



Soil water availability effects on the distribution of 20 tree species in western North America



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ABSTRACT

The distribution of tree species is largely shaped by regional variation in climate and soils. Current models make very simple assumptions about soil water availability with limited inclusion into the predicted distribution of species. Recently, methods have been developed that integrate observations from satellites on maximum leaf area index. These remote sensing estimates, when combined with physiology can provide more detailed maps of available soil water holding capacity (ASWC) and soil fertility. By allowing soil properties as well as climate to vary across western North America, our process-based decision tree models predicted the occurrence of 20 tree species with an average accuracy of 84% ($\kappa = 0.79$), based on their recorded presence and absence on 43,404 field plots. Changes in productivity and distributions were assessed with varying soil water inputs. ASWC was increased and decreased by 50% from the originally mapped values to evaluate the effects on predicted species distributions. Soil water availability helped explain the variation in the distribution of 75% of the tree species. We found that 30% of the species were very to extremely sensitive to changes in ASWC, while 45% were somewhat sensitive. We conclude that knowledge of soil properties generally improves overall accuracy of species distribution models. Our sensitivity analysis identified the most sensitive species to changes in water availability, and indicated where additional information on soil properties would be most critical to verify.

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1. Introduction

Most ecologists and botanists recognize that the distribution of tree species within a region is shaped by both climate and soil properties (Syphard and Franklin, 2009). Increased climate change on a global scale is altering the hydrological cycle (IPCC, 2007) and affecting the amount of water available for tree growth. Differences in soil depth and water holding capacities are becoming increasingly important to identify with changes in climatic conditions (Ganey and Vojta, 2011; Peterman et al., 2013).

In the Pacific Northwest, the regional climate has become warmer since 2000 compared to a cooler phase in 1950–1975 (Waring et al., 2011). Such climate alterations are affecting forest ecosystems and their vulnerability to changes in disturbance regimes (Raffa et al., 2008; Westerling et al., 2006). In southwestern parts of the United States, extended periods of drought have been observed, leading to higher rates of tree mortality of pinyon pine–juniper (*Pinus edulis* and *Juniperus* spp.) forests caused by low water content in the soils (Peterman et al., 2013). Ganey and Vojta (2011) reported a die off in mixed-conifer and ponderosa

pine species (*Pinus ponderosa*) in Arizona during a drought event in 1997–2007. They found a high mortality of 85% quaking aspen (*Populus tremuloides*) and 28% white fir (*Abies concolor*) and attributed this to elevated temperatures associated with climate change as well as insect attack. Soil water deficits during the growing season are also prevalent in low elevation areas causing a decline in productivity (Latta et al., 2010). Water stress is known to affect plant growth by inhibiting photosynthesis and transpiration and can lead to mortality under severe conditions (Reichstein et al., 2007). There has been an expressed need to better understand the link between tree responses associated with increased exposure to drought conditions and use this to predict areas where species shifts will occur (Allen et al., 2010). Available soil water content is an essential requirement for successful tree occurrence and productivity, providing a means to quantify tree responses to hydrological changes (Weltzin et al., 2003).

Foresters and ecologists have long recognized species-specific requirements with regard to soils. For example, ponderosa pine, a widely distributed species in the Pacific Northwest, is known to be drought tolerant and can effectively compete in well-drained sandy soils (Tarrant, 1953). Douglas-fir (*Pseudotsuga menziesii*) grows in a wide variety of soils although it prefers sandy loams with good drainage (Farrar, 1995). In contrast, western red cedar

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(*Thuja plicata*) is able to survive anaerobic conditions but has a low tolerance to drought (Harlow and Harrar, 1950). Knowledge about how soil water availability influences tree species establishment and growth plays an important role for forest managers seeking to conserve biodiversity while also increasing forest resources. Soil properties determine the water available to trees and the soil type influences the amount of rainfall that evaporates or infiltrates into the soil and the amount of plant available water released in the rooting zone. A better understanding of the interaction between tree species types and soil moisture can thus improve the ability to maintain healthy, productive forests.

Whilst the importance of soil attributes on tree growth and species distributions is well known, inclusion of this information into predictive models is less common (Syphard and Franklin, 2009) and even rarer in models designed to assess the impact of climate change (Rehfeldt et al., 2009; McKenney et al., 2007). Instead species distribution models often utilize climate data and focus on climatic controls on species occurrence. McKenney et al. (2007) used the climate envelope approach to model the climate niche of 130 tree species in North America. The study did not utilize soil data due to limited maps available on a continental scale. Rehfeldt et al. (2009) modeled the distribution of quaking aspen in western USA using only climate parameters and noted that inclusion of soil factors are also important for accurate model predictions. The challenge to do so is great due to the low spatial resolution of available digitized data sets, however attempts to improve the situation continue through the development of a global digital soil map (Sanchez et al., 2009). In North America, the State Soil Geographic (STATSGO) database is the source that most species distribution modellers utilize (Iverson et al., 2008; Coops and Waring, 2001). Iverson et al. (2008) mapped species habitat in the eastern United States using soil properties derived from STATSGO, indicating that soil parameters influenced tree species distributions. However, they did not provide any further explanation on how soils might assist or constrain species range shifts under climate change. Coops and Waring (2001) also employed STATSGO to derive soil water content in Oregon. They found soil water to have an important impact on forest growth especially during summer drought conditions. All above cited authors agreed that variation in soil parameters influence the predicted distribution and growth of tree species and that coarse-resolution maps of soil properties were insufficient and need to be refined.

