WOODLAND RESEARCH REPORT

Oak Woodland Restoration: Understory Response to Removal of Encroaching Conifers

Warren D. Devine, Constance A. Harrington, and David H. Peter

ABSTRACT

Oregon white oak (or Garry oak, *Quercus garryana*) woodlands and savannas of the coastal Pacific Northwest are legacies of an anthropogenic fire regime that ended with European settlement in the mid-1800s. Historically, these oak stands had a sparse overstory and an understory dominated by fire-tolerant grasses and forbs. Post-settlement fire suppression resulted in widespread invasion and subsequent overstory dominance by conifers, causing mortality of shade-intolerant oak trees and shifting understory plant communities to shade-tolerant species. In a study on four southwestern Washington sites, our objective was to determine the effects of overstory conifer removal, primarily Douglas-fir (*Pseudotsuga menziesii*), on microclimate, native and non-native understory cover, and sapling growth. Overstory conifer removal created a warmer, drier understory microclimate during summer months. Conifer removal had little effect on native understory cover during five years post-treatment; however, cover of non-native plants, primarily grasses and woody understory species, increased significantly during the same period. Height growth of Oregon white oak and Douglas-fir saplings exhibited a delayed, but positive, response to overstory conifer removal, although the treatment response of Douglas-fir was 133% greater than that of oak. Increases in non-native understory cover and the rapid growth of young Douglas-fir indicate the importance of pre- and post-treatment understory management to control undesirable plants and promote native species such as Oregon white oak.

Keywords: Douglas-fir (*Pseudotsuga menziesii*), microclimate, Oregon white oak (*Quercus garryana*), restoration, savanna, understory

Introduction

The Oregon white oak (or Garry oak; *Quercus garryana*) woodlands, savannas, and associated prairies of the coastal Pacific Northwest are part of an anthropogenic ecosystem, historically maintained by frequent, low-intensity fires set by Native Americans (Agee 1993). After European settlement in the mid-1800s, the lack of regular burning allowed fire-intolerant conifers, primarily Douglas-fir (*Pseudotsuga menziesii*), to regenerate in prairies and oak stands where they were previously excluded (Thysell and Carey 2001). Growth and survival of Oregon white oak trees are substantially reduced where these conifers have invaded (Stein 1990, Devine and Harrington 2006). Conifers overtop and suppress the shade-intolerant oak trees, leading to crown die-back and eventual mortality of the oak.

Restoration of Oregon white oak woodlands and savannas to presettlement conditions requires removal of the conifer overstory to "release" the suppressed oak trees from competition and to restore a more open stand structure (Harrington and Devine 2006). Results from a companion study have shown that large oak trees (diameter at breast height over 20 cm) respond to release from overtopping Douglas-fir by increasing their rate of growth, expanding leaf area through formation of new (i.e., epicormic) branches, and increasing acorn production (Devine and Harrington 2006). Preservation of existing oak trees is a priority when restoring these stands because the trees provide an important structural component and would take decades or centuries to replace due to their slow growth (Stein 1990). Where former canopy oak trees are already dying as a result of suppression, promoting the growth and survival of oak seedlings and saplings becomes critical.

This encroachment of conifers is widespread, and substantial losses of prairie and oak habitats also have resulted from conversion of land to agricultural and urban uses (Crawford and Hall 1997). In British Columbia, less than five percent of pre-settlement Oregon white oak habitat remains (Lea 2006) (Figure 1). Recognizing the loss of this ecosystem, private landowners, conservation organizations, and state and federal land managers in Oregon's Willamette Valley, the Puget Sound region of Washington, and Vancouver Island, British Columbia, have become involved in various aspects of restoring Oregon white oak communities. Two non-profit organizations, the Oregon

Ecological Restoration Vol. 25, No. 4, 2007
ISSN 1522-4740 E-ISSN 1543-4079

Figure 1. An Oregon white oak (*Quercus garryana*) woodland (dormant season) with encroaching Douglas-fir (*Pseudotsuga menziesii*) in the background. In the foreground is our most problematic invasive shrub, Scotch broom (*Cytisus scoparius*). Photo by Warren Devin

Oak Communities Working Group and the Garry Oak Ecosystems Recovery Team (British Columbia), have focused on preserving and restoring Oregon white oak ecosystems since the late 1990s. When Oregon white oak is released from overtopping conifers, the intensity of release ranges from individual-tree treatment (removing only the conifers adjacent to selected oak trees) to total removal of conifers at the stand level. These practices are influenced by the fact that on many private lands the invading conifers represent a source of timber revenue while the oak trees may have little monetary value. Thus, depending on the merchantability of the conifers, a release treatment may require an expenditure, allow the owner to break even, or even yield a profit.

