

Combining a generic process-based productivity model and a statistical classification method to predict the presence and absence of tree species in the Pacific Northwest, U.S.A.

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ABSTRACT

Although long-lived tree species experience considerable environmental variation over their life spans, their geographical distributions reflect sensitivity mainly to mean monthly climatic conditions. We introduce an approach that incorporates a physiologically based growth model to illustrate how a half-dozen tree species differ in their responses to monthly variation in four climatic-related variables: water availability, deviations from an optimum temperature, atmospheric humidity deficits, and the frequency of frost. Rather than use climatic data directly to correlate with a species' distribution, we assess the relative constraints of each of the four variables as they affect predicted monthly photosynthesis for Douglas-fir, the most widely distributed species in the region. We apply an automated regression-tree analysis to create a suite of rules, which differentially rank the relative importance of the four climatic modifiers for each species, and provide a basis for predicting a species' presence or absence on 3737 uniformly distributed U.S. Forest Services' Forest Inventory and Analysis (FIA) field survey plots. Results of this generalized rule-based approach were encouraging, with weighted accuracy, which combines the correct prediction of both presence and absence on FIA survey plots, averaging 87%. A wider sampling of climatic conditions throughout the full range of a species' distribution should improve the basis for creating rules and the possibility of predicting future shifts in the geographic distribution of species.

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1. Introduction

A region's flora and fauna reflect the interplay of dispersal, colonization, and competition for resources under a specific range of environments. Within the Pacific Northwest (PNW) region of the United States, the distribution of the flora is well described by Franklin and Dyrness (1973) in terms of temperature and precipitation patterns, physiography, and associated plant communities. These descriptions, however, lack predictive power, and this deficiency, in a region where the climate may already be changing (Mote et al., 2005; Westerling et al., 2006), makes plans for conservation, as well as exploitation of natural resources, highly uncertain. In the extreme, climatically induced disturbance might cause major structural transformations from one type of vegetation to another, and through changes in the energy balance, further alter the region's climate (Pielke et al., 1998).

At present, there are two divergent approaches that incorporate climatic information to predict the distribution of species. One

approach relies on empirical correlations while the other attempts to acquire a mechanistic understanding on which to base predictions. The first, and most widely accepted approach, consists of "niche" or "bioclimatic envelope" models (Austin, 1985; Iverson and Prasad, 1998; McKenzie et al., 2003; Thuiller et al., 2008). Such models usually relate presence/absence data empirically to environmental variables, most often climate (but sometimes including soil and physiographic features), using an array of statistical methods including multiple regression techniques, neural networks, and regression-tree analysis (Iverson and Prasad, 2001). The capacity of these empirical models to provide accurate predictions of species' distributions under future, possibly novel climatic combinations is unclear (Williams et al., 2007).

At the other extreme are mechanistic models that predict the growth of individual species or even clones under any specified environment (Sands et al., 2000; Rodriguez et al., 2002; Almeida et al., 2004; Dye et al., 2004). The advantage of such mechanistic, process-based models is that they identify the relevant environmental constraints on growth and other processes. Such models are specifically designed to be able to predict performance of a species outside its present natural range (Waring, 2000; Coops et al., 2005; Waring et al., 2008). Their disadvantage is that detailed

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information is required by these models to define a species' tolerance and response to deviations from optimum temperature, frost, drought, and atmospheric humidity deficits, and in how resources are partitioned to leaves, roots, stems, and branches.

We questioned whether it might be possible to combine the automated, statistically sophisticated component of empirical models with the process-based understanding imbedded in the mechanistic type models. To address this question, we recognize that we must first simplify the mechanistic approach by referencing environmental responses of any number of species to one that is widely distributed. We also know that climatic data must be extrapolated across landscapes in an appropriate form and at a spatial resolution that match model requirements and the availability of biological information recorded on ground-based field survey plots. To automate the process of seeking rules to define the distribution of different tree species, we chose regression-tree analysis because of its efficiency and transparency in recognizing those physiological variables and their thresholds that separate one tree species from another in its adaptation to environment. Based on the analysis of a half-dozen species, the results of this hybrid approach were sufficiently encouraging to share, although we recognize the need to expand the analysis to include the full environmental range that each species now occupies.

2. Methods

2.1. Hybrid model

All ecosystem process-based models are simplified versions of reality with the choice of which model to utilize dependent a number of factors including the minimum spatial and temporal units of operation and the number and type of output parameters (Nightingale et al., 2004). Likewise 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 (Wulder et al., 2007). Given the need to predict species distribution over large spatial extents 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 (Nightingale et al., 2004) including HYBRID (Friend et al., 1997), FOREST-BGC (Running and Coughlan, 1988), BIOME-BGC (Running and Hunt, 1993) amongst others.

The 3-PG model (physiological principles predicting growth) was selected as a basis for the test because it contains a number of simplifying assumptions that have emerged from studies conducted over a wide range of forests (Landsberg et al., 2003). These include:

- Climatic data can be summarized at monthly intervals with little loss in the accuracy of model predictions.
- Each month, the most limiting climatic variable on photosynthesis is selected, based on departure from conditions that are optimum (expressed as unity) or completely limited (expressed as zero).
- Maximum canopy stomatal conductance approaches a plateau above a leaf area index (LAI) of 3.0.
- The ratio of actual/potential photosynthesis decrease in proportion to the reductions in the most limiting environmental factor.
- The fraction of production not allocated to roots can be partitioned among foliage, stem and branches based on allometric relationships and knowledge of annual leaf turnover.