Recognizing the need for more accurate spatial information, a new soil map was produced from the relationship between soils, climate and forest productivity (Coops et al., 2012). The spatial variation in available soil water storage capacity (ASWC) and soil fertility (FR) were inferred at 1 km resolution by optimizing the predictive maximum leaf area index (LAI_{max}) derived with a process-based growth model with values acquired from satellite measurements.

In this study, we utilize these derived layers of soil properties to model the occurrence of tree species across the Pacific Northwest. We expand the number of native tree species evaluated and extend the area to include most of western North America. We also assess the sensitivity of model predictions to variations in soil water availability by analyzing species predictions when ASWC is increased and decreased by 50%. Finally, we evaluate the implications of recent climatic change on species distributions by comparing shifts in ranges under stable and variable soil water conditions.

2. Methods

2.1. Study region

The Pacific Northwest Region (PNW) of North America contains a number of diverse ecoregions, with varying climate and

landforms. This diversity in landforms, climate and vegetation gives rise to a wide variety of soil types (Franklin and Dyrness, 1973).

Extending from Alaska to Northern California, the Marine West Coast Forest, is the most productive PNW zone with high annual precipitation. These temperate coastal forests contain tree species such as sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and Douglas-fir, with western red cedar (*T. plicata*), grand fir (*Abies grandis*), Alaska yellow cedar (*Chamaecyparis nootkatensis*) and coast redwood (*Sequoia sempervirens*) abundant in certain areas as well. Soils in this ecoregion can vary from infertile, well-drained shallow soils to nutrient-rich bogs with high organic matter content (Valentine et al., 1978).

In the Interior, the Northwest Forested Mountains has a drier climate and is the second most productive zone. Species such as Douglas-fir, western hemlock, noble fir (*Abies procera*), western larch (*Larix occidentalis*) and pacific silver fir (*Abies amabilis*) are well distributed in this area. The subalpine environment contains species such as lodgepole pine, whitebark pine (*Pinus albicaulis*), mountain hemlock (*Tsuga mertensiana*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). The soils range from nutrient-poor to moderately rich depending on both parent material and soil formation rates (CEC, 1997).

The North American Deserts found in eastern BC and California has an arid to semi-arid climate caused by the rain shadow of the Sierra Nevada and Cascade Mountains. Species such as ponderosa pine are widely distributed, in addition to pinyon pines and junipers. Only about 2% of the ecoregion is covered by forests (McLaughlin, 1986). The ecological zone contains some very dry soils with low organic matter content associated with sparse vegetation (CEC, 1997).

2.2. Climate data

Mean monthly climate data were obtained using ClimateWNA, where long-term measurements of temperature and precipitation are interpolated spatially. PRISM (Parameter-elevation Regressions on Independent Slopes Model) records were downscaled to 1 km through bilinear interpolation and elevation adjustments (Wang et al., 2006; Daly et al., 2002) and elevation data for ClimateWNA were generated by resampling a 90 m Digital Elevation Model (DEM) from the Shuttle Radar Topography Mission (SRTM). Average monthly atmospheric vapor pressure deficits (VPD) during the daytime were calculated with the assumption that daytime water vapor concentrations are the same as those at mean minimum temperature (Kimball et al., 1997). Maximum VPD was obtained as the difference between the saturated vapor pressure at the mean maximum and minimum temperatures. Average daytime VPD was estimated as two thirds of the maximum, in order to obtain a mean daytime value instead of one derived from the daily extremes (Waring, 2000). The number of days per month with sub-freezing temperatures ($\leq 2^\circ\text{C}$) was calculated from empirical equations with mean minimum temperature (Coops et al., 1998). Similar to the methodology applied by Schroeder et al. (2009), monthly mean incoming short-wave radiation was estimated by combining the synoptic and zonal variation captured by the North American Regional Reanalysis (NARR) with topographically-driven variation based on Fu and Rich (2002). Spatial biases found through comparison with station networks from the National Solar Radiation Database (NREL) and Environment Canada (ECGC) were then removed.