The goal of this study was to evaluate the influence of oak release treatments on the understory, as the effects of release are currently not well understood. We compared overtopped and released conditions to determine how removal of conifers affects microclimate, native and non-native understory cover, and growth of Oregon white oak and Douglas-fir saplings. Our hope is that information on understory response will facilitate selection of appropriate restoration techniques in similar plant communities.

Study Area

The study took place in four stands of Oregon white oak and Douglas-fir on the Fort Lewis Military Reservation in southwestern Washington, east of the city of Tacoma. The four sites, located 10 to 15 km apart, are on glacial outwash terraces and moraines, at elevations from 85 to 135 m. Soils are gravelly to very gravelly sandy loams, and loamy fine sands, and are moderately to somewhat excessively drained. Annual precipitation in Tacoma is 995 mm, but total precipitation from 1 May through 30 September averages only 158 mm (WRCC 2005). Mean temperatures in January and July are 5 and 19°C respectively.

The four stands were similar in species composition, with an overstory primarily composed of Douglas-fir averaging 167 ± 46 trees/ha (mean ± one standard deviation) and a midstory of suppressed Oregon white oak averaging 115 ± 66 trees/ha. This is the first generation of Douglas-fir to colonize these former oak savanna and woodland sites. The Douglas-fir had been lightly thinned two to three times before this study at 10- to 15-year intervals, most recently immediately prior to the study (2000–2001). Stand basal area averaged 34.3 ± 8.2 m^2/ha for Douglas-fir and 4.7 ± 2.4 m^2/ha for oak. Approximate age range for the suppressed oak was 90 to 150 years, while Douglas-fir averaged 65 to 90 years. A detailed description of these oak trees appears in Devine and Harrington (2006).

The understory of the oak woodland and savanna stands in the Puget Sound region was historically dominated by grasses and forbs in a plant community likely similar to the Oregon white oak, long-stolon sedge (*Carex inops*), common camas (*Camassia quamash*) community (Chappell and Crawford 1997). A lack of regular fire and increasing conifer dominance results in a more shade-tolerant, shrubby understory community such as the Oregon white oak, Douglas-fir/snowberry (*Symphoricarpos albus*), swordfern (*Polystichum munitum*) community (Chappell and Crawford 1997) which was present at our study sites. The most common understory species present across all treatments and years are listed in Table 1. Control of the invasive shrub Scotch broom (*Cytisus scoparius*) is part of nearly all oak savanna and prairie restoration efforts in the region; we performed a one-time removal of Scotch broom from the study by cutting (at groundline to prevent sprouting) or uprooting all plants within one tree-height radius of the study trees at the beginning of the study in June 2001. The number of Scotch broom plants per study tree was variable, averaging 43 ± 80 and ranging from zero to 350.

Study Design and Sampling

At each of four sites, we selected 18 oak trees for the study that were each overtopped by at least two Douglas-fir trees. Average height of these 72 oak

Table 1. Shade tolerance and percent coverage in years 1 and 5 by treatment for species occurring on at least 5% of microplots. Shade tolerance classification is tolerant (T), intermediate (M), or intolerant (I). The symbol * indicates a significant change in cover ($p < 0.05$) between year 1 and year 5.

Group / Species	Shade Tolerance	Cover (%) Control Yr 1	Control Yr 5	Full Release Yr 1	Full Release Yr 5
Native forbs					
Polystichum munitum (swordfern)	T	16.6	20.1	7.2	12.1
Galium aparine (stickywilly)	M	7.0	1.6*	6.0	3.4
Clinopodium douglasii (yerba buena)	T	2.8	2.0	1.1	2.2
Nemophila parviflora (smallflower nemophila)	M	2.4	0.3	2.8	1.2
Fragaria vesca (woodland strawberry)	M	0.5	1.1	1.1	1.6
Native grasses					
Carex inops (long-stolon sedge)	M	1.9	2.1	2.2	3.6
Bromus vulgaris (Columbia brome)	M	1.1	0.5	2.0	1.3
Native woody species					
Symphoricarpos albus (snowberry)	M	32.7	42.4*	25.5	37.2*
Rubus ursinus (California blackberry)	M	32.6	36.9	24.1	41.6*
Corylus cornuta var. *californica* (California hazelnut)	T	13.8	16.3	14.5	20.2*
Mahonia aquifolium (tall Oregongrape)	M	2.5	3.7	2.3	6.7*
Lonicera ciliosa (orange honeysuckle)	M	4.9	7.4	3.7	5.8
Non-native forbs					
Hypochaeris radicata (hairy catsear)	M	0.7	1.5	0.6	2.2
Hypericum perforatum (common St. Johnswort)	M	0.3	0.5	0.4	1.5*
Mycelis muralis (wall-lettuce)	M	0.4	0.6	1.8	0.6*
Non-native grasses					
Agrostis capillaris (colonial bentgrass)	I	2.8	2.2	3.5	8.9*
Holcus lanatus (common velvetgrass)	M	0.8	2.2	3.1	8.9*
Dactylis glomerata (orchardgrass)	M	0.8	3.5	1.3	0.8
Poa pratensis (Kentucky bluegrass)	M	0.0	1.6	0.0	1.2
Non-native woody species					
Cytisus scoparius (Scotch broom)	M	0.3	4.2	0.6	14.9*

