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Release of Oregon White Oak from Overtopping Douglas-fir: Effects on Soil Water and Microclimate

Abstract

Many former Oregon white oak (*Quercus garryana*) woodland and savanna stands in the coastal Pacific Northwest have been invaded by Douglas-fir (*Pseudotsuga menziesii*) during the past century as a result of fire suppression. Douglas-fir overtop and suppress the shade-intolerant oak, causing its eventual mortality. Removal of Douglas-fir is necessary for restoration of these oak ecosystems, but such action will influence belowground and near-ground conditions, affecting residual trees and understory communities. In a three-year study on a glacial outwash soil near Olympia, Washington, we compared soil and microclimate conditions near overtopped and released oak trees to determine how soil water content (SWC), throughfall, soil and air temperature, and vapor pressure deficit (VPD) are affected when oak is released from overtopping Douglas-fir. In each year, volumetric SWC near all trees declined from ~0.25 $m^3 m^{-3}$ to ~0.10 $m^3 m^{-3}$ during the growing season, but this decline was delayed approximately one month in the released condition. Additionally, minimum SWC during late summer was 0.02 to 0.03 $m^3 m^{-3}$ greater near released trees than near overtopped trees. The understory in the released condition consumed more soil water than that in the overtopped condition, but only in the first year after release. During light rain events from May through July, throughfall was 170% greater in the released condition than in the overtopped condition. Release from Douglas-fir increased soil temperature, maximum air temperature, and maximum VPD. Release of oak trees from overtopping Douglas-fir reduced early- to mid-summer competition for soil water, which will likely benefit the formerly suppressed oak trees.

Introduction

The extent of Oregon white oak (*Quercus garryana*) woodlands and savannas in the Pacific Northwest has significantly diminished since Euro-American settlers arrived in the mid-1800s (Crawford and Hall 1997). Stands formerly maintained by frequent, low-intensity fires set by Native Americans have become dominated by conifers, particularly Douglas-fir (*Pseudotsuga menziesii*), which have invaded in the absence of fire (Agee 1993, Tveten and Fonda 1999, Thysell and Carey 2001). Douglas-fir has overtopped and subsequently suppressed the shade-intolerant oak, and, without intervention, the oak will not survive or regenerate. Oregon white oak stands and associated prairies are unique habitats in a conifer-dominated landscape, and their loss and fragmentation may negatively impact species such as the western gray squirrel (*Sciurus griseus*) and other animal and plant species associated with these more open habitats (Wilson et al. 1997, Bayrakci et al. 2001).

Long-suppressed Oregon white oak trees, even those with extensive crown dieback, respond positively to release from (i.e., removal of) Douglas-fir competition (Devine and Harrington 2006). In the first several years following release, stem growth and acorn production increase, and crowns expand through epicormic branching. The understory response to Douglas-fir removal indicates that conditions become favorable for non-native, invasive graminoid and shrub species (Devine et al. 2007). These vegetation responses to release are likely influenced by changes in soil water content (SWC) and near-ground microclimate, but these variables have not been studied in this context.

Removal of forest canopy trees typically reduces stand-level evapotranspiration, thus increasing SWC (Minckler and Woerheide 1965, Adams et al. 1991, Bréda et al. 1995, Beckage et al. 2000, Ritter et al. 2005). Because these changes in SWC are primarily a function of plant transpiration, they are also seasonal in nature, often occurring only after cumulative depletion of soil water during the growing season (Gray et al. 2002, Ritter et al. 2005). The rapid, positive effect of canopy removal on SWC typically diminishes over time as vegetation develops (Minckler et al. 1973, Stone et al. 1978, Adams et al. 1991).

Douglas-fir canopies may intercept a significant fraction of precipitation, reducing the amount of

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water entering the soil profile (Schaap et al. 1997). Interception rates may be especially high during light rain events in summer (Rothacher 1963). Crowns of broadleaf species, due to their typically decurrent form, affect throughfall differently than crowns of conifers (Voigt 1960, Iroumé and Huber 2002). Throughfall rates beneath crowns of oak trees have been reported to be similar to or greater than rates beneath crowns of conifers (Fenn and Bytnerowicz 1997, Cantu and Gonzalez 2001).

Manipulation of the forest overstory alters near-ground microclimate and soil temperature, which in turn may influence soil biological processes and affect understory composition and growth of tree regeneration (Chen et al. 1999, Aussenac 2000, Singsaas et al. 2000, Proe et al. 2001). In the absence of a forest canopy, air temperatures typically become more extreme, with warmer summer temperatures and greater diurnal fluctuation (Carlson and Groot 1997, Gray et al. 2002, Ritter et al. 2005). Overstory removal increases near-ground vapor pressure deficit (VPD) which is associated with an increase in plant transpiration rate; although, at higher VPD levels, this increase is attenuated by stomatal closure (Martin et al. 1997, Bond and Kavanagh 1999, Oren et al. 1999, Davies-Colley et al. 2000).

The objectives of this study were to determine how release of Oregon white oak trees from overtopping Douglas-fir influences SWC, throughfall, soil temperature, near-ground air temperature and VPD. Such information may facilitate management and restoration of Oregon white oak stands following the significant changes in structure that occur when invading conifers are removed from the overstory.

Methods

Study Area

The study area is in a Douglas-fir–Oregon white oak stand located in the Puget Trough physiographic province in western Washington on Fort Lewis Military Reservation (46°55' N, 122°42' W). The site is a glacial outwash terrace, and the soil is a Spanaway gravelly sandy loam (sandy-skeletal, mixed, mesic Typic Melanoxerand), classified as somewhat excessively drained (Pringle 1990). This type of soil is characteristic of oak savanna and prairie sites in the Puget Sound lowlands. A typical soil profile at the study site consists of a 2-cm-thick O horizon over a 50-cm-thick sandy loam A horizon containing 35% pebbles by volume. This is underlain by a 20-cm-thick Bw horizon (sandy; 55% pebbles; 5% cobbles) and a C horizon from 70 to 200+ cm (sandy; 75 to 85% pebbles; 5% cobbles) (Devine and Harrington 2005). Long-term mean annual precipitation in the nearby city of Olympia is 1291 mm, with 191 mm occurring between 1 May and 30 September (Western Regional Climate Center 2007). Mean annual air temperature is 10°C, and mean temperatures in January and July are 3°C and 17°C, respectively (Western Regional Climate Center 2007).