2.3. Tree species plot data

Tree species presence and absence information were acquired from various sources across the PNW. In British Columbia,

species data were derived from the centroids of stand-level polygons located in protected forested areas and from vegetation resource inventory plots collected across all forest lands using a three-phase, photo- and ground-based sampling design (Schroeder et al., 2010). In Alberta, data were provided by Alberta Environment and Sustainable Resource Development. For the Canadian plots, only mature trees were considered and the spatial accuracy of the plot coordinates was approximately ± 500 m. Tree species data in the USA were acquired from Forest Inventory and Analysis (FIA) survey plots from the US Forest Service. As described in Schroeder et al. (2010), a permanent sampling grid was used to record FIA data at a density of about one plot per 2400 ha (Bechtold and Patterson, 2005). The samples included only trees of DBH > 2.54 cm and no seedlings. We used the publically available coordinates, which have been swapped between similar plots and reduced in spatial accuracy. The tree species data of Canada and USA, which were acquired from a total of 43,404 field plots, were compiled in a database for further analysis.

2.4. The 3-PG model

The 3-PG model (Physiological Principles Predicting Growth) was developed by Landsberg and Waring (1997) as a means to assess forest productivity and implications of forest disturbance across landscapes (Mäkelä et al., 2000; Nightingale et al., 2004). The model uses a number of biophysical factors and simplifications that have developed from studies over a wide range of forest types (Landsberg et al., 2003). The basic model assumptions include: (a) climate data can be used in monthly time intervals to capture major trends, (b) net primary production (NPP) and autotrophic respiration (R_a) are constant fractions of gross primary production (GPP), (c) maximum canopy conductance becomes constant when LAI > 4.0 and (d) the proportion of photosynthate decreases linearly with nutrient availability to a minimum of $\sim 25\%$ of NPP (Landsberg and Sands, 2010).

The 3-PG model calculates forest growth, GPP, NPP, LAI, transpiration, and litterfall on a monthly basis. Absorbed photosynthetically active radiation (APAR) is estimated from global solar radiation and LAI. The actual portion of APAR used for photosynthesis is constrained by environmental factors that are applied to the model, ranging from 0 being most limiting to 1 representing no constraint on photosynthesis. The environmental modifiers include (a) average daily temperature, (b) soil water limitations, (c) mean vapor pressure deficits (VPD) during the daytime and (d) the frequency of frost. Drought effects are determined with a monthly soil water balance that is continuously updated based on the amount of precipitation, evaporation from the canopy and transpiration calculated with the Penman–Monteith equation (Landsberg and Waring, 1997; Monteith, 1965). The most limiting climate variable on photosynthesis is defined each month based on maximum deviation from optimum conditions.

We parameterized the 3-PG model for Douglas-fir, the most widely distributed species in the region using forestry yield tables and field-based observations that are reported in Coops et al. (2012). The seasonal constraints on photosynthesis derived from the model were then applied to other species to predict their suitable ranges using a hybrid modeling approach described by Coops et al. (2009). Unlike most previous studies, where soil properties were assumed to be uniform, soil maps produced by Coops et al. (2012) account for variations in soil fertility and moisture on a regional scale. The 3-PG model defines the fertility-dependent growth modifier as a function of the soil fertility rating, where the poorest soils were ranked zero and the most fertile as one

(Landsberg and Waring, 1997). ASWC was allowed to vary across the region from 0 to 300 mm.

In this study, we analyzed the effect of soil water availability on LAI_{max} by generating spatial layers of LAI with varying soil variables. We compared the simulation results of baseline conditions using spatially variable maps of ASWC (Coops et al., 2012) with FR values held constant at 0.5 to modeled values of LAI_{max} when both soil variables were held constant (FR = 0.5, ASWC = 200 mm). The maximum photosynthetic efficiency was set to $0.04 \text{ mol C mol}^{-1} \text{ photon}^{-1}$ when FR was held constant.

2.5. Predicting species distributions with decision tree models

We combined the 3-PG process-based growth model outputs with a decision tree analysis to map species distributions following methods of Coops et al. (2009). Monthly mean climate from 1950–1975 acquired from ClimateWNA was used in the 3-PG model, which was run for 50 years following establishment of a stand planted with 300 seedling ha⁻¹. The long-term climate record was chosen to match the plot data of tree species occurrences. Model outputs included four monthly environmental constraints with the potential to limit photosynthesis for Douglas-fir. The seasonal averages of the climate modifiers were then related to the field-based observations by extracting this information at each of the 43,404 plots distributed within the PNW. Using Decision Tree Regression (DTREG, Sherrod, 2010) software, we determined the relative importance of the four variables for each tree species and predicted their presence and absence across the landscape. Model accuracies were calculated as a weighted value of the percentage of plots where the species occurrence was correctly assigned, proportional to the number of plots corresponding to the two categories, presence and absence. For species that had a low presence value, the categories were balanced by increasing the weight of data rows of the minority category so as to make the sum of all of the target categories equal. Accuracy was assessed through a 10-fold cross-validation technique, where the data were divided into 10 random groups of equal size. Nine of the groups were used in the model and tested against the remaining 10% of the data. The procedure was repeated 10 times and the overall accuracy was determined from the average of the 10 results in a process known as k-fold partitioning (Breiman et al., 1984). The Kappa statistic (κ) statistic was also calculated to evaluate the accuracy of the species models. When the predicted values were in agreement with the observed plots, $\kappa = 1$ and when there was no agreement, $\kappa = 0$. If one category has a significantly larger class size, then κ will be less than one, in which case κ can be rescaled to match the observed marginal frequencies (Ben-David, 2008). Species distribution results were also visually compared to field survey plots and to existing range maps (Little, 1971).