"study trees" was 16.0 ± 3.1 m, and crown diameter averaged 7.5 ± 2.3 m. Height of the two largest overtopping Douglas-fir per oak averaged 40.6 ± 6.9 m.

We applied three levels of treatment, replicated six times per study site, in April and May of 2001. The "full-release" treatment was removal of all Douglas-fir trees within a distance of one tree-height (an average of 16 m) of the study tree, an average of 15 ± 8 Douglas-fir trees per oak. The "half-release" treatment was removal of all Douglas-fir trees within a distance of one-half tree-height (an average of 8 m) of the study oak tree, an average of 6 ± 3 Douglas-fir trees per oak. In the control treatment, no Douglas-fir trees were removed. An average of one to two Douglas-fir trees within one tree-height radius of each study tree was removed across all treatments in a light commercial thinning that took place prior to the study in 2000–2001, removing approximately 15% of stand basal area. The full-release treatment represents a near-total removal of overstory competition, while the half-release represents an individual-tree release that has been applied by some landowners to prolong the life of oak trees while removing relatively few overstory conifers. During thinning and treatment, trees were cut with chainsaws and moved to the landings with skidders.

We measured air temperature and relative humidity every two hours near 18 randomly selected full-release and control treatment trees using HOBO® Pro dataloggers (Onset Computer Corp., Bourne, MA). Dataloggers were mounted 25 cm above the forest floor, 1 m south of the study oak tree. Vapor pressure deficit (VPD), which influences plant-water relations and photosynthesis rate (Elliott and Vose 1994, Singsaas et al. 2000), was calculated from relative humidity and air temperature (Lee 1978). Data presented are from 2002 and 2003 and are representative of the collection period (July 2001 through May 2005).

We conducted vegetation surveys near 24 study trees in the full-release and control treatments in June of 2001, 2003, and 2005 (study years one, three, and five). We established a permanent transect from east to west, bisected by the study tree, with 20- × 50-cm microplot frames every two meters. Transect length was equal to twice the study tree height, and the number of microplots per transect averaged 16 ± 3. Within each microplot, experienced surveyors measured duff layer thickness and visually estimated percent total understory cover, percent exposed soil, and percent cover by species for vascular plants.

In spring 2001, we tagged, mapped, and measured the height of naturally established oak and Douglas-fir saplings (height = 0.5 to 3.0 m; n = 288) within one tree-height of the study trees. We remeasured the height of these saplings after each growing season from 2001 to 2005. For oak saplings, we classified the level of understory competition in 2002 and crown shape in 2003. Crown shape was classified as 1) a vertically oriented crown with one dominant leader; 2) a vertically oriented crown with multiple competing leaders; or 3) a flat-topped, horizontally oriented crown.

The study followed a randomized complete-block design (site = block). Data were analyzed by analysis of variance and correlation analysis (details of analysis available upon request). Significance was judged at the 95% confidence level.

Results and Discussion

Understory microclimate

The full-release treatment increased maximum daily air temperature, particularly from June through August when the maximum temperature averaged 5.2°C higher than in the control (Figure 2a). Conversely, daily minimum air temperature was slightly but consistently lower in the full-release treatment than in the control throughout the year. Mean daily air temperature did not differ between the full-release and control treatments. Maximum daily VPD was significantly higher in the full-release treatment than in the control during summer months, particularly from June through August (Figure 2b). Mean daytime VPD did not differ by treatment. Air temperature and VPD during a typical clear summer day (12 July 2002) are shown in Figure 2c. Both air temperature and VPD peaked slightly earlier in the day in the full-release treatment than in the control.

