P. ponderosa* for the past century, as shown in Fig. 6, correspond close to the published geographic distribution of the species (Little, 1971). There is a one area in South Western Oregon (Latitude  $43^{\circ}$ N, Longitude  $121^{\circ}$ E) where ponderosa pine currently exhibits a wider distribution than our analyses. We suspect that our estimation of soil water storage capacity may be high, and sensitivity analyses suggest that adjusting soil water holding capacity downward would bring agreement between predicted and observed distributions. Previous model evaluation in the larger area with pumice-derived soils suggest that our estimates of water holding capacity are reasonable (Law et al., 2000a).

The 3-PG model simulations undertaken for this study are based on well documented parameter values for pure stands of *P. ponderosa* (Law et al., 2001a). For other species, particularly those growing on the west side of the Cascade Mountains, different parameter values would apply, which in most cases would lead to slightly higher LAI values than those predicted for ponderosa pine (Coops and Waring, 2001a).

Where an adequate supply of water is available throughout the growing season, soil fertility becomes an important limitation on growth. We parameterized 3-PG with soil fertility set to a constant 0.4, because where *P. ponderosa* forest dominate, soil fertility is generally low and slight variation in this parameter have little effect on growth (Law et al., 2003). Using this value also leads to an underestimate of LAI in the maritime environments of western Oregon and Washington (Coops and Waring, 2001a).

Our analysis indicates that there has been, and should continue to be, considerable variation in the suitability of the landscape to support *P. ponderosa* dominance across the PNW. In the first decade of the 1900s, the climate favored expansion of *P. ponderosa* to include potentially as much as 25% of the area. In contrast, the drought of the 1920s and 1930s, if extended, was predicted to reduce the distribution of the species by 30–18% of the total landscape. The area most sensitive to climatic variation is that situated along the eastern flank of the Cascade Mountains, where the pine type is confined by a steep climatic gradient that hems in the pine by competition with mixed conifers to the west and with juniper to the east.

How long might it take to shift the range of ponderosa pine? We would assume more than a decade would be required. During that time, insect and disease outbreaks, or fire, might hasten the demise of the pine (Keane et al., 1996; Ogle et al., 2000), or continued drought would result in unsuccessful pine seedling establishment, but invasion of other species would also require time, as large seed crops are irregular events in most forested regions and seed dispersal by wind and animals, probabilistic. Reversal in a following decade to less favorable conditions could return pine to a dominant position if a few trees were to survive because the invading species would be of small stature and more prone to frost, drought, ground fires, and herbivory.

When utilizing the HADLEY future climate scenario we did not incorporate the effect of increasing atmospheric CO<sub>2</sub>. Numerous studies have assumed in evergreen conifers that stomatal behavior under this condition would not differ significantly from the present and that the major change would be a modest increase in canopy quantum efficiency, assuming sufficient nitrogen was available (Ellsworth, 1999). The degree to which quantum efficiency would increase is unknown, with increases of a third above current levels suggested from experiments with Scots pine (*Pinus sylvestris* L.) (Overdieck et al., 1998), to zero in loblolly pine (*Pinus taeda* L.) forests (Oren et al., 2001). Thornton et al. (2002) concluded, however, that changes in fluxes (Net Ecosystem Exchange) due to increasing CO<sub>2</sub> were highly dependent on disturbance events intensity and post harvest management rather than increasing CO<sub>2</sub> alone. In our analyses, canopy quantum efficiency was assumed to remain at 0.04 mol C/mol photon over the next 100 years.