2.6. Sensitivity analysis

A sensitivity analysis was conducted to determine the effects of varying ASWC across the study area on the distributions of selected tree species. ASWC was increased and decreased by 50% from baseline conditions while fertility was held constant at 0.5. Simulations were run using contemporary monthly climate data (1976–2009), which includes the available decade of reprocessed MODIS LAI_{max} values to produce the spatial soil layers (Coops et al., 2012). The environmental constraints were then applied to the decision tree analysis to generate the resulting tree species models. The extent that the spatial distribution of each tree species was altered was assessed by comparing consecutive runs of the species distribution models.

3. Results

Comparison of predicted LAI_{max} resulting from different values of soil properties helped identify where a more accurate assessment of ASWC appears critical to predict the distribution of tree species. The difference between LAI_{max} with constant FR (0.5) and when both variables were held constant is shown in Fig. 1. The greatest difference in LAI_{max} occurred in parts of Marine West Coast Forests in Washington and Oregon, with increases of $>0.8 \text{ m}^2 \text{ m}^{-2}$ observed when using the spatial map of ASWC. In these areas, values of ASWC $> 200 \text{ mm}$ are required to maintain LAI_{max} commensurate with forest productivity (Waring et al., 2008). LAI_{max} values were $>0.8 \text{ m}^2 \text{ m}^{-2}$ lower in the North American desert zone to the east of the Cascade and Sierra Mountains

when using variable compared with fixed values of ASWC. Low rainfall in these areas combined with shallow soils lead to sparse vegetation and low productivity. Over much of the study area, LAI was at least $0.2 \text{ m}^2 \text{ m}^{-2}$ higher when ASWC was allowed to vary over the landscape.

The accuracies of the predicted species distributions using the variable soil layers from Coops et al. (2012) are displayed in Table 1. The overall accuracy of the species models averaged 84% with a kappa value of 0.79. Generally, the overall presence accuracy was slightly higher (88%) than the absence accuracy (81%) of the species. Sitka spruce had the highest overall accuracy of 94% ($\kappa = 0.92$) with a presence accuracy of 96%. The lowest model accuracy of 70% was for lodgepole pine with a κ value of 0.62 indicating only moderate agreement of model predictions with the plot values.