The pre-treatment stand consisted of an overstory of Douglas-fir, averaging 215 trees ha^{-1} [trees $\geq$10 cm diameter at breast height (dbh)] and a midstory of Oregon white oak averaging 124 trees ha^{-1} (trees $\geq$10 cm dbh), many of which exhibited some degree of crown dieback resulting from decades of overtopping. Other tree species (mostly broadleaf) totaled 40 trees ha^{-1}, but rarely occurred on study plots. Basal area was 40.3 and 9.3 m^2 ha^{-1} for Douglas-fir and oak, respectively. A sample of typical midstory oak trees (n=7) ranged in age from 89 to 111 years at 15 cm above groundline. Overstory Douglas-fir trees were generally between 60 and 80 years of age. While the oak trees in this study originated after Euro-American settlement, the large, spreading crowns of several older oak trees near the study area suggest that a savanna condition existed prior to settlement. The current Douglas-fir overstory is the first generation of conifers to colonize this former savanna site. At the time of study installation in January-February 2003, a light commercial thinning of Douglas-fir occurred. Two similar thinnings took place prior to 2003, the most recent in 1988.

The site is characterized by the Oregon white oak-Douglas-fir/snowberry (*Symphoricarpos albus*)/swordfern (*Polystichum munitum*) plant community type (Chappell and Crawford 1997). The most prevalent woody understory species in 2003 were snowberry, trailing blackberry (*Rubus ursinus*), and beaked hazelnut (*Corylus cornuta* var. *californica*). The most prevalent herbaceous species were swordfern, white insideout flower (*Vancouveria hexandra*), California nettle (*Urtica dioica* ssp. *gracilis*), long-stolon sedge (*Carex inops*), cleavers (*Galium aparine*), and smallflower nemophila (*Nemophila parviflora*).

Study Design

The study followed a completely randomized, split-plot design with 12 study plots (the experimental units). Each circular study plot was centered on a midstory oak tree, hereafter called a "study tree." Each study plot radius was equal to the height of its study tree at the time of study installation (mean=17.0 m). The study trees were typical of the larger oak trees in the stand (dbh=22.2-46.4 cm; height=11.1-24.5 m), and all were partially or completely overtopped by Douglas-fir prior to treatment. The two tallest Douglas-fir trees on each study plot averaged 39.5 m in height and 83.6 cm dbh.

The whole-plot treatment was presence or absence of release from overtopping conifers (i.e., "released" and "overtopped" conditions), assigned randomly with six replications. On plots assigned to the released condition, all Douglas-fir were removed from the plot in January-February 2003; an average of 21 trees were removed per plot. In each of the plots assigned the overtopped condition, two or fewer Douglas-fir trees were removed as part of a concurrent stand-level commercial thinning. Removed trees were cut with chainsaws and yarded with skidders. No oak trees were removed.

Three split-plot treatments were used to determine the effects of the study tree's crown and the understory vegetation on various dependent variables. Split-plot treatment A was a location beneath the study tree's crown, 1.0 m from the stem base (Figure 1). Split-plot treatments B and C were each randomly assigned to one of two locations, 2.0 m apart and 2.0-3.0 m beyond the dripline of the study tree's crown, at an azimuth of 360 degrees. The distance from the study tree's stem to the location of treatments B and C was 6.6 to 8.1 meters, depending on crown size. In treatments A and B, understory vegetation was not disturbed. Treatment C consisted of understory exclusion from a circular plot, 1.0 m in diameter, centered on a soil water sensor. To exclude roots of understory plants, the perimeter of this plot was trenched to a depth of 35 cm at study installation, lined with 0.075-mm plastic sheeting, and backfilled. All vegetation was manually removed from plots in treatment C at two-week intervals in years one and two and at four-week intervals in year three. At the end of year three, soil within the treatment C plots was excavated to a depth of 35 cm at three randomly selected locations and visually assessed for the presence of root ingrowth.

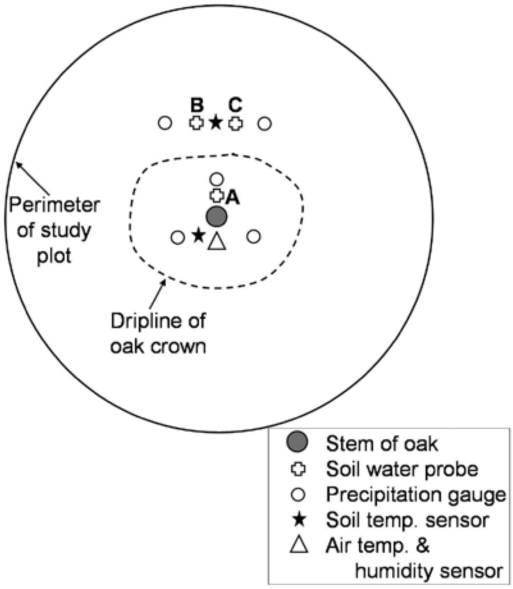

Figure 1 Study plot layout, showing locations of sensors and precipitation gauges in relation to the study tree.

As part of a separate study, 50% of the study plots in each whole-plot treatment were randomly chosen for fertilization (150 kg N ha^{-1}; 75 kg ha^{-1} each of P_2O_5, K_2O, and S) which was applied in January 2003. Fertilization results are not included here; analysis showed no fertilization effect and no fertilization x treatment interactions affecting the reported variables.

Data Collection

Volumetric SWC was measured by installing one Ech$_2$o® EC-20 capacitance probe (Decagon Devices, Pullman, Washington) in each split-plot treatment (*n*=36) and taking readings with an Ech$_2$o Check® meter (Decagon Devices) every two weeks during the growing season for oak (approximated as 1 May to 30 September) in years one and two and every four weeks in year three. Readings were taken at four- to eight-week intervals during the dormant season (1 October to 30 April). Each probe was installed to measure SWC over the soil depth interval of 10-25 cm, within the A horizon. We measured SWC at this depth because tree root density in this soil type was much higher in the A horizon, particularly the upper A horizon, than lower in the soil profile (Devine and Harrington 2005). The finer soil texture and the lower coarse fragment content in the A horizon result in greater water-holding capacity than lower soil horizons.

All SWC data were derived from a soil-specific calibration equation. Calibration was performed by collecting four minimally disturbed soil samples from the study site in August 2005. In the laboratory, a probe was installed in each sample, and the samples were incrementally wetted, with a probe reading made 48 hours after each wetting. Known soil volume and measured water content allowed calculation of volumetric SWC for each probe reading. The relationship between volumetric SWC and probe output was:

$$\mathrm{SWC} = 0.00101X - 0.328 \quad (R^2 = 0.962)$$

where SWC is measured in $m^3\ m^{-3}$ and X is the millivolt reading from the Ech$_2$o® EC-20 probe. Pebbles greater than 6 mm diameter were removed from the probe's zone of influence in the field and during calibration. This pebble fraction was measured (0.202 $m^3\ m^{-3}$), and all reported SWC values have been adjusted to represent soil with pebbles present. A soil water retention curve was created from series-specific particle size distribution and soil water retention data (Soil Survey Staff 2007) using the ROSETTA model (Schaap et al. 2001). Based on this curve, tensions of 10, 100, 200, and 1500 kPa are equivalent to SWC of 0.29, 0.18, 0.15, and 0.08 $m^3\ m^{-3}$.