In the model, absorbed photosynthetically active radiation (APAR) is estimated from global solar radiation and LAI; the utilized portion, APAR_u, is calculated by reducing APAR by an amount

determined by a series of modifiers that take values between 0 (system 'shutdown') 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, (c) soil drought and (d) temperature. Limitations on APAR_u 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 are significantly less than transpiration estimated with the Penman–Monteith equation (Coops et al., 2005). Gross primary production (PG) is calculated by multiplying APAR_u by a canopy quantum efficiency coefficient, 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 (Ra) and total net primary production (PN) in temperate forests are approximately fixed fractions (0.53 and 0.47, SE ± 0.04) of PG (Landsberg and Waring, 1997; Waring et al., 1998; Law et al., 2001). The model partitions PN into root and aboveground biomass. Under more favorable climatic conditions, the fraction of photosynthate allocated to roots increases with infertility of the soil (Landsberg and Waring, 1997).

We further simplified the approach by selecting Douglas-fir (*Pseudotsuga menziesii*), the most widely distributed species in the region, to characterize the importance of climatic constraints on photosynthesis and growth across all forested environments, as we have done previously for other purposes (Swenson et al., 2005; Waring et al., 2005; Coops et al., 2007). Rather than utilizing climatic data directly, we use 3-PG to assess the implications of seasonal limitations of water availability, deviations from an optimum temperature of 20 °C, frost frequency, and atmospheric humidity deficits on photosynthesis and growth. The link to photosynthesis is critical because the potential varies seasonally. The upper limits are set by the amount of light absorbed by the canopy's foliage. Although we recognize that soil fertility and soil water storage capacity vary considerably across the region (Swenson et al., 2005), in this paper we chose to keep soil properties constant to simplify the analysis of the effects of climatic variation on tree distributions. We did this by setting the maximum available soil water storage capacity at 200 mm and giving a moderately high rank to a soil fertility index (0.7), which generates a maximum photosynthetic quantum efficiency of 0.05 mol C mol photon⁻¹ (2.75 g C MJ⁻¹ of absorbed photosynthetically active radiation).

We used parameters for equations describing the physiological responses of Douglas-fir reported in a previous publication (Coops et al., 2007). The extent that different species encounter environments that would impose restrictions on the performance of Douglas-fir is incorporated through an automated regression-tree analysis, described in more detail below. This statistical procedure generates a suite of rules for each species that differentiates the relative importance of the four climatic modifiers (maximum impact imposed through the year by: water availability, deviations from an optimum temperature of 20 °C, frost frequency, and atmospheric humidity deficits).

2.2. Climatic data

Monthly mean climatic data, registered at a resolution of 1 km², were obtained for precipitation, minimum and maximum temperature, frost occurrence, and short wave radiation over the 18-year period from 1980 to 1997 from the DAYMET US climatological database (Thornton et al., 1997; Thornton and Running, 1999).¹

¹ URL: (<http://www.daymet.org>).

2.3. Species occurrence data

Information on species occurrence was obtained from records on 3737 United States Department of Agriculture (USDA), Forest Service (USFS) Forest Inventory and Analysis (FIA) field survey plots. These plot records contain detailed information regarding the size, basal area, mortality, and frequency of tree species. To maintain privacy the publically available spatial locations of the FIA plots are randomly moved by up to 800 m within the 1 km spatial resolution of this application. We chose presence/absence data alone, however, as the most reliable to establish the environmental distribution of a species.

2.4. Delineating limiting climatic factors

Across the region, we applied the model to predict stand growth and LAI, using the mean 18-year DAYMET averages, for each year of the 50 years of stand development with an initial stocking density of 1000 tree seedlings ha^{-1} . At the end of the 50th year, by which time stands have obtained maximum LAI, the simulations were stopped and the most climatically restricting variables on photosynthesis determined for each of the preceding 12 months.

2.5. Regression-tree analysis

To assess the extent that the annual maximum constraints of the 3-PG environmental modifiers, expressed as fractions of optimum conditions (unity), might serve to predict presence or absence of each of six selected tree species, a classification tree analysis was applied. This type of analysis is increasingly advocated for ecological research because it is not dependent on the assumption of a normalized distribution, is well suited to dealing with collinear datasets, and efficiently excludes variables that are insignificant (De'ath, 2002; Schwalm et al., 2006; Melendez et al., 2006). The technique automatically separates the dependent variables (presence or absence of a tree species) into a series of choices that not only identifies the importance of each constraining variable, but also establishes thresholds that best separate one species from another (diagrams for two species appear later, Fig. 3).

We execute the regression-tree analysis with a 10-fold cross validation technique, similar to a jackknifing procedure, which starts by using all available data (the reference tree). The total dataset is partitioned randomly into 10 equally sized groups (or folds). One set is held in reserve, while the other nine are pooled and a model developed. The accuracy of the model is assessed using the remaining 10% of the data which were not used in model development. This process is then repeated 10 times, resulting in 10 different test trees and 10 different accuracy assessments. The average of the accuracy of the 10 test trees is provided as the training accuracy, and the average accuracy of runs using the 10% reserved dataset is the validation accuracy. The decision rules of the 10 models are then merged to produce a final classification tree with an overall accuracy accessed by averaging the independent results of the 10 simulations (Breiman et al., 1984).