The interpretation of regional changes in future climate agree in general with those of Bachelet et al. (2001), who, using a dynamic general vegetation model, predicted higher than normal precipitation during the winter and warmer temperatures with a longer growing season in the pine transition zone in future decades. This would, according to our rule-based model, lead to conditions favoring expansion to the east by ponderosa pine, with general accumulation of fuels throughout its range. If these conditions were to persist, an increase in the intensity of fire, as well as the frequency, might be expected (Drapek and Bachelet, personal communication). At higher elevations to the west, continued climatic warming might reduce the amount of snow and favor expansion of pine into the current subalpine zone. On the western side of the Cascades, however, an increase in precipitation would favor growth of Douglas-fir (*P. menziesii*), hemlock (*T. heterophylla*), grand fir (*A. grandis*), and white fir (*A. concolor*) and restrict pine to recently disturbed sites.

The approach presented in this paper, we believe, has more general application. It could obviously be improved by acquiring finer spatial estimates of future climatic conditions with the full compliment of meteorological data required to drive a physiologically based process model. Tension zones, such as we have identified for dominance of ponderosa pine, are excellent areas on which to evaluate predictions of climatic change in the future. The availability of Earth orbiting satellites offers a means of evaluating both predicted changes in climatic conditions and vegetation over the next century.

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## References

- Aber, J.D., Ollinger, S.V., Federer, C.A., Reich, P.B., Goulden, M.L., Kicklighter, D.W., Melillo, J.M., Lathrop Jr., R.G., 1995. Predicting the effects of climate change on water yield and forest production in the northeastern US. *Climate Res.* 5, 207–222.
- Bachelet, D., Neilson, R.P., Lenthan, J.M., Drapek, R.J., 2001. Equilibrium and dynamic models agree about impacts of global warming on US ecosystems. *Ecosystems* 4, 164–185.
- Cayan, D.R., Webb, R.H., 1992. El Niño/Southern Oscillation and streamflow in the western United States. In: Diaz, H.F., Markgraf, V. (Eds.), *El Niño—Historical and Paleoclimatic Aspects of the Southern Oscillation*. Cambridge University Press, Cambridge, pp. 29–68.
- Coops, N.C., Waring, R.H., Landsberg, J.J., 1998. Assessing forest productivity in Australia and New Zealand using a physiologically-based model driven with averaged monthly weather data and satellite derived estimates of canopy photosynthetic capacity. *Forest Ecol. Manage.* 104, 113–127.
- Coops, N.C., Waring, R.H., 2001a. Assessing forest growth across southwestern Oregon under a range of current and future global change scenarios using a process model, 3-PG. *Global Change Biol.* 7, 15–29.
- Coops, N.C., Waring, R.H., 2001b. Estimating maximum potential site productivity and site water stress of the eastern Siskiyou using 3-PGS. *Can. J. Forest Res.* 31, 143–154.
- Ellsworth, D.S., 1999. CO<sub>2</sub> enrichment in a maturing pine forest: are CO<sub>2</sub> exchange and water status in the canopy affected? *Plant Cell Environ.* 22, 461–472.
- Franklin, J.F., Dyrness, C.T., 1973. *Natural Vegetation of Oregon and Washington*. Oregon State University Press, Oregon, USA.
- Friend, A.D., Stevens, A.K., Knox, R.G., Cannell, M.G.R., 1997. A process-based, biogeochemical, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). *Ecol. Modell.* 95, 249–287.
- Gifford, R.M., 2003. Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. *Funct. Plant Biol.* 30, 171–186.
- Hunt Jr., E.R., Martin, F.C., Running, S.W., 1991. Simulating the effect of climatic variation on stem carbon accumulation of a *P. ponderosa* stand: comparison with annual growth increment data. *Tree Physiol.* 9, 161–172.
- Irvine, J., Law, B.E., 2002. Seasonal soil CO<sub>2</sub> effluxes in young and old ponderosa pine forests. *Global Change Biol.* 8, 1183–1194.
- Johns, T.C., Carnell, R.E., Crossley, J.F., Gregory, J.M., Mitchell, J.F.B., Senior, C.A., Tett, S.F.B., Wood, R.A., 1997. The second Hadley Centre coupled ocean-atmosphere GCM: model description, spinup and validation. *Climate Dyn.* 13, 103–134.