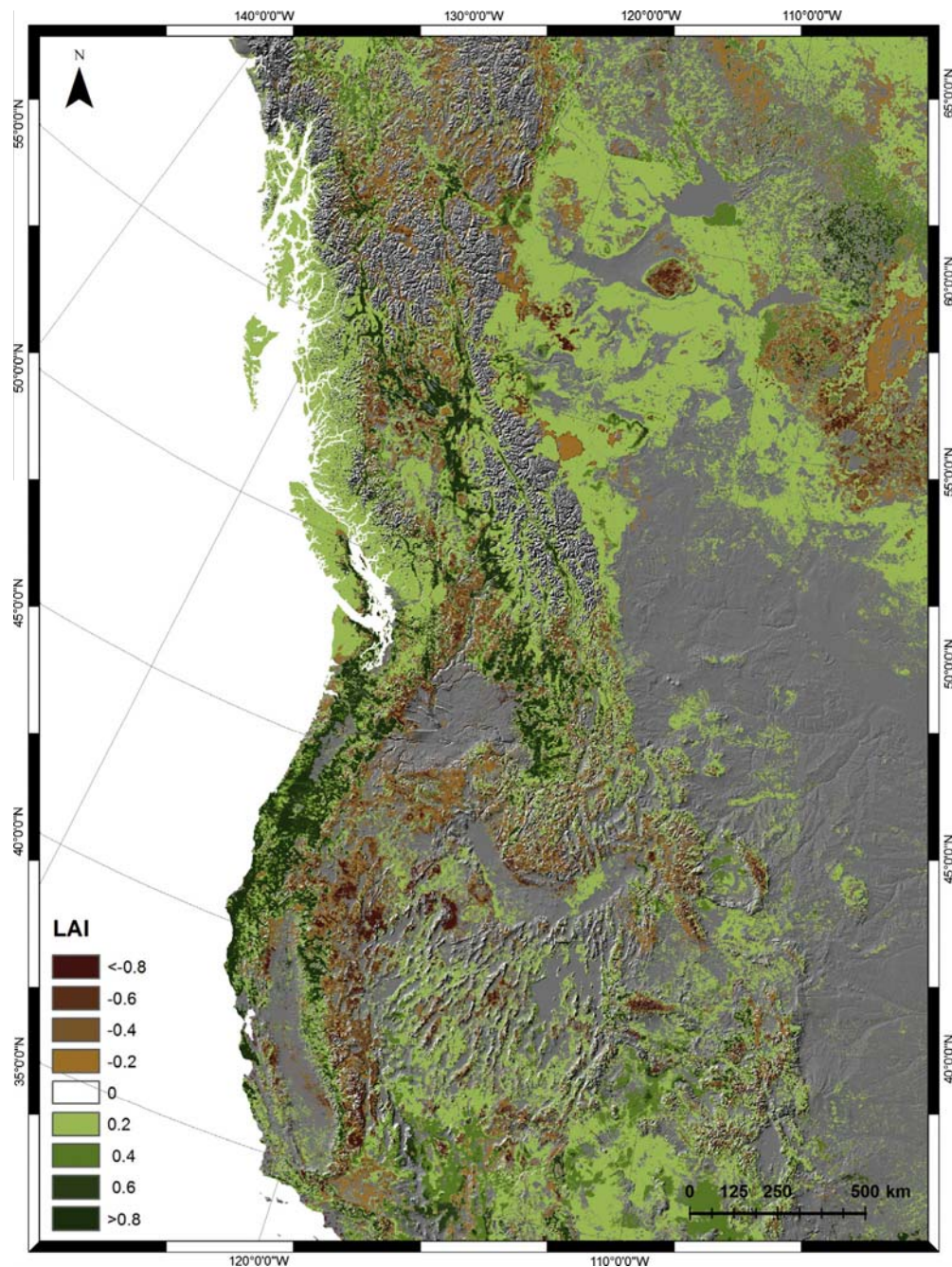


Fig. 1. Predicted changes in LAI ($\text{m}^2 \text{ m}^{-2}$) when available soil water content was first allowed to vary from 0–300 mm and then held constant at 200 mm. In both simulations, soil fertility was held constant at a median level of 0.5.

Table 1

The accuracy of decision tree models derived for each of 20 tree species based on mean monthly climate conditions during the period 1950–1975.

Species	Presence accuracy (%)	Absence accuracy (%)	Overall average (%)	κ
Lodgepole pine	68	78	70	0.626
Douglas-fir	74	80	78	0.599
Pinyon pine	84	96	90	0.910
Subalpine fir	95	62	79	0.856
Engelmann spruce	84	72	78	0.887
Whitebark pine	91	81	86	0.805
Western larch	88	83	85	0.742
Pacific silver fir	90	87	88	0.790
White fir	93	80	87	0.839
Grand fir	85	79	81	0.675
Noble fir	93	90	91	0.858
Alaska yellow cedar	95	90	92	0.895
Utah juniper	95	82	89	0.890
Sitka spruce	96	92	94	0.922
Western white pine	81	70	75	0.570
Western red cedar	87	79	83	0.718
Western hemlock	95	80	87	0.883
Mountain hemlock	85	88	87	0.754
Ponderosa pine	91	73	82	0.779
Quaking aspen	82	71	77	0.895

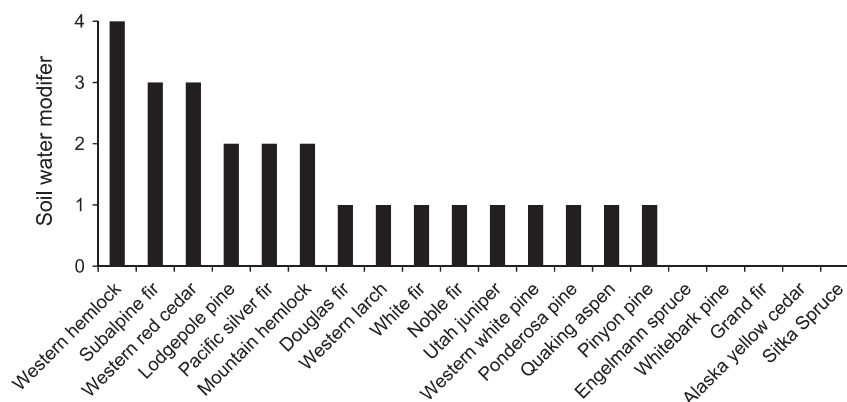


Fig. 2. Occurrence of soil water modifiers (annual, spring, summer, fall, winter) in decision tree models for each of 20 tree species native to the Pacific Northwest Region.

Fig. 2 presents the number of times the soil water modifiers were included in a decision tree model for each species. ASWC explained the variation of 75% of the tree species, where 30% were extremely sensitive and 45% somewhat sensitive to changes in water availability. Of these, western hemlock had the most sensitivity to a soil water modifier, with all four seasons contributing to predicting its presence across the PNW. The occurrence of western red cedar was also highly affected by ASWC during the summer, winter, and averaged annually. Douglas-fir and ponderosa pine, the two most widely distributed species, were relatively insensitive to variation in seasonal ASWC values, with the variable appearing only once in their respective decision tree models. Engelmann spruce, whitebark pine, grand fir, sitka spruce and Alaska yellow cedar appear completely insensitive to ASWC (Fig. 2).