2.6. Spatial validation of models

To provide a visual comparison of model accuracy with referenced sources, we generated maps of current species' distributions and compared these with recorded presence of each species on FIA survey plots as well as with more general range distributions (Critchfield and Little, 1966; Little, 1971).²

3. Results

Spatial variation in the four climatic modifiers as they constrain photosynthesis of Douglas-fir during the most unfavorable month is shown in Fig. 1(A)–(D). All the modifiers are scaled between 0 and 1, where 1 indicates optimum conditions for photosynthesis, and 0 indicates complete shutdown for at least 1 month out of each year. According to model predictions, late summer drought is typical throughout most of the interior of the Pacific Northwest region with soil water storage capacity set at 200 mm (Fig. 1A). There are isolated mountain ridges in the southern interior where precipitation in the form of snow provides ample recharge of the water supply throughout the growing season. In the Rocky Mountains, the northwestern Cascades and Coastal Ranges, summer precipitation is sufficient to limit soil water stress on photosynthesis, in some cases to zero.

High evaporative demand during the summer is typical throughout the central valley in California, and for much of the areas on the eastern sides of the Cascade and Sierra Mountains. Mountainous areas toward the interior part of the region remain sufficiently cool resulting in deviations in optimum temperature (Fig. 1B), reducing evaporative demand (Fig. 1C) and limitations imposed by frequent frost (Fig. 1D) show similar patterns, with the areas most unfavorable for Douglas-fir located to the east of the Cascades and Sierra mountain ranges. The coastal mountains are buffered from extremes in temperature, whereas diurnal variation increases with elevation and with movement inland.

Based on presence data recorded on FIA plots for the selected species, we contrast seasonal variation in the climatic modifiers in Fig. 2. In regard to tolerance to soil water stress, western juniper appears the most adapted as it experiences 4 months in the year where photosynthesis is reduced to less than 20% of its potential (Fig. 2A). In contrast, Sitka spruce, which occurs along the coast, is present in areas where precipitation is sufficient to maintain a soil water balance within 10% of optimum throughout the year.

With temperature, most of the species analyzed are adapted to considerable variation throughout the year (Fig. 2B). Sitka spruce is present where temperature extremes are rare, in conjunction with its distribution close to the Pacific Coast. Lodgepole pine, on the other hand, is well adapted to survive, if not grow well, in areas where seasonal variations in temperature are extreme. Douglas-fir, the reference species, inhabits environments that are predominantly mild, with departures from its optimum temperature (20 °C) on average, of less than 50%. In regard to seasonal variation in atmospheric humidity deficits (VPD), the species show similar ranking, although with less extreme variation than they exhibit to drought (Fig. 2C). Sitka spruce experiences the least limitations and juniper the most. The environmental distribution of species in reference to monthly constraints imposed by frost (Fig. 2D) follows the general pattern exhibited for deviation from optimum temperature (Fig. 2B). The separation among species is accentuated, with lodgepole pine associated most with the occurrence of frost and Sitka spruce the least.

Decision trees were developed to predict presence and absence of each of the species, based on the maximum effect each of the four climate modifiers have on photosynthesis throughout the year. Examples of decision trees constructed for Sitka spruce and ponderosa pine are presented in Fig. 3. In the case of Sitka spruce (Fig. 3A), the first decision is based on the temperature modifier being >0.68. The second decision separates sites that are rarely water stressed (modifier >0.82). A third separation is made to include only those site where the temperature modifier is <0.82, and among those selected, a further delineation is based on the frost modifier being >0.47.

The decision tree constructed for ponderosa pine (Fig. 3B) sorts the climate variables in a different order, and assigns different

² URL: (<http://esp.cr.usgs.gov/data/atlas/little/>).