- Keane, R.E., Ryan, K.C., Running, S.W., 1996. Simulating effects of fire on northern Rocky Mountain landscapes with the ecological process model FIRE-BGC. *Tree Physiol.* 15, 319–331.
- Kittel, T.G.F., Royle, J.A., Daly, C., Rosenbloom, N.A., Gibson, W.P., Fisher, H.H., Schimel, D.S., Berliner, L.M., VEMAP2 Participants, 1997. A gridded historical (1895–1993) bioclimate dataset for the conterminous United States. In: Proceedings of the 10th Conference on Applied Climatology, 20–24 October, Reno, NV. American Meteorological Society, Boston.
- Landsberg, J.J., 2003. Modelling forest ecosystems: state of the art, challenges and future directions. *Can. J. Forest Res.* 33, 385–397.
- Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecol. Manage.* 95, 209–228.
- Landsberg, J.J., Waring, R.H., Coops, N.C., 2003. Performance of the forest productivity model 3-PG applied to a wide range of forest types. *Forest Ecol. Manage.* 172, 199–214.
- Law, B.E., Cescatti, A., Baldocchi, D.D., 2001a. Leaf area distribution and radiative transfer in open-canopy forests: implications to mass and energy exchange. *Tree Physiol.* 21, 777–787.
- Law, B.E., Goldstein, A.H., Anthoni, P.M., Unsworth, M.H., Panek, J.A., Bauer, M.R., Fracheboud, J.M., Hultman, N., 2001b. Carbon dioxide and water vapor exchange by young and old *P. ponderosa* ecosystems during a dry summer. *Tree Physiol.* 21, 299–308.
- Law, B.E., Sun, O., Campbell, J., Van Tuyl, S., Thornton, P., 2003. Changes in carbon storage and fluxes in a chronosequence of ponderosa pine. *Global Change Biol.* 9, 510–524.
- Law, B.E., Van Tuyl, S., Cescatti, A., Baldocchi, D.D., 2001c. Estimation of leaf area index in open-canopy *Pinus ponderosa* forests at different successional stages and management regimes in Oregon. *Agric. Forest Meteorol.* 108, 1–14.
- Law, B.E., Waring, R.H., 1994. Combining remote sensing and climatic data to estimate net primary production across Oregon. *Ecol. Appl.* 4, 717–728.
- Law, B.E., Waring, R.H., Anthoni, P.M., Aber, J.D., 2000a. Measurement of gross and net ecosystem productivity and water vapor exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biol.* 6, 155–168.
- Law, B.E., Williams, M., Anthoni, P.M., Baldocchi, D.D., Unsworth, M.H., 2000b. Measuring and modeling seasonal variation of carbon dioxide and water vapor exchange of a *Pinus ponderosa* forest subject to soil water deficit. *Global Change Biol.* 6, 613–630.
- Little, E.L. Jr., 1971. Atlas of United States Trees, vol. 1, Conifers and Important Hardwoods. U.S. Department of Agriculture Miscellaneous Publication 1146, 9 pp., 200 maps.
- Mitchell, J.F.B., Johns, T.C., Gregory, J.M., Tett, S., 1995. Climate response to increasing levels of greenhouse gases and sulphate aerosols. *Nature* 376, 501–504.
- Neilson, R.P., King, G.A., Koerper, G., 1992. Toward a rule-based biome model. *Landscape Ecol.* 7, 27–43.
- Nightingale, J.M., Phinn, S.R., Held, A.A., 2004. Ecosystem process models at multiple scales for mapping tropical forest productivity. *Prog. Phys. Geography* 28, 241–281.
- Ogle, K., Whitham, T.G., Cobb, N.S., 2000. Tree-ring variation in pinyon pine predicts likelihood of death following record drought. *Ecology* 81, 3237–3243.
- Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., Schafer, K.V.R., McCarthy, H., Hendrey, G., McNulty, S.G., Katul, G.G., 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO<sub>2</sub>-enriched atmosphere. *Science* 441, 469–472.