In each plot, throughfall was measured beneath the crown of the study tree and outside the dripline. Precipitation gauges were metal cans (15.5 cm diameter x 16.0 cm tall; n=60) containing a layer of mineral oil to prevent evaporation of accumulated water. Three gauges were located beneath the crown of each study tree at one-half of the distance from crown center to the dripline along azimuths of 120, 240, and 360 degrees, and two were located in the sensor cluster beyond the study tree's dripline (Figure 1). The water in each gauge was measured at two-week intervals from 28 April through 17 July of year one, and from 30 April through 21 July of year two. During this period from late spring to early summer, plant growth rates are high and SWC declines rapidly; thus, throughfall rate becomes increasingly relevant to SWC.

Soil temperature was recorded at two-hour intervals during the growing season with Ibutton® sensors (model DS1920, Maxim Integrated Products, Inc., Sunnyvale, California) located 5 cm below the surface of the A horizon. Sensors were installed at two locations per plot: *i*) 1.0 meter from the base of the study tree's stem, and *ii*) in the sensor cluster beyond the dripline. Air temperature and relative humidity were recorded at two-hour intervals from 20 May 2003 to 13 May 2005 using Hobo Pro® dataloggers (Onset Computer Corporation, Bourne, Massachusetts) installed 1.0 m from the study tree in three randomly chosen plots in each release treatment. Dataloggers were mounted 25 cm above the forest floor and were sheltered by a circular, 18-cm diameter, white plastic canopy to prevent direct exposure to sunlight and precipitation. Vapor pressure deficit was calculated from simultaneous temperature and relative humidity readings (Lee 1978).

Cover of understory vegetation was visually estimated on 10 September of year one to determine whether coverage was correlated with SWC. Percent coverage was recorded by species within a circular plot (radius=0.5 m) around each soil water probe in split-plot treatments A and B. Estimates were to nearest 5 percent from 5 to 95 percent and to nearest 1 percent outside this range.

Data Analysis

Repeated-measures analysis of variance (ANOVA) was used to analyze the fixed effects (i.e., release in the whole-plot and location and vegetation treatments in the split-plot, where applicable) on SWC, throughfall, soil temperature, air temperature, and VPD (Table 1; PROC MIXED; SAS Institute Inc. 2005). Soil water content, air temperature, and VPD were measured year-round but analyzed separately for the growing season and the dormant season. Soil temperature and throughfall were measured only during the growing season, and because the period of measurement differed slightly among years, years were analyzed separately. In analysis of SWC, year was the repeated unit of time, and in analysis of soil temperature, air temperature, and VPD, the repeated unit of time was month. In throughfall analysis, the repeated unit of time was the two-week sampling period. Protected mean separations were performed using single-degree-of-freedom contrasts. Correlation analysis was used to assess relationships between understory cover and SWC (PROC CORR; SAS

TABLE 1. Analysis of variance table used to test fixed effects on soil water content (SWC), throughfall, soil temperature, air temperature, and vapor pressure deficit (VPD).

	Degrees of freedom			
Source	SWC	Throughfall	Soil temp.	Air temp. & VPD[a]
Release	1	1	1	1
Error	10	10	10	-
Location	2	1	1	-
Release x Location	2	1	1	-
Error	20	10	10	-
Time	2[b]	5	4[c]	9
Release x Time	2	5	4	9
Location x Time	4	5	4	-
Release x Location x Time	4	5	4	-
Error	60	100	80	40
Total	107	143	119	59

[a] For dormant-season analysis: df=13 for Time and Release x Time, df=56 for Error, and total df=83.

[b] For dormant-season analysis, df=1 for Time effect.

[c] In year two, df=3 for Time effect.

Institute Inc. 2005). Significance was judged at the *P*=0.05 level.

Results

Soil Water Content

Dormant-season SWC remained between approximately 0.25 and 0.29 m^3 m^{-3} (equivalent to soil water potentials of -30 to -10 kPa) throughout the study (Figure 2). The early-to-mid growing season was characterized by a period of rapid decline in SWC, beginning around May and ending when SWC reached a minimum in August of 0.08 to 0.12 m^3 m^{-3} (-1500 to -400 kPa), depending on treatment and year. Soil water content then increased abruptly, in October of years one and three and in late August of year two, following periods of significant precipitation.

Growing-season SWC was significantly greater in the released condition than in the unreleased condition during the three years of this study (*F*=19.7, df=1, *P*=0.002; Figure 2). Growing-season SWC was greater in year two than in years one or three (*F*=130.6, df=2, *P*<0.001), but there was no release treatment x year interaction. During the dormant season, SWC was not significantly affected by the release treatment, and there was no release treatment x year interaction for dormant-season SWC.

In year one, understory removal (location B vs. C) increased growing-season SWC in the released condition (*F*=4.5, df=1, *P*=0.046) but not in the overtopped condition (Figure 2). The effect of understory removal was greatest from late July through September. Understory removal did not affect growing-season SWC in years two or three. Within both the released and overtopped conditions, growing-season SWC never differed between locations beneath the oak crown and beyond the dripline (location A vs. B; data not shown).

Total understory cover, estimated on locations A and B (*n*=24) on 10 September of year one, was significantly and positively correlated with SWC measured on dates from May through August of that year. The highest correlation between total understory cover and SWC was for the 17 July measurement of SWC (r=0.55, *n*=24, *P*=0.006).

Our assessment of root ingrowth in the understory exclusion plots (split-plot treatment C) revealed that, by December of year three, roots of woody plants, including Douglas-fir, had grown beneath the plastic-lined trenches and upward into the soil of the plot.