The importance of each soil water modifier in determining the distribution of the tree species is indicated in Fig. 3. Out of the 20 species, 15 had at least 1 variable involving soil water in their respective decision tree model. Of these, 6–38% of the variance was explained by soil water related variables. Soil water deficits during the summer were the most limiting on species occurrences, accounting for 38% of the variance in the species range-prediction models. Drought during this time of the year provided a major constraint on the distribution of western red cedar and western hemlock. The amount of moisture in the soil during the wintertime was also an important constraint, reducing the distribution of some of the species by 21%. Because we did not account for accumulation

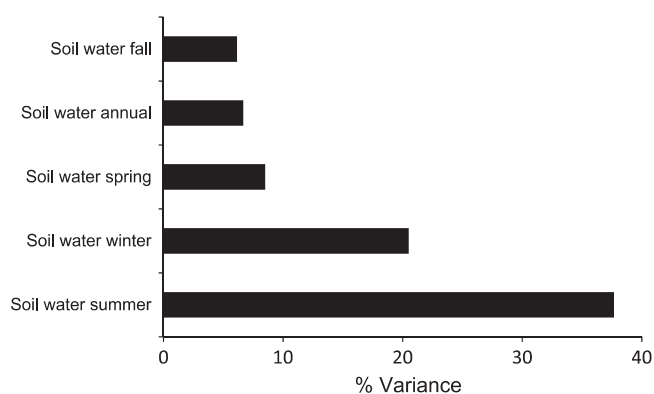


Fig. 3. Importance of each soil water modifier in determining the mean % variance of the tree species.

of a snowpack when temperatures remain below freezing, the 3-PG model predicts that soils will remain at field capacity in much if not most of the subalpine forest zone in the winter. As a result, soils with high winter water contents are surrogates for areas where a heavy snowpack normally accumulates and thus are important in defining the range of lodgepole pine, subalpine fir, and four other snow-adapted species. ASWC annually and during

the spring and fall played a lesser role in defining species distributions, contributing between 6% and 9% of the prediction's accuracy (Fig. 3). Below we discuss the results in relation to Douglas-fir and western white pine, two tree species with different soil water tolerances.

Changing the soil water holding capacity had varying effects on the species distributions. Western white pine, a species that grows on productive sites and has a low tolerance to drought conditions, exhibited a contraction of its range, with 50% reduction in baseline ASWC in Idaho, Montana, and the Interior of BC (Fig. 4a). Decreasing ASWC by half reduced the overall range of western white pine by 6% (Table 2), whereas increasing ASWC by 50% had no measurable effect. Among the water deficits, those in the spring were most important in defining the range of western white pine. The range of the tree species extends from the coast of BC to the east of the Cascade and Sierra Mountains in Washington, Oregon and Idaho (Fig. 4c).

Increasing ASWC by 50% resulted in the expansion of predicted Douglas-fir distributions along the coast of BC and Vancouver Island, while simultaneously decreasing it in parts of California and Oregon, where such changes may favor other species (Fig. 4b). Douglas-fir is moderately drought tolerant and does not grow well on water-logged soils. Increasing ASWC by 50% reduced its overall range by 13%, whereas decreasing ASWC compressed its range by only 3% (Table 2). Douglas-fir is well represented in the Marine West Coast Forests of BC, Oregon, and Washington, and extends southward to California. It is also found in the Northwest Forested Mountains to the east of the Rocky Mountains in the United States and Canada (Fig. 4d).

Sensitivity analysis of western red cedar showed the largest potential change in species distribution. When ASWC was reduced by half, its range expanded by 27%. Western hemlock produced the greatest change when ASWC was increased by 50%, with its range reduced by 21% of baseline ASWC values. Both Engelmann spruce and whitebark pine displayed no change in distribution with varying ASWC. In general, the tree species were more sensitive to the presence or absence of excess soil moisture conditions (representing heavy winter snowpack) because they normally experience little soil water deficit (Runyon et al., 1994).

4. Discussion

Species distribution models are most useful to not only predict but also to improve our understanding of potential shifts in range. As demonstrated in this paper, the degree that soil water deficits occur seasonally has a measurable effect on the accuracy of predictions for a majority of the 20 native tree species. We also showed in predicting LAI_{max} that ASWC becomes a critical variable to include in models of forest productivity (Coops et al., 2012). Climate change affects soil properties and depending on the soil type, texture and depth impacts their ability to retain and release water. Changes in temperature and precipitation patterns can affect the soil water balance, which as we have shown, changes the predictions of species distributions. In combination, climate and soils also may alter the vulnerability of forests to disturbance from insects, pathogens and wildfires (Westerling et al., 2006; Raffa et al., 2008).

In this study, we demonstrated the important link between forest productivity and soil water storage capacity, reinforcing the growing need for quantitative information on soil properties. Soil water has an impact on LAI, which in turn affects photosynthetic uptake and evapotranspiration of the trees (Landsberg and Waring, 1997). The soil maps derived by Coops et al. (2012) and used in this study are a step forward in providing continuous spatial information across large regions. The extent to which the approach can

be refined is unknown but worth pursuing as remote sensing techniques become more sensitive.