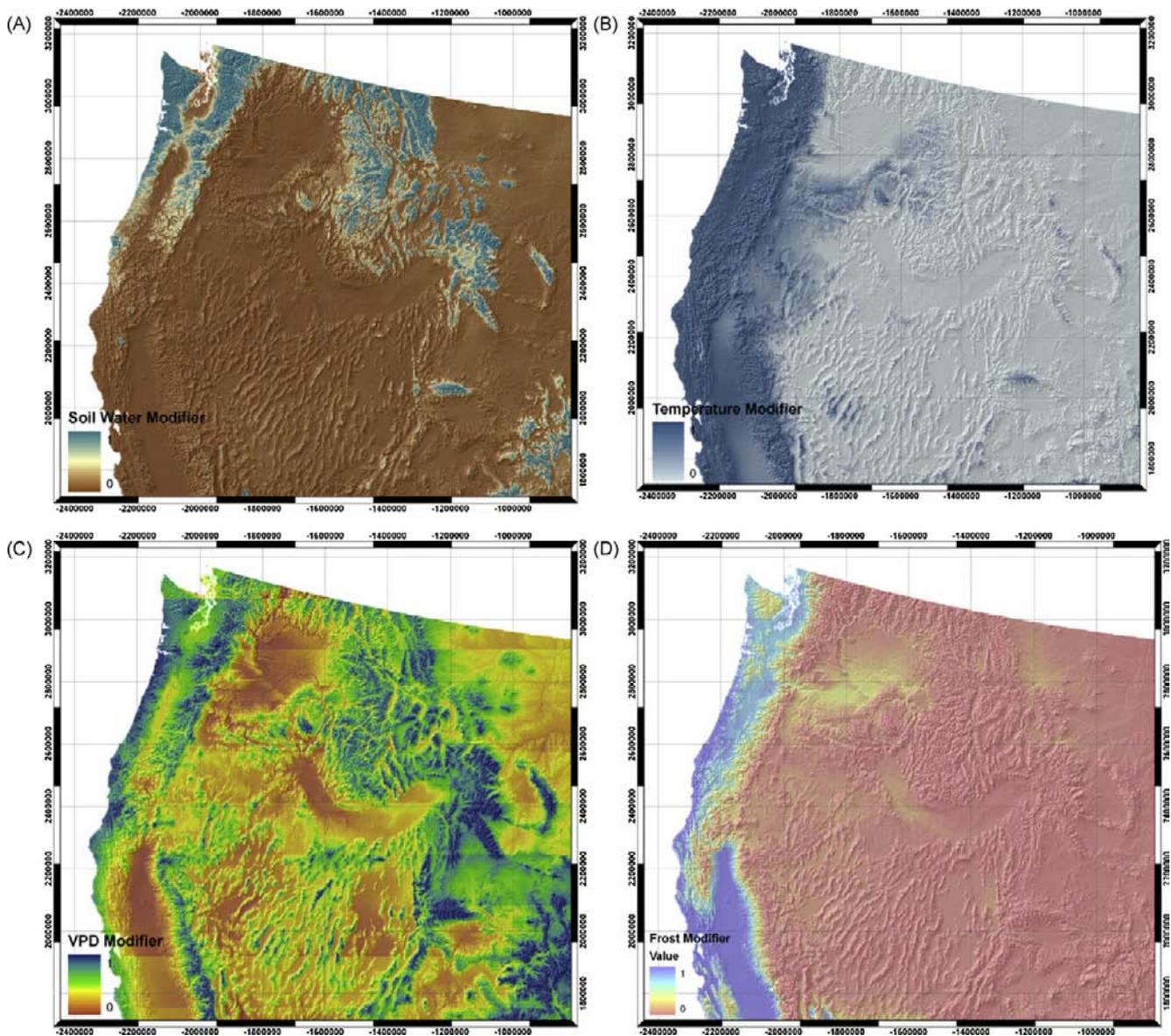


Fig. 1. (A–D) Geographic variation in the maximum effect on photosynthesis of the four climatic modifiers throughout the year, referenced to responses by Douglas-fir stands at 50 years of age. Modifiers are scaled between 0 (complete restriction in growth) and 1 (optimum).

thresholds than those presented for Sitka spruce. The first level of discrimination for ponderosa pines is water availability with the modifier ranked at <0.1 of optimum during late summer. The second decision level is based on the temperature modifier being <0.36 during part of the growing year, with a third level decision that identifies sites with the frost modifier at >0.1 . The fourth and last decision is based on the vapor pressure deficit modifier being >0.35 .

Although all four modifiers were used in the decision tree analysis, their importance differs, as shown in Fig. 4. For three species, one modifier accounts for 60–90% of the predictive power of the

regression-tree analysis. For lodgepole pine the critical modifier is frost, for western hemlock it is temperature, and for ponderosa pine it is soil water availability. Douglas-fir and Sitka spruce have two variables that account for $>30\%$ of the model's predictive power, but the variables differ: frost and VPD are important for Douglas-fir, whereas soil water and temperature help define the distribution for Sitka spruce (Table 1).

Accuracy assessments of the models were similar whether the data sets were for training or for validation (Table 2). Accuracies are referenced to the percentage of FIA plots on which a species was cor-

Table 1
Common and scientific names, and limiting environmental conditions of six common tree species in the Pacific Northwest region.

Common name	Scientific name	Environmental limiting factors
Sitka spruce	<i>Picea sitchensis</i> (Bong.) Carr	Most sensitive to humidity deficits and temperature extremes
Ponderosa pine	<i>Pinus ponderosa</i> Dougl. ex Loud.	Less sensitive to drought, frost, and humidity deficits than Douglas-fir
Western juniper	<i>Juniperus occidentalis</i> Hook.	Least sensitive to drought and high VPD
Lodgepole pine	<i>Pinus contorta</i> Dougl. ex Loud.	Most tolerance of frost
Douglas-fir	<i>Pseudotsuga menziesii</i> (Mirb.) Franco	Suited to intermediate environmental conditions
Western hemlock	<i>Tsuga heterophylla</i> (Raf.) Sarg.	More sensitive to humidity deficits and to drought than Douglas-fir