Throughfall

Significant three-way interactions between release treatment, crown location, and measurement period occurred in both year one and year two (*F*=2.3, df=5, *P*=0.042 and *F*=4.6, df=5, *P*<0.001, respectively). Beneath the crowns of released oak trees, throughfall was less than outside the dripline, but for overtopped oak trees, throughfall was similar

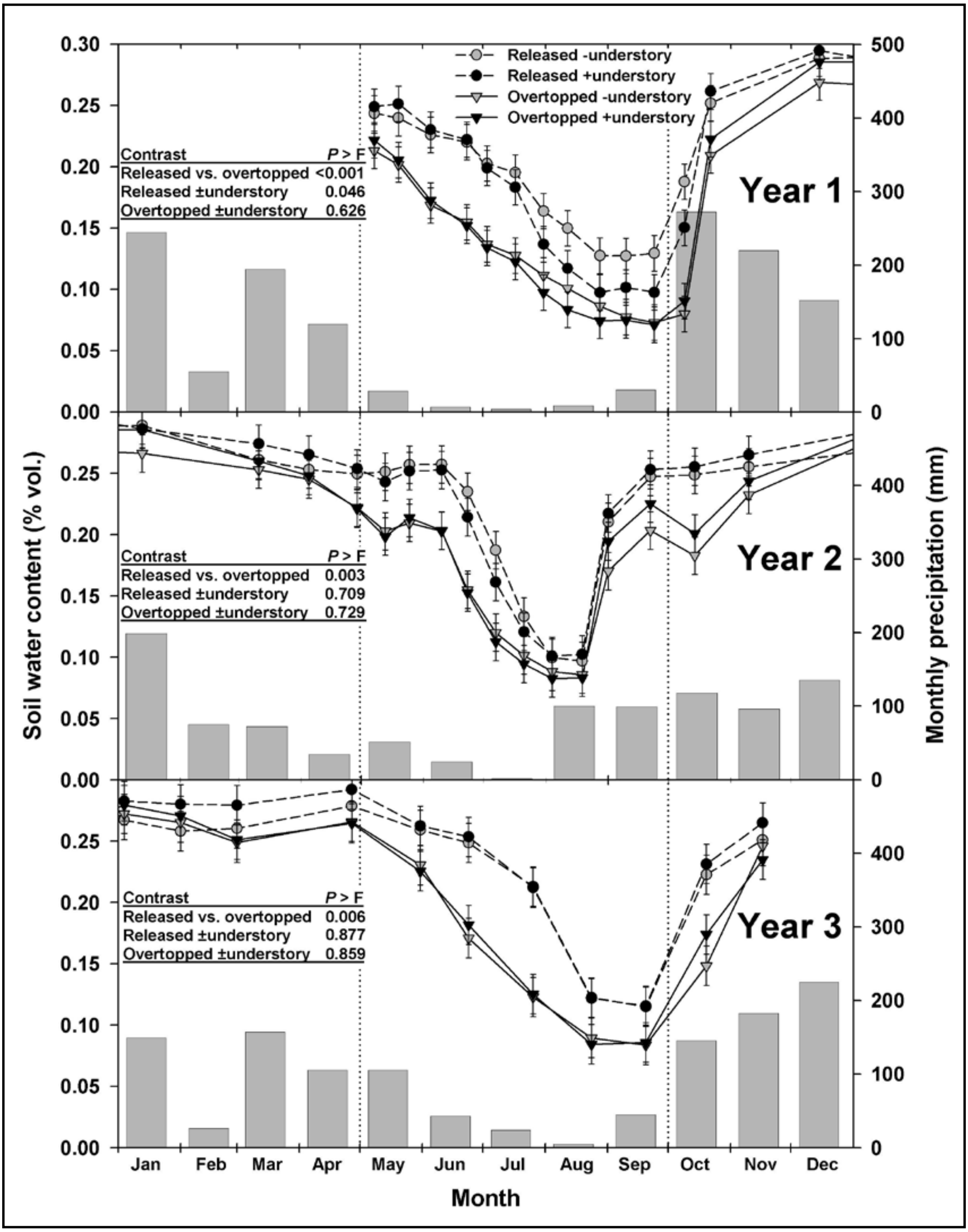

Figure 2. Soil water content (10-25 cm depth interval; represented by symbols and lines), under four combinations of overstory and understory treatments, and total monthly precipitation in Olympia, WA (vertical bars). Vertical dotted lines indicate an approximation of the growing season. Contrasts test the effects of release and the presence/absence of the understory (sensor locations B and C) within the released and overtopped conditions during the growing season of each year. None of the contrasts were significant during the dormant season.

beneath the oak crowns and outside the dripline (Figure 3). Additionally, the magnitude of the crown location effect varied by measurement period. Relative to precipitation values outside the oak dripline in the released condition (i.e., no canopy cover), throughfall beneath the Douglas-fir canopy (46%) was lower than beneath oak crowns alone (74%).

Linear contrasts revealed that, overall, throughfall beneath the crowns of released oak trees was significantly greater than that beneath the crowns of overtopped oak trees in years one and two (F=35.4, df=1, P<0.001 and F=4.3, df=1, P=0.042, respectively). However, during the two-week measurement periods with total precipitation greater than the study's median value of 11.2 mm (as measured in the release treatment outside the oak dripline), throughfall in the released condition was 98% greater than in the overtopped condition. During the measurement periods with precipitation below the median value, throughfall in the released condition was 170% greater than in the overtopped condition.

Microclimate

Soil temperature was significantly greater in the released condition than in the overtopped condition in years one and two (F=39.9, df=1, P<0.001 and

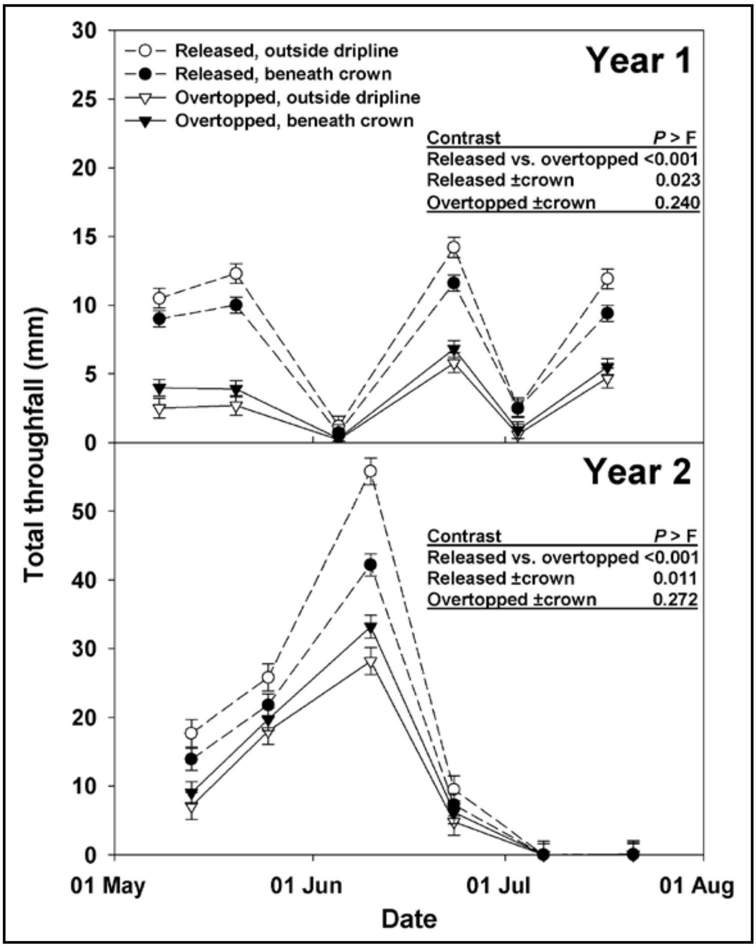

Figure 3. Total throughfall for two-week measurement periods in locations beneath and outside the dripline of Oregon white oak crowns released from (dashed lines) or overtopped by (solid lines) Douglas-fir. Contrasts test the effects of release and position relative to the oak crown (beneath crown vs. outside dripline) within the released and overtopped conditions. Note different scales of y-axes between years.