- Overdieck, D., Kellomaki, S., Wang, K.Y., 1998. Do the effects of temperature and CO<sub>2</sub> interact? In: Jarvis, P.G. (Ed.), *European Forests and Global Change*. Cambridge University Press, London.
- Peterson, D.L., Waring, R.H., 1994. Overview of the Oregon transect ecosystem research project. *Ecol. Appl.* 4, 211–225.
- Running, S.W., 1994. Testing FOREST-BGC ecosystem process simulations across a climatic gradient in Oregon. *Ecol. Appl.* 4, 238–247.
- Running, S.W., Coughlan, J.C., 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecol. Model.* 42, 125–154.
- Running, S.W., Hunt Jr., E.R., 1993. Generalization of a forest ecosystem process model for other biomes. BIOME-BGC and an application for global scale models. In: Ehleringer, J.R., Field, C. (Eds.), *Scaling Physiological Processes: Leaf to Globe*. Academic Press, San Diego, pp. 141–158.
- Running, S.W., Nemani, R.R., Hungerford, R.D., 1987. Extrapolation of synoptic meteorological data in mountainous terrain, and its use for simulating forest evapotranspiration and photosynthesis. *Can. J. Forest Res.* 17, 472–483.
- Runyon, J., Waring, R.H., Goward, S.N., Welles, J.M., 1994. Environmental limits on net primary production and light-use efficiency across the Oregon transect. *Ecol. Appl.* 4, 226–237.
- Schimel, D., Melillo, J., Tian, H., McGuire, A.D., Kicklighter, D., Kittel, T., Rosenbloom, N., Running, S.W., Thornton, P., Ojima, D., Parton, W., Kelly, R., Sykes, M., Neilson, R., Rizzo, B., 2000. Contribution of increasing CO<sub>2</sub> and climate to carbon storage by ecosystems of the United States. *Science* 287, 2004–2006.
- Swetnam, T.W., Betancourt, J.L., 1998. Mesoscale disturbance and ecological response to decadal climate variability in the American southwest. *J. Climate* 11, 3128–3147.
- Thornton, P.E., Law, B.E., Gholz, H.L., Clark, K.L., Falge, E., Ellsworth, D.S., Goldstein, A.H., Monson, R.K., Hollinger, D., Falk, M., Chen, J., Sparks, J.P., 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needle-leaf forests. *Agric. Forest Meteorol.* 113, 185–222.
- Thornton, P.E., Running, S.W., White, M.A., 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *J. Hydrol.* 190, 214–251.
- Thornton, P.E., Running, S.W., 1999. An improved algorithm for estimating incident daily solar radiation from measurements of temperature, humidity, and precipitation. *Agric. Forest Meteorol.* 93, 211–228.
- Van Tuyl, S., Law, B.E., Turner, D.P., Gitelman, A.I., submitted for publication. Variability in net primary production and carbon

- storage in biomass across Oregon forests—an assessment integrating data from forest inventories, intensive sites, and remote sensing. *Forest Ecol. Manage.*
- Waring, R.H., 1969. Forest plants of the eastern Siskiyou: their environmental and vegetational distribution. *Northwest Sci.* 43, 1–17.
- Waring, R.H., 2000. A process model analysis of environmental limitations on the growth of Sitka spruce plantations in Great Britain. *Forestry* 73, 65–79.
- Waring, R.H., Emmingham, W.H., Running, S.W., 1975. Environmental limits of an endemic spruce, *Picea breweriana*. *Can. J. Bot.* 53, 1550–1613.
- Waring, R.H., Coops, N.C., Ohmann, J.L., Sarr, D.A., 2002. Interpreting woody plant richness from seasonal ratios of photosynthesis. *Ecology* 83, 2964–2970.
- Waring, R.H., Landsberg, J.J., Williams, M., 1998. Net primary production of forests: a constant fraction of gross primary production? *Tree Physiol.* 18, 129–134.