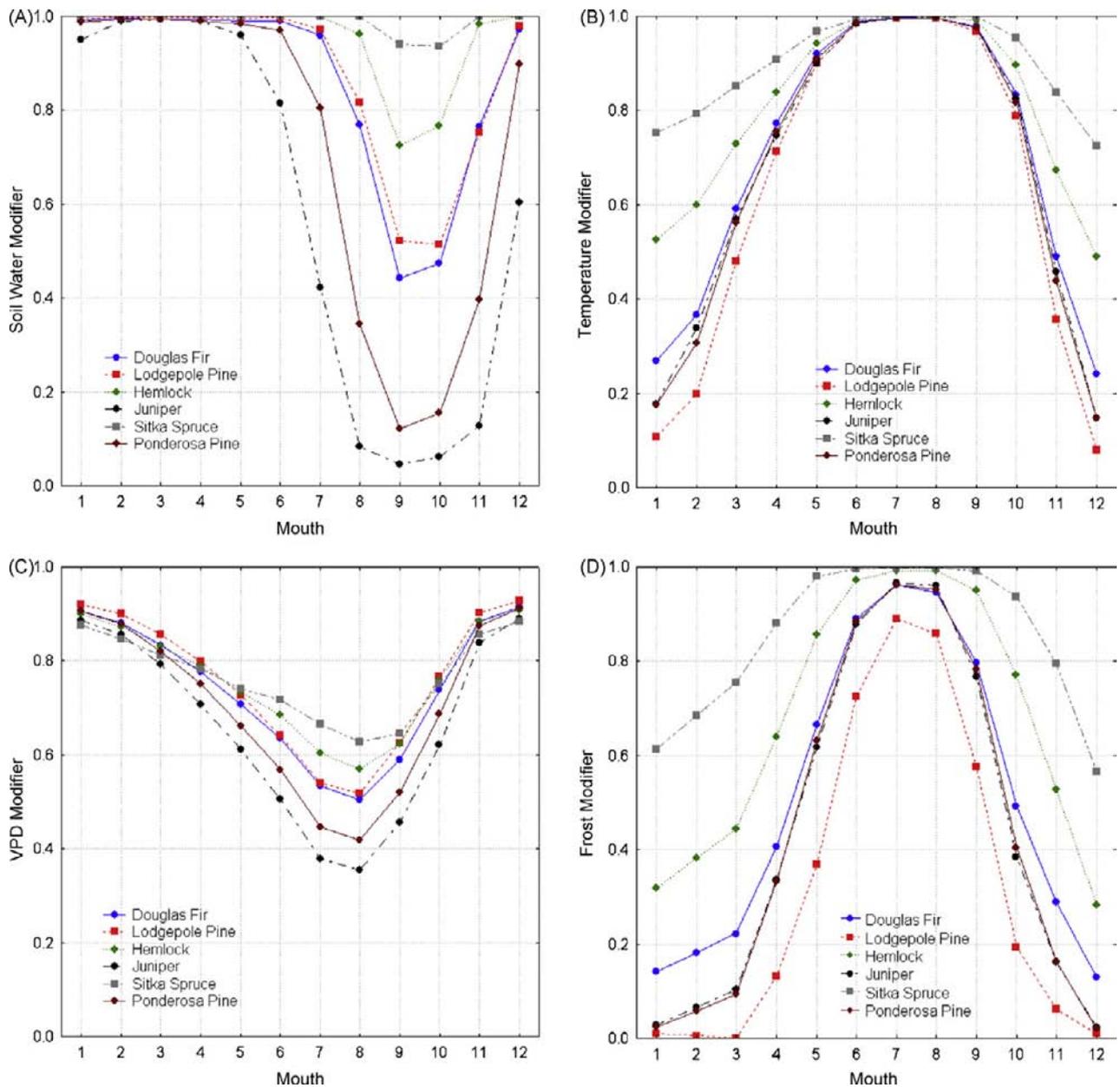


Fig. 2. (A–D) Monthly mean variation in the four climatic modifiers for each of six selected tree species.

rectly assigned as being present or absent, and then combined into a weighted value, proportionately to the number of plots associated with each of the two categories. The overall accuracy of the six models averaged 87%. The approximate location of the presence/absence FIA survey data plots are shown in Fig. 5 and graphic presentations

of model predictions of current species' distributions are presented in Fig. 6. Predictions based on the modifiers, and the Little (1971) range maps are independent of current land-use, whereas the FIA plots used in this study only occurred in areas recognized as forest. The predicted range of Sitka spruce is more confined than that sam-

Table 2
Percent correct classification for training and validation classification trees for the six selected species.

Data sets	Sitka spruce	Ponderosa pine	Western juniper	Western hemlock	Lodgepole pine	Douglas-fir	Averages
% of cases presence	2	21	5	15	30	40	19
Training							
Presence	68	56	56	49	69	82	63
Absence	99	93	99	97	78	67	89
Overall	98	86	97	90	75	76	87
Validation							
Presence	67	56	53	49	64	82	62
Absence	99	93	99	97	78	66	89
Overall	98	86	96	90	74	76	87

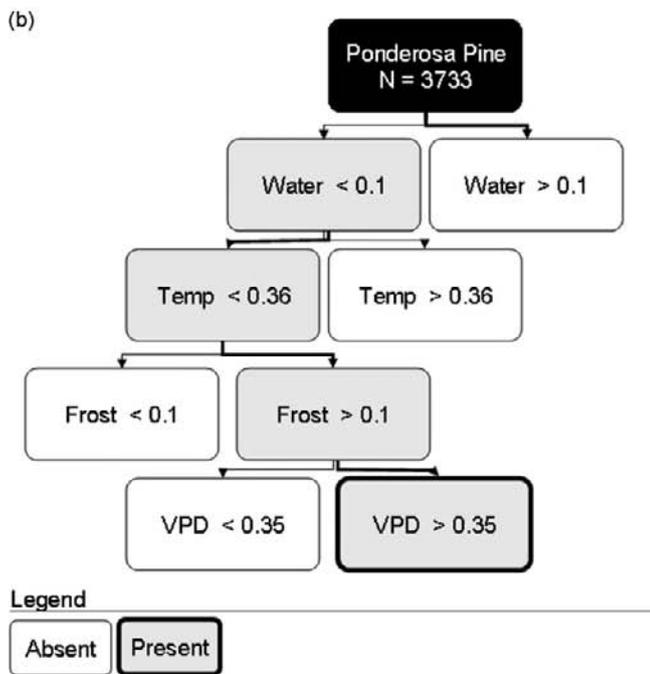
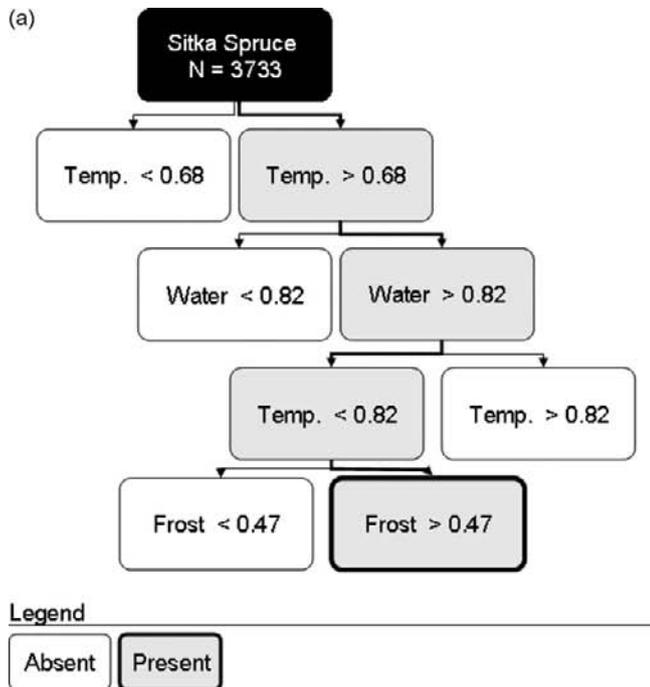