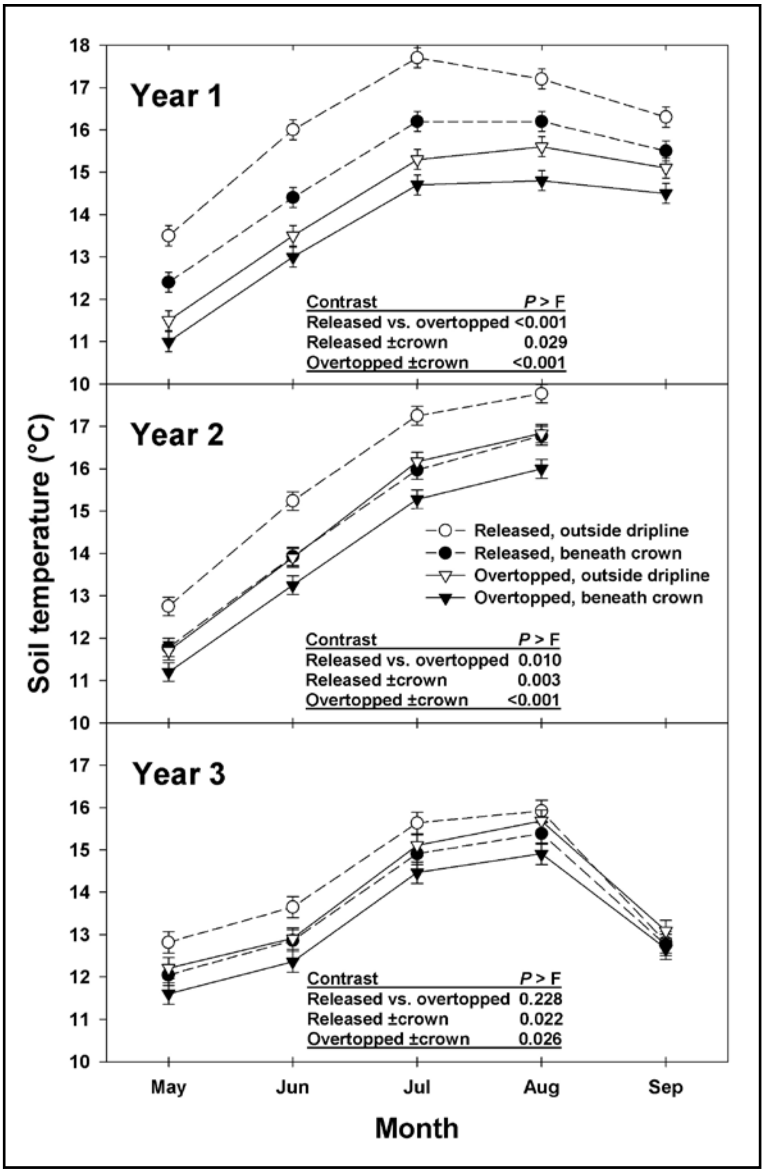

Figure 4. Soil temperature at 5 cm below the surface of the mineral soil in locations beneath and outside the dripline of the crowns of Oregon white oak trees released from (dashed lines) or overtopped by (solid lines) Douglas-fir. Contrasts test the effects of release and position relative to the oak crown (beneath crown vs. outside dripline) within the released and overtopped conditions. September data are missing in year two.

F=10.6, df=1, *P*=0.010, respectively) but not in year three (Figure 4). There was a release treatment x month interaction in years one and three: the positive effect of release on soil temperature was greatest in the early-to-mid growing season (*F*=10.7, df=4, *P*<0.001 and *F*=8.0, df=4, *P*<0.001, respectively). In all three years, there was a significant crown location effect indicating that soil temperatures were higher outside the dripline of the oak crown than beneath the crown.

During the growing season, maximum daily air temperature was greater in the released condition than in the overtopped condition (Figure 5; *F*=12.5, df=1, *P*=0.024). Growing-season mean and minimum daily air temperatures, and dormant-season mean, maximum, and minimum daily air temperatures, were not affected by release. Maximum daily VPD during the growing season was greater in the released condition (Figure 5; *F*=9.6, df=1, *P*=0.036). Growing-season mean and minimum VPD, and dormant-season mean, maximum, and minimum VPD, did not differ between release treatments.

Discussion

Soil Water Content

Release from overstory Douglas-fir delayed the depletion of soil water during the growing season. For example, when SWC in the released condition fell to a given value in July (e.g., 0.15 m^3 m^{-3} or -200 kPa), the overtopped condition had reached the same value approximately one month earlier. Because June and July soil water potentials were within a range that can be growth-limiting for oak trees (i.e., -200 to -1200 kPa), the delay of soil water depletion in the released condition may have contributed to greater tree growth during these months (Reich et al. 1980, Bréda et al. 1995). Improved soil water availability during this period also has the potential to positively influence reproductive growth in oak, specifically the level of acorn production (Sork et al. 1993). Oregon white oak trees receiving the same release treatment on four other sites had significantly greater diameter growth and acorn production than