We predicted the occurrence of tree species in the Pacific Northwest by increasing the tree species number to 20 and expanding the area to include Alberta and U.S. states in the Western Rockies. Inclusion and employment of the soil map helped increase the model accuracy of the tree species compared to the previous study, where soil properties were held constant. Studies have found that combining climate, soil, and satellite imagery produced highest model accuracies than when omitting any of these variables (Salajano et al., 2010; Iverson et al., 2008). Meyer and Thuiller (2006) also reported that inclusion of variables at different spatial scales can increase the overall accuracy of model predictions. Sensitivity analysis revealed that the distribution of many of the tree species is variable with soil water holding capacity. The range of western white pine contracted slightly with reduced ASWC, while increasing water availability had no effect. It used to dominate the Interior Northwest forests of North America, however drought has made western white pine prone to disease and its distribution has been greatly reduced due to white pine blister rust (Harvey et al., 2008). In our analysis, Douglas-fir was more vulnerable to excess soil moisture in the rooting zone than to drought conditions. Field measurements and model predictions confirm the species to be tolerant to drought by accessing soil water in deeper soil layers and in fractured bedrock (Waring et al., 2008). The species generally prefers soils with good drainage and has a lower tolerance to waterlogged conditions (Farrar, 1995). Ponderosa pine was also sensitive to ASWC, with varying soil moisture content altering its spatial distribution. The tree species is known to be drought tolerant and grows best in sandy soils with good drainage. Reduction of ASWC enabled expansion of the Ponderosa pine range, indicating that increased water stress associated with climate change will enable drought-adapted species such as ponderosa pine and Douglas-fir to thrive in a changing environment.

Changes in ASWC did not affect all tree species. Engelmann spruce was insensitive to increases and decreases in soil moisture. The species is frequently found in saturated soils with a high water table and has a moderate tolerance to drought (Alexander and Shepperd, 1990). Summer frost and air temperatures during the fall and annually were more important in the decision tree model in determining its presence over the landscape. In our analysis, pinyon pine was also not affected by reduced available soil water conditions. A decline in pinyon pine in southwestern USA has been previously attributed to increased drought exposure (Peterman et al., 2013). Soil water availability did not seem to be the main cause of species decline in our study, and long term increases in vapor pressure deficits associated with a warming trend may play an equally important role (Waring et al., 2011).

It is recognized that climate is the main control on species distributions at broad spatial scales (Salajano et al., 2010). Temperature variables are important indicators of climate change and its impact on species distributions. Elevated minimum winter air temperatures have been associated with increased bark beetle activity (Raffa et al., 2008), leading to widespread tree mortality such as the mountain pine beetle attack on lodgepole pine trees in BC. Tree species such as whitebark pine were shown to be more vulnerable to changes in air temperature than to changes in precipitation and the ASWC (Schrage et al., 2008). In our study, whitebark pine was also unaffected by ASWC and its distribution was mainly determined by suitable climate conditions. Nonetheless, our results indicate that water availability to trees also plays an important role in the decision tree models and can provide further insight into species-specific requirements. Climate and soil variables are spatially interrelated and it can be challenging to examine their importance on model predictions separately. For example, an increase in temperature is likely associated with greater runoff from