Fig. 3. (A) and (B) Decision tree rules (shown in lightest shade of gray) for Sitka spruce and for ponderosa pine indicate different orders of importance and different threshold values for the four climatically related modifiers (scaled between 0 and 1) to predict the species presence and absence. Temp = temperature modifier, Frost = frost modifier, Water = soil water modifier and VPD = vapor pressure modifier.

pled by FIA surveys and indicated on Little's range maps, although the overall accuracy was 98%. A larger sample that included areas in Canada and Alaska might improve model accuracy in estimating presence (67–68%). In the case of ponderosa pine, the model predictions closely match the distribution of FIA plots recording the species' presence, but a wider sampling is obviously required to improve predictions in California, Arizona, and New Mexico. Predictions of western juniper distribution were rarely placed in areas where the species was not recorded on FIA plots (accuracy 99%) but were predicted in areas where FIA plots were not available in

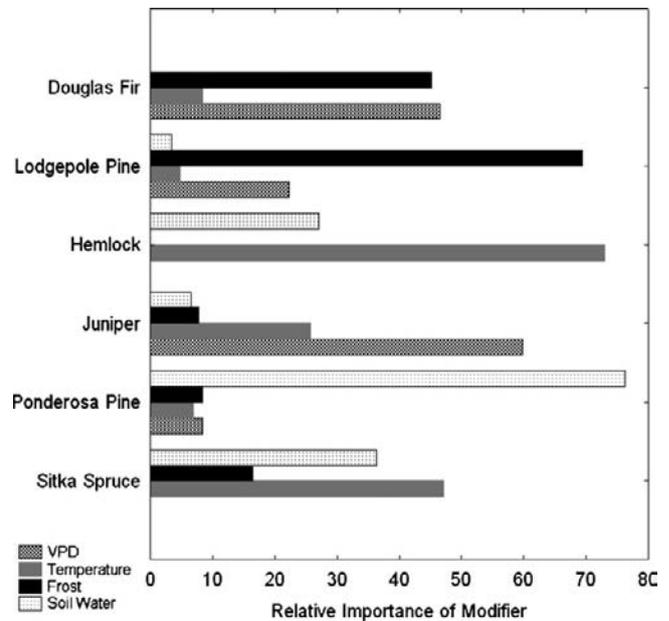


Fig. 4. Importance of the four modifiers for the six modeled species.

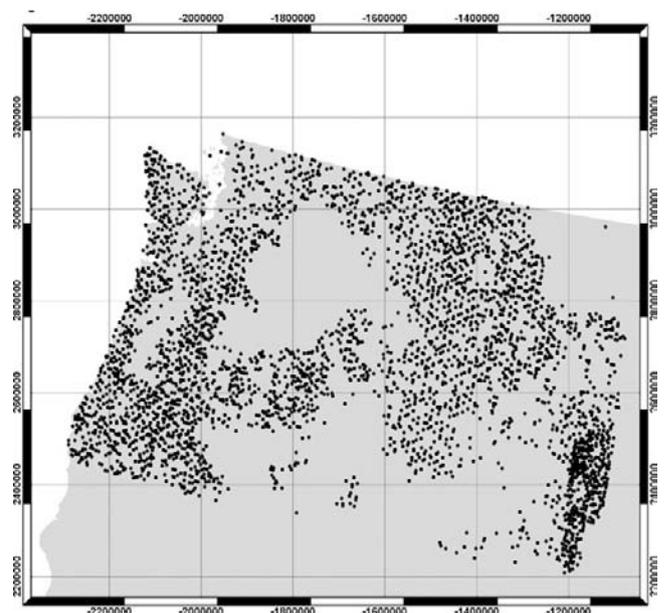


Fig. 5. The location of the 3737 FIA survey data plots used in this analysis.

the 18-year period (1980–1997) selected for this analysis. Model prediction of the distribution of western hemlock show the best correspondence to Little's range map of any of the species evaluated and had an overall accuracy of 90%. Lodgepole pine predictions were also in general agreement with Little's maps, although the distribution of the coastal subspecies *Pinus contorta* var. *contorta* was not captured. Model predictions of Douglas-fir presence on FIA survey plots were 82% correct, but the distribution is extended to areas where the species was not recorded, with a resulting drop in accuracy (66–67%).