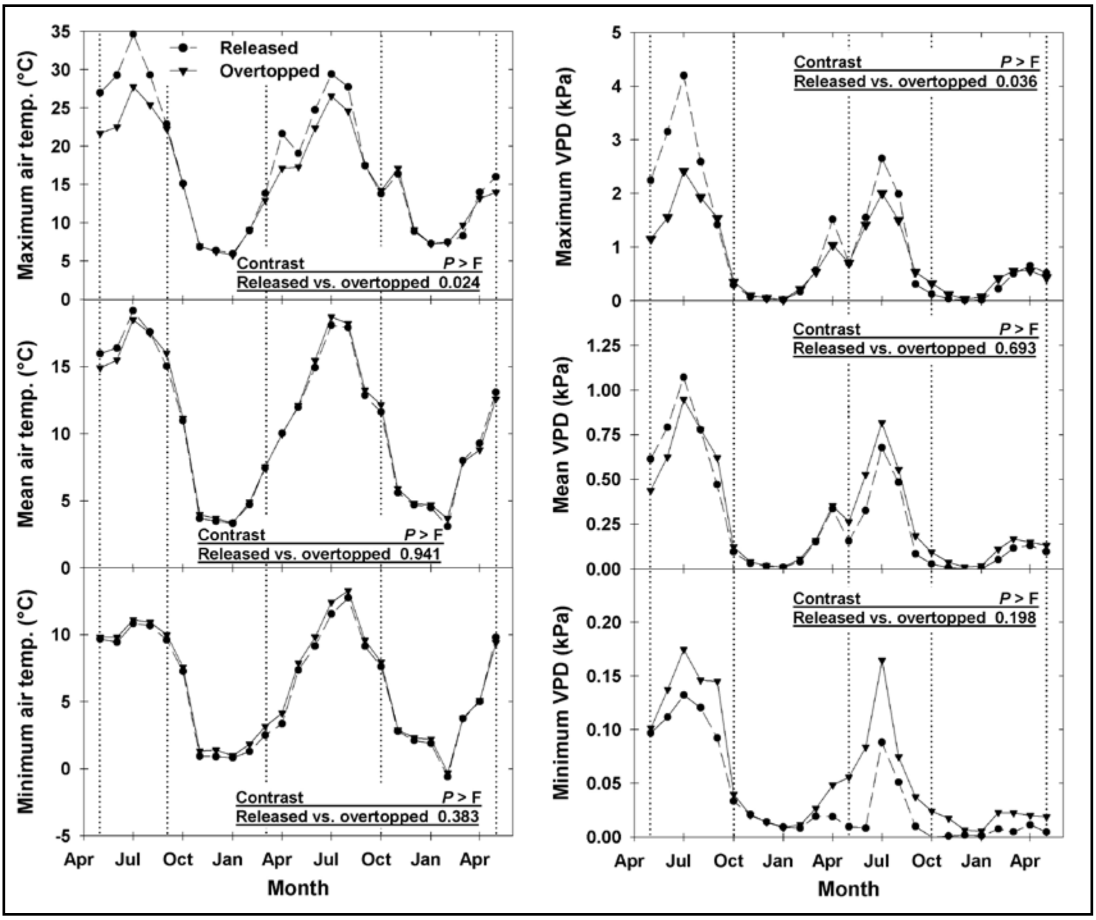

Figure 5 Maximum, mean, and minimum daily air temperature and vapor pressure deficit (VPD) by month, measured 25 cm above the forest floor beneath Oregon white oak crowns released from or overtopped by Douglas-fir. Dotted vertical lines indicate the approximate beginning and end of the growing season for oak. Contrasts test release effect during the growing season. Note different scales of y-axes.

overtopped trees in the first five years post-treatment (Devine and Harrington 2006). While soil water uptake by these oak trees was certainly not limited to the A horizon (where our sensors were located), the majority of their roots were located in this horizon, where water-holding capacity is higher than in underlying horizons (Devine and Harrington 2005).

The Douglas-fir overstory constituted over 80% of stand basal area at the study site and was probably responsible for the majority of the annual transpiration in the stand (Kline et al. 1976, Granier 1987). After above-average rainfall in late summer of year two wetted the soil, the effect of release on SWC was evident as late as October (Figure 2). This pattern was not surprising, as transpiration rates of overstory Douglas-fir trees in the region remain relatively high at that time of year (Moore et al. 2004), and it illustrates the influence that the Douglas-fir overstory exerts on SWC in these rapidly draining soils.

The Douglas-fir overstory also influenced the minimum value to which soil water was depleted in summer. The minimum SWC was 0.02-0.03 m^3 m^{-3} lower in the overtopped condition than in the released condition, equivalent to minimum soil water potentials of -1200 kPa in the overtopped condition, but only -400 to -600 kPa in the released condition. Therefore, it appears that the understory plus the midstory oak trees were not capable of depleting the SWC to the extent to which the Douglas-fir overstory did. Thus, competition for soil water, in addition to competition for light, may be an important factor in the decline of Oregon white oak trees in stands invaded by Douglas-fir.

Soil water content was similar for microsite locations beneath the crowns and outside of the driplines of released oak trees. This contrasts with findings from Wisconsin oak savannas and pastures, where summer SWC was greater beneath crowns, a trend attributed to lower evapotranspiration resulting from reduced solar radiation and cooler soils (Ko and Reich 1993). The lack of such a crown effect in the present study may have been due to the moderate to severe crown dieback that many of the study trees suffered, combined with the influence of shade from the Douglas-fir bordering the study plots. Furthermore, roots from these neighboring Douglas-fir may have extended well into the study plots, as they have the potential to reach to 35% of tree height (Eis 1987). If this occurred, our estimates of the effect of release on SWC are conservative.

Significant depletion of soil water by the understory was detected only in the released condition and only in the first year. We expected greater understory water use in the released condition than in the overtopped condition due to increased rates of plant transpiration under the warmer temperatures and greater insolation. We attribute the absence of the understory exclusion effect in years two and three to declining efficacy of our root exclusion treatment, as tree roots had invaded these plots by the third year of the study.

Throughfall

The lower rate of throughfall beneath the Douglas-fir canopy compared to beneath oak crowns is in agreement with research comparing canopy interception in Douglas-fir and broad-leafed forest types (Iroumé and Huber 2002). The throughfall rate for the oak crowns was comparable to or slightly higher than rates reported previously for savanna and forest oaks of North America and Europe (Ko and Reich 1993, Cantu and Gonzalez 2001, Moreno et al. 2001, Rodrigo et al. 2003). The low rate of throughfall for overtopped oak trees during periods of light rainfall suggests that, for trees in this condition, little precipitation reaches the soil profile during the typically light summer rain events of this region. Furthermore, because the bark of Oregon white oak is relatively rough and therefore probably has a high capacity for water storage, the light rain events likely produce little stemflow (Kimmins 1987, Cantu and Gonzalez 2001, Levia and Frost 2003).

Microclimate

Soil temperature was greater in the released condition than in the overtopped condition, although this difference declined from year one to year three, perhaps due to development of the understory during this period and its shading of the forest floor (Oliver et al. 1987, Carlson and Groot 1997). Given the soil temperature range in our study, it is possible that the warmer soil temperatures resulting from release could increase rates of root growth and nutrient cycling (Teskey and Hinckley 1981, Reynolds et al. 2000).