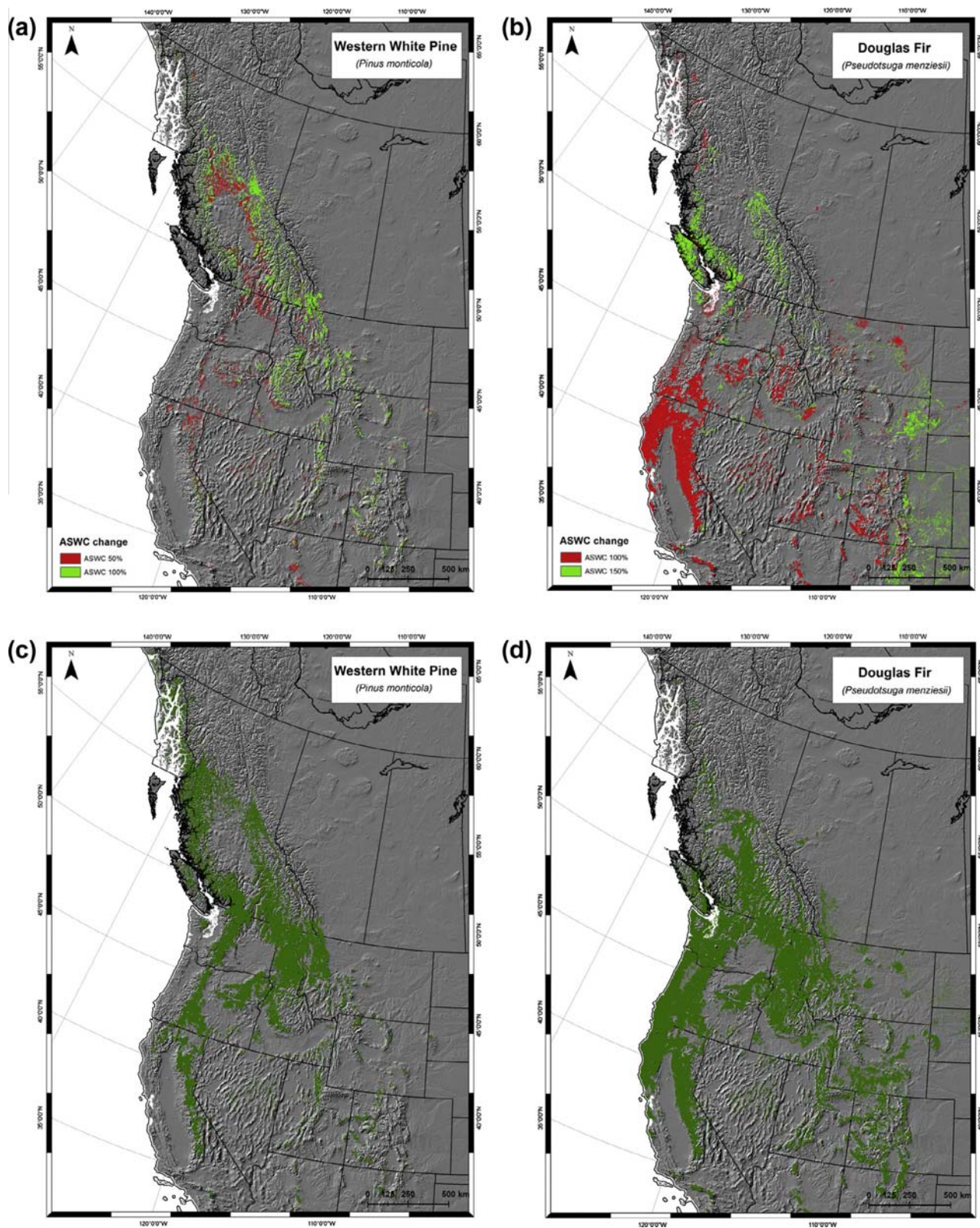


Fig. 4. Changes in the distributions of two species with varying available soil water content (ASWC) during the period 1976–2009. The expansion of (a) western white pine range for ASWC at baseline conditions (green) and when reduced by 50% (red) and (b) Douglas-fir range at baseline conditions and when increased by 50%. The current range of (c) western white pine and (d) Douglas-fir at baseline ASWC values are also shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

snowmelt and early soil water recharge, which in turn could cause soil water depletion earlier in the growing season (Hamlet et al., 2007). We expect adaption to changes in heavy snowpack to be

an important constraint on the distribution of subalpine species, which is currently not included in the 3-PG model and thus may diminish the effects of drought.

Table 2

Current predicted ranges and percent change in species distributions when increasing or decreasing ASWC by 50% compared with baseline values with variable ASWC maps (Coops et al., 2012) and constant FR (0.5).

Species	Total range (km ²)	Decrease ASWC 50 (%)	Increase ASWC 50 (%)
Western white pine	527,791	–6	0
Douglas-fir	915,579	–3	–13
Western hemlock	475,097	+14	–21
Pinyon pine	140,244	+17	+9
Ponderosa pine	115,130	+21	+9
Western red cedar	478,509	+27	–9
Engelmann spruce	965,623	0	0
Whitebark pine	788,490	0	0

Future work can help to continuously improve the quality of the soil data. Currently, MODIS derived estimates of LAI_{max} saturate at values >7.0 m² m^{–2} and cannot identify LAI values that extend to 10 m² m^{–2} and higher. Therefore, the soil maps used in this study were likely unable to portray the most productive and fertile sites in the PNW. As remote sensing techniques are improved, more accurate estimates of LAI can be achieved which, in turn, will improve the spatial soil maps. Airborne Light Detection and Ranging (LiDAR) can capture the full spectrum of LAI and quantify values exceeding 7 m² m^{–2} (Lefsky et al., 2002). With increased accessibility to LiDAR data, more accurate soil properties can be determined which will help to improve species model predictions. Disturbances caused by insect, fires, and disease are processes interrelated with climate and soil and are currently not considered in species models. Incorporating these into future species distribution models is beneficial when determining the presence of tree species and the effects of changing climate and soil conditions (Malmström and Raffa, 2000).

This study highlights the importance of soil water availability in successful species occurrence over the landscape. It emphasizes the sensitivity of certain tree species to changes in ASWC and others that are adapted to fluctuations. Current models often lack adequate soil data and an understanding of the mechanisms controlling species distributions. Uncertainties in data inputs can have a large impact on predicted distributions of certain species as shown in the sensitivity analysis. Changes in climate are altering precipitation patterns and the amount of plant available water, which has an impact on species occurrences. The study informs us where future field surveys will benefit in validating the model predictions and where soil management is required for climate change adaptation. Improving our knowledge on species requirements in terms of water availability and their tolerance to drought will be beneficial to improving the accuracy of model predictions in a changing climate scenario. This will help forest managers and ecologists to maintain forest productivity and adopt silvicultural practices that can preserve forest resources in western North America.

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