4. Discussion

The approach developed here in this paper makes the inherent assumption that the species presence or absence at a given site is a

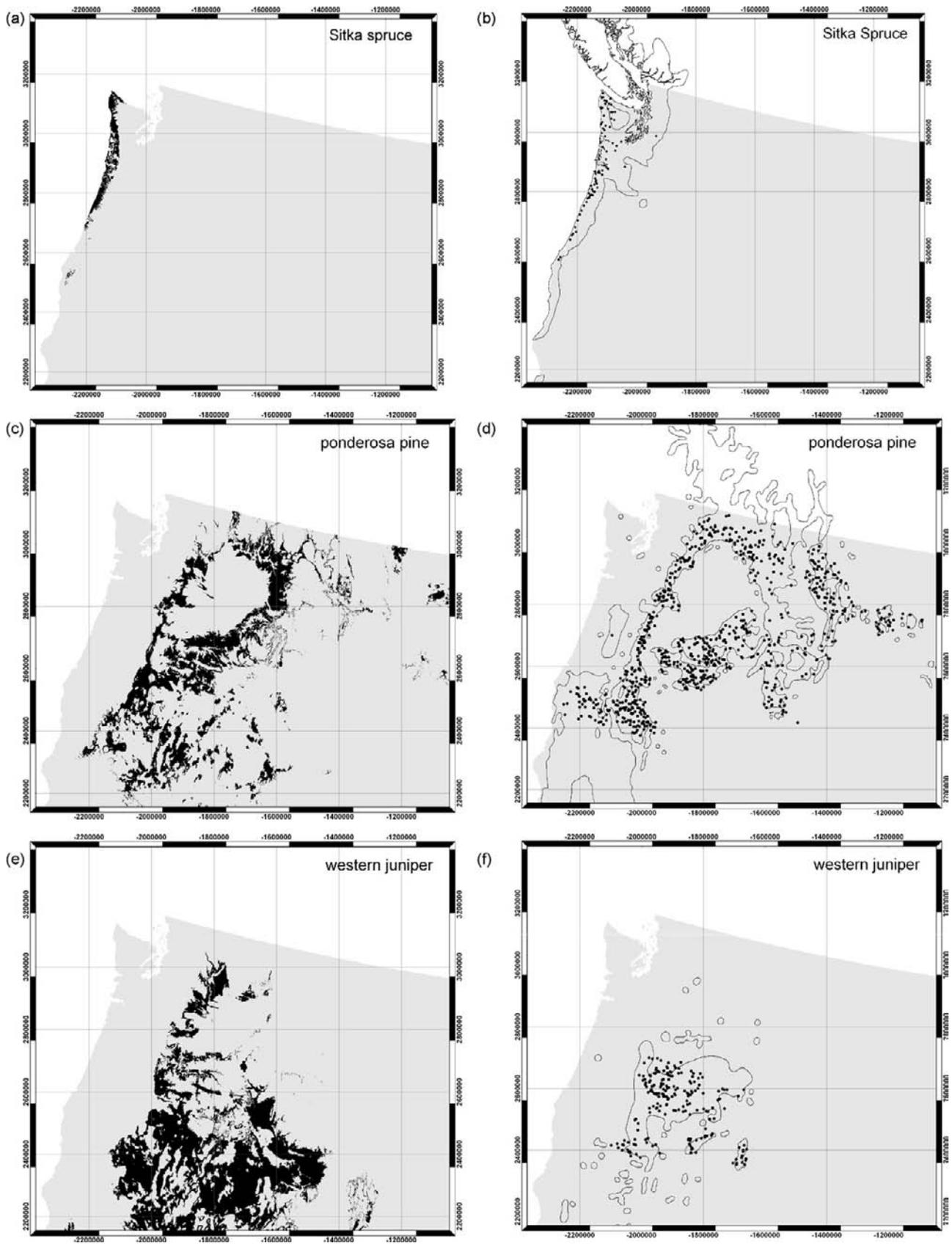


Fig. 6. (A)–(L) Maps of predicted species occurrence using regression-tree decision rules (left) in reference to presence data recorded on FIA survey plots (●), and to more general range distributions from Little (1971) (right).