Greater maximum air temperatures in the released condition, relative to the overtopped condition, likely are a result of increased solar radiation. Elsewhere, maximum air temperatures increased and minimum air temperatures decreased in forest openings, relative to closed canopy conditions, due to greater solar radiation during the daytime and greater radiative cooling at night (Carlson and Groot 1997; Barg and Edmonds 1999; Gray et al. 2002; Ritter et al. 2005). Maximum daily VPD, which peaked in the month of July, also was increased by the release treatment. Vapor pressure deficit is positively (but non-linearly) related to plant transpiration rate; thus, the increased VPD in the released condition may have increased understory water use (Elliott and Vose 1994, Oren et al. 1999, Singsaas et al. 2000). However, the magnitude of this effect would likely be minor relative to the effect of Douglas-fir removal on SWC.

Implications

The potential for invading plants, particularly trees, to alter the hydrologic cycle of an ecosystem is well documented in temperate and tropical regions (Vitousek 1992). In our study the removal of invasive conifers from a stand historically dominated by oak increased SWC during the growing season. It is not known whether this soil water increase represents a return to the historical soil water pattern prior to Douglas-fir invasion or whether the increase is a temporary phenomenon associated with the post-release vegetative condition. In either case, the increased growing-season SWC suggests improved water availability, likely favorable for the growth and recovery of the formerly suppressed oak trees, particularly if changes in solar radiation, temperature, and humidity cause post-release transpiration rates to increase (Ogink-Hendriks 1995).

The changes in sunlight, soil water, and microclimate that follow Douglas-fir removal affect the competitive environment of the understory. The removal of a conifer overstory may result in understory conditions more susceptible to invasion by non-native species (Devine et al. 2007), but over time, species composition will be a function of the disturbance regime (the historical precedent here being frequent anthropogenic fire) as well as resource availability (Holmes and Rice 1996, MacDougall and Turkington 2004). The disturbance regime will be affected by SWC and microclimate through their influences on understory growth rates, resultant fuel loads, and fuel moisture content, which in turn affect the planning and efficacy of prescribed fire (Miller and Urban 1999, Higgins et al. 2000, MacDougall et al. 2004). It is not certain how post-release changes in resource availability will influence future understory composition, given the abundance of non-native species that have entered these plant communities during the last century. For example, increased SWC in early summer could benefit native plants or non-native plants as many competing species in these ecosystems share similar phenologies (MacDougall et al. 2004). However, release from Douglas-fir, and the resulting environmental changes, are a necessary early step in restoring the native plant community.

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Literature Cited

Adams, P. W., A. L. Flint, and R. L. Fredriksen. 1991. Long-term patterns in soil moisture and revegetation after a clearcut of a Douglas-fir forest in Oregon. Forest Ecology and Management 41:249-263.

Agee, J. K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, D. C.

Aussenac, G. 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. Annals of Forest Science 57:287-301.

Barg, A. K., and R. L. Edmonds. 1999. Influence of partial cutting on site microclimate, soil nitrogen dynamics, and microbial biomass in Douglas-fir stands in western Washington. Canadian Journal of Forest Research 29:705-713.

Bayrakci, R., A. B. Carey, and T. M. Wilson. 2001. Current status of the western gray squirrel population in the Puget Trough, Washington. Northwest Science 75:333-341.

Beckage, B., J. S. Clark, B. D. Clinton, and B. L. Haines. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. Canadian Journal of Forest Research 20:1617-1631.

Bond, B. J., and K. L. Kavanagh. 1999. Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. Tree Physiology 19:503-510.

Bréda, N., A. Granier, and G. Aussenac. 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). Tree Physiology 15:295-306.

Cantu, S. I., and R. H. Gonzalez. 2001. Interception loss, throughfall and stemflow chemistry in pine and oak forests in northeastern Mexico. Tree Physiology 21:1009-1013.

Carlson, D. W., and A. Groot. 1997. Microclimate of clear-cut, forest interior, and small openings in trembling aspen forest. Agricultural and Forest Meteorology 87:313-329.

Chappell, C. B., and R. C. Crawford. 1997. Native vegetation of the South Puget Sound prairie landscape. *In* P. Dunn and K. Ewing (editors), Ecology and Conservation of the South Puget Sound Prairie Landscape. The Nature Conservancy of Washington, Seattle. Pp. 107-122.

Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Mroz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. BioScience 49:288-297.

Crawford, R. C., and H. Hall. 1997. Changes in the South Puget Sound prairie landscape. *In* P. Dunn and K. Ewing (editors), Ecology and Conservation of the South Puget Sound Prairie Landscape. The Nature Conservancy of Washington, Seattle. Pp. 11-15.

Davies-Colley, R. J., G. W. Payne, and M. van Elswijk. 2000. Microclimate gradients across a forest edge. New Zealand Journal of Ecology 24:111-121.

Devine, W. D., and C. A. Harrington. 2005. Root system morphology of Oregon white oak on a glacial outwash soil. Northwest Science 79:179-188.

Devine, W. D., and C. A. Harrington. 2006. Changes in Oregon white oak (*Quercus garryana* Dougl. ex Hook.) following release from overtopping conifers. Trees 20:747-756.

Devine, W. D., C. A. Harrington, and D. H. Peter. 2007. Unpublished report on file at Olympia Forestry Sciences Laboratory, Olympia, WA.

Eis, S. 1987. Root systems of older immature hemlock, cedar, and Douglas-fir. Canadian Journal of Forest Research 17:1348-1354.

Elliott, K. J., and J. M. Vose. 1994. Photosynthesis, water relations, and growth of planted *Pinus strobus* L. on burned sites in the southern Appalachians. Tree Physiology 14:439-454.

Fenn, M. E., and A. Bytnerowicz. 1997. Summer throughfall and winter deposition in the San Bernardino Mountains in southern California. Atmospheric Environment 31:673-683.

Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiology 3:309-320.

Gray, A. N., T. A. Spies, and M. J. Easter. 2002. Microclimate and soil moisture responses to gap formation in coastal Douglas-fir forests. Canadian Journal of Forest Research 32:332-343.

Higgins, S. I., Bond, W. J., and W. S. W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. Journal of Ecology 88:213-229.

Holmes, T. H., and K. J. Rice. 1996. Patterns of growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. Annals of Botany 78:233-243.

Iroumé, A., and A. Huber. 2002. Comparison of interception losses in a broadleaved native forest and a *Pseudotsuga menziesii* (Douglas-fir) plantation in the Andes Mountains of southern Chile. Hydrological Processes 16:2347-2361.

Kimmins, J. P. 1987. Forest Ecology. Macmillan Publishing Company, New York.

Kline, J. R., K. L. Reed, R. H. Waring, and M. L. Stewart. 1976. Field measurement of transpiration in Douglas-fir. Journal of Applied Ecology 13:273-283.

Ko, L. J., and P. B. Reich. 1993. Oak tree effects on soil and herbaceous vegetation in savannas and pastures in Wisconsin. American Midland Naturalist 130:31-42.

Lee, R. 1978. Forest Microclimatology. Columbia University Press, New York.

Levia, D. F., and E. E. Frost. 2003. A review and evaluation of stemflow literature in the hydrologic and biogeochemical cycles of forested and agricultural ecosystems. Journal of Hydrology 274:1-29.

MacDougall, A. S., and R. Turkington. 2004. Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. Journal of Ecology 92:422-434.

MacDougall, A. S., B. R. Beckwith, and C. Y. Maslova. 2004. Defining conservation strategies with historical perspectives: a case study from a degraded oak grassland ecosystem. Conservation Biology 18:455-465.

Martin, T. A., K. J. Brown, J. Cermák, R. Ceulemans, J. Kucera, F. C. Meinzer, J. S. Rombold, D. G. Sprugel, and T. M. Hinckley. 1997. Crown conductance and tree and stand transpiration in a second-growth *Abies amabilis* forest. Canadian Journal of Forest Research 27:797-808.

Miller, C., and D. L. Urban. 1999. A model of surface fire, climate and forest pattern in the Sierra Nevada, California. Ecological Modelling 114:113-135.

Minckler, L. S., and J. D. Woerheide. 1965. Reproduction of hardwoods 10 years after cutting as affected by site and opening size. Journal of Forestry 63:103-107.

Minckler, L. S., J. D. Woerheide, and R. C. Schlesinger. 1973. Light, soil moisture, and tree reproduction in hardwood forest openings. USDA Forest Service Research Paper NC-89. North Central Forest Experiment Station, St. Paul, MN.

Moore, G. W., B. J. Bond, J. A. Jones, N. Phillips, and F. C. Meinzer. 2004. Structural and compositional controls on transpiration in 40- and 450-year-old riparian forests in western Oregon, USA. Tree Physiology 24:481-491.

Moreno, G., J. F. Gallardo, and F. Bussotti. 2001. Canopy modification of atmospheric deposition in oligotrophic

Quercus pyrenaica forests of an unpolluted region (central-western Spain). Forest Ecology and Management 149:47-60.

Ogink-Hendriks, M. J. 1995. Modelling surface conductance and transpiration of an oak forest in The Netherlands. Agricultural and Forest Meteorology 74:99-118.

Oliver, S. A., H. R. Oliver, J. S. Wallace, and A. M. Roberts. 1987. Soil heat flux and temperature variation with vegetation, soil type and climate. Agricultural and Forest Meteorology 39:257-269.

Oren, R., J. S. Sperry, G. G. Katul, D. E. Pataki, B. E. Ewers, N. Phillips, and K. V. R. Schäfer. 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapor pressure deficit. Plant, Cell and Environment 22:1515-1526.

Pringle, R. F. 1990. Soil survey of Thurston County, Washington. USDA Soil Conservation Service, Olympia, WA.

Proe, M. F., J. H. Griffiths, and H. M. McKay. 2001. Effect of whole-tree harvesting on microclimate during establishment of second rotation forestry. Agricultural and Forest Meteorology 110:141-154.

Reich, P. B., R. O. Teskey, P. S. Johnson, T. M. Hinckley. 1980. Periodic root and shoot growth in oak. Forest Science 26:590-598.

Reynolds, P. E., N. V. Thevathasan, J. A. Simpson, A. M. Gordon, R. A. Lautenschlager, W. F. Bell, D. A. Gresch, and D. A. Buckley. 2000. Alternative conifer release treatments affect microclimate and soil nitrogen mineralization. Forest Ecology and Management 133:115–125.

Ritter, E., L. Dalsgaaard, and K. S. Einhorn. 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. Forest Ecology and Management 206:15-33.

Rodrigo, A., A. Avila, and F. Roda. 2003. The chemistry of precipitation, throughfall and stemflow in two holm oak (Q*uercus ilex* L.) forests under a contrasted pollution environment in NE Spain. The Science of the Total Environment 305:195-205.

Rothacher, J. 1963. Net precipitation under a Douglas-fir forest. Forest Science 9:423-429.

SAS Institute Inc. 2005. The SAS System for Windows. Version 9.1. Cary, NC.

Schaap, M. G., W. Bouten, and J. M. Verstraten. 1997. Forest floor water content dynamics in a Douglas fir stand. Journal of Hydrology 201:367-383.

Schaap, M. G., F. J. Leij, and M. T. van Genuchten. 2001. ROSETTA: a computer program for estimating soil hydraulic parameters with hierarchical pedotransfer functions. Journal of Hydrology 251:163-176.

Singsaas, E. L., D. R. Ort, and E. H. DeLucia. 2000. Diurnal regulation of photosynthesis in understory saplings. New Phytologist 145:39-49.

Soil Survey Staff. 2007. National Soil Survey Characterization Data. Soil Survey Laboratory, National Soil Survey Center, USDA Natural Resources Conservation Service, Lincoln NE. Available online at http://ssldata.nrcs.usda.gov/ (accessed 8 February 2007).

Sork, V. L., J. Bramble, and O. Sexton. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology 74:528-541.

Stone, E. L., W. T. Swank, and J. W. Hornbeck. 1978. Impacts of timber harvest and regeneration systems on streamflow and soils in the eastern deciduous region. *In* C. T. Youngberg (editor), Forest Soils and Land Use. Colorado State University, Fort Collins. Pp. 516-535

Teskey, R. O., and T. M. Hinckley. 1981. Influence of temperature and water potential on root growth of white oak. Physiologia Plantarum 52:363-369.

Thysell, D. R., and A. B. Carey. 2001. *Quercus garryana* communities in the Puget Trough, Washington. Northwest Science 75:219-235.

Tveten, R. K., and R. W. Fonda. 1999. Fire effects on prairies and oak woodlands on Fort Lewis, Washington. Northwest Science 73:145-158.

Vitousek, P. M. 1992. Effects of alien plants on native ecosystems. *In* C. P. Stone, C. W. Smith, and J. T. Tunison (editors), Alien plant species in native ecosystems of Hawai'i: management and research. University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. Pp. 29-41.

Voigt, G. K. 1960. Distribution of rainfall under forest stands. Forest Science 6:2-10.

Western Regional Climate Center. 2007. Washington climate summaries. Available online at http://www.wrcc.dri.edu/summary/climsmwa.html (accessed 8 February 2007).

Wilson, M. V., P. C. Hammond, and C. B. Schultz. 1997. The interdependence of native plants and Fender's Blue butterfly. In T. N. Kaye, A. Liston, R. M. Love, D. Luomo, R. J. Meinke, and M. V. Wilson (editors), Conservation and management of native flora and fungi. Native Plant Society of Oregon, Corvallis. Pp. 83-87.

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