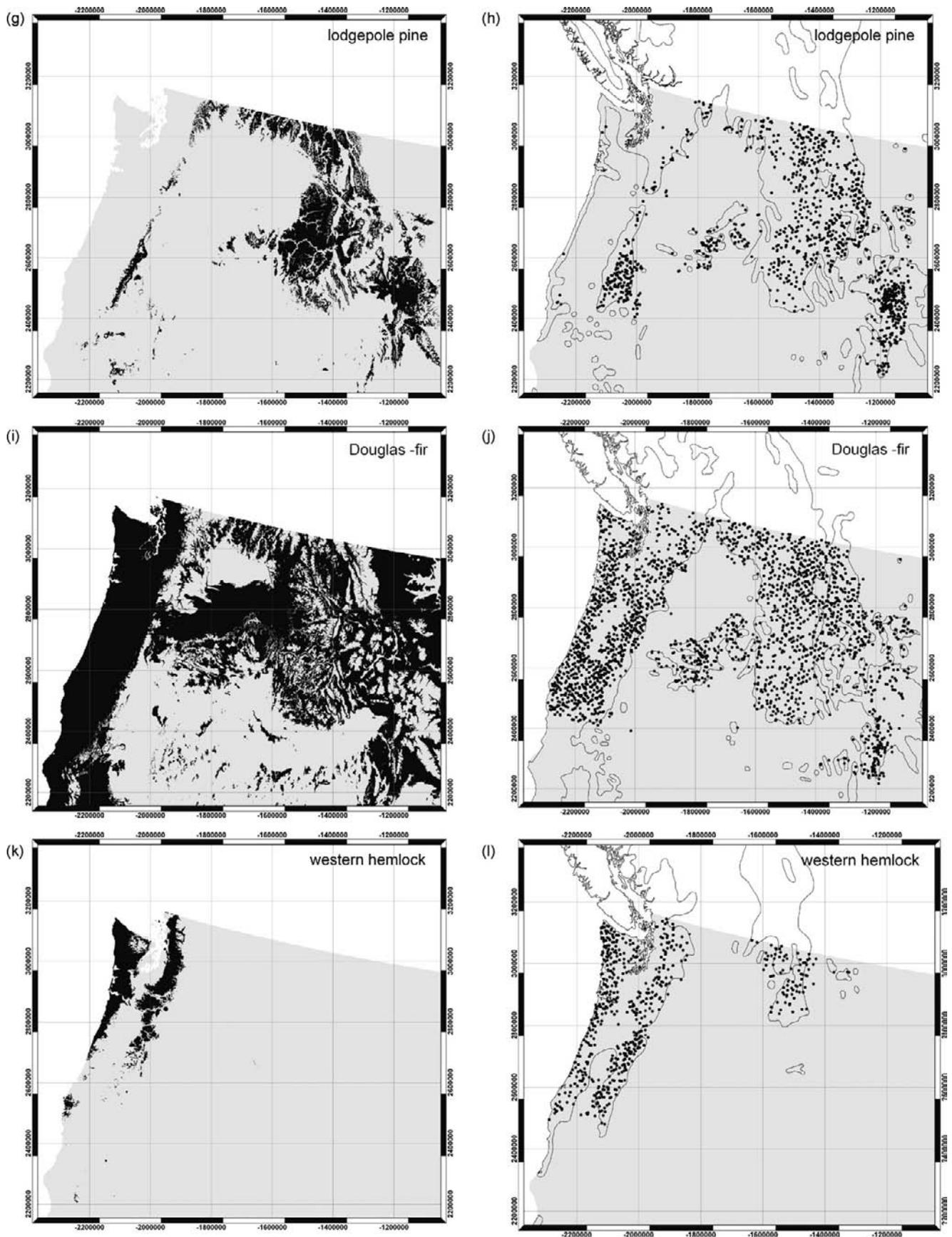


Fig. 6. (Continued).

function of plants' physiological responses (most specifically photosynthesis) to climate. Thus the idea of choosing a widely distributed tree species such as Douglas-fir as a surrogate for other evergreen conifers seems reasonable based on the results of these analyses. To adapt the approach for deciduous trees, we might choose big-leaf maple (*Acer macrophyllum* Pursh), which is also widely distributed. One of our big concerns was that presence data would not be as good of metric as abundance (or frequency of occurrence on FIA plots) to define the environments where a species is best adapted. Our preliminary analysis suggests that presence data may be adequate but a comparison needs to be made. A number of models are suited to this including, for example, the CLIMEX model (Sutherst and Maywald, 1985) which predicts the responses of species to climate, based on its current geographical distribution. The model develops a series of response functions which can then be applied to new climate data from future climate scenarios or from other locations (Sutherst, 2003).

By combining information on species abundance with predictions of stand growth we meet two of the most critical data needs for sustainable forest management activities, and this approach has potential for both species mapping efforts, as well as productivity studies. The regression tree-analysis using the four climatically related constraints on photosynthesis appears to be a powerful approach, but also requires further evaluation to see how stable the order of variables selected and thresholds defined remain as the area sampled increases (McKenzie et al., 2003). While the locations of the FIA plots are spatially smoothed, and only average an area of 0.067 ha, their benefit is that they are available across the U.S.A. in increasing numbers (Swenson and Waring, 2006; Nightingale et al., 2008). Similar surveys are also conducted in Canada (Gillis, 2001). We propose to extend the approach presented here to include more species and to incorporate data from a wider sampling area. Although a wider sample may increase the predictive power of the model, it might require recognition of subspecies and varieties that are adapted to a more restricted climatic environment (e.g. *P. contorta* var. *contorta*).

We could find some species, as they approach the limits of their range, to be restricted to environments where competition is limited. This is the case for Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) in Oregon where it grows naturally only on ultramafic soils (Whittaker, 1960). The 3-PG model includes a soil fertility index, but the mapping of soil properties is inaccurate at the scale we need (Swenson et al., 2005). Similarly, soil water holding capacity varies from <100 to >300 mm across the region. Although 200 mm has been shown to be a reasonable average, a more accurate assessment would be desirable in drought-prone areas, as demonstrated through sensitivity analyses (Nightingale et al., 2007).

There are physical stresses associated with wind, ice, snow, and selective predation by animals that also affect tree distributions that are not currently incorporated in most process-based models. Indirectly, sites where snow accumulates might be recognized through the regression-tree analysis as they rarely experience drought, high evaporative demand, or seasonally favorable temperatures for growth of Douglas-fir. High winds and salt spray typical of coastal regions might be correlated with the environmental characteristics associated with the performance of Sitka spruce, in lieu of direct measurement. Similarly, factors of succession and competition are not explicitly modeled using this approach, as we are simply looking at the presence and absence of species based on the current climatic conditions at a site.

The extent that the hybrid modeling approach will provide an adequate basis for predicting a species' performance under a changing environment, particularly one beyond that experienced in the natural range, is unknown. Paleobotanical studies suggest that many species have altered their competitive status under changing climates (Raven and Axelrod, 1974). Several Pacific NW conifers are

also known to grow as well or better in climates not commonly encountered in their home range (Waring, 2000; Waring et al., 2008). In New Zealand and in South America, some species such as lodgepole pine have escaped to invade national parks, as a result of being much better adapted to current temperatures than other endemic species (Hawkins and Sweet, 1989).

If the climate were gradually to shift to one less favorable for a native species, we would expect a hybrid model to predict constrictions on a species' range in a consistent manner. The 3-PG model, parameterized for Douglas-fir, will, under such circumstances, also predict a reduction in LAI and growth efficiency (NPP produced per unit of absorbed light). Remote sensing techniques are available to confirm reductions in LAI and to identify areas where reductions in growth efficiency are associated with major outbreaks of fire, disease, and insects (Mildrexler et al., 2006).

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