We assessed direct sunlight reaching the study trees and found that the half-release and full-release treatments approximately doubled and quadrupled, respectively, the duration of direct sunlight that the oak trees received each day in summer (Devine and Harrington 2006). The overtopped oak trees in the control treatment received, on average, only 13% of the photosynthetically active radiation that would have been available

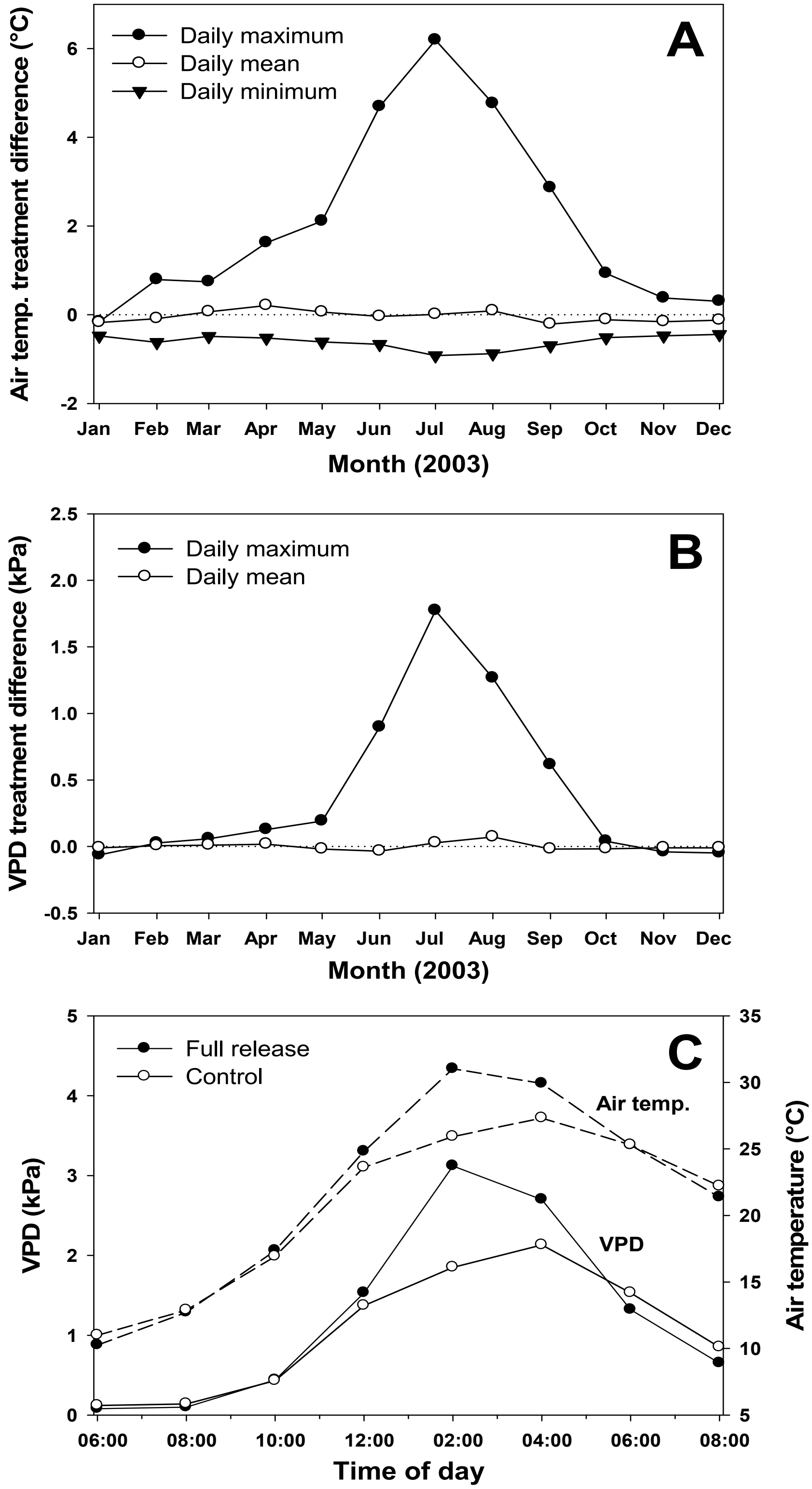

Figure 2. The effect of full release, relative to the control treatment on A) average daily maximum, mean, and minimum air temperatures at 25 cm (positive values indicate full release was warmer than the control and negative values indicate full release was cooler); B) daytime maximum and mean vapor pressure deficit (VPD) at 25 cm. C) mean VPD (solid line) and air temperature (dashed line) for control and full-release treatments on a typical clear summer day (12 July 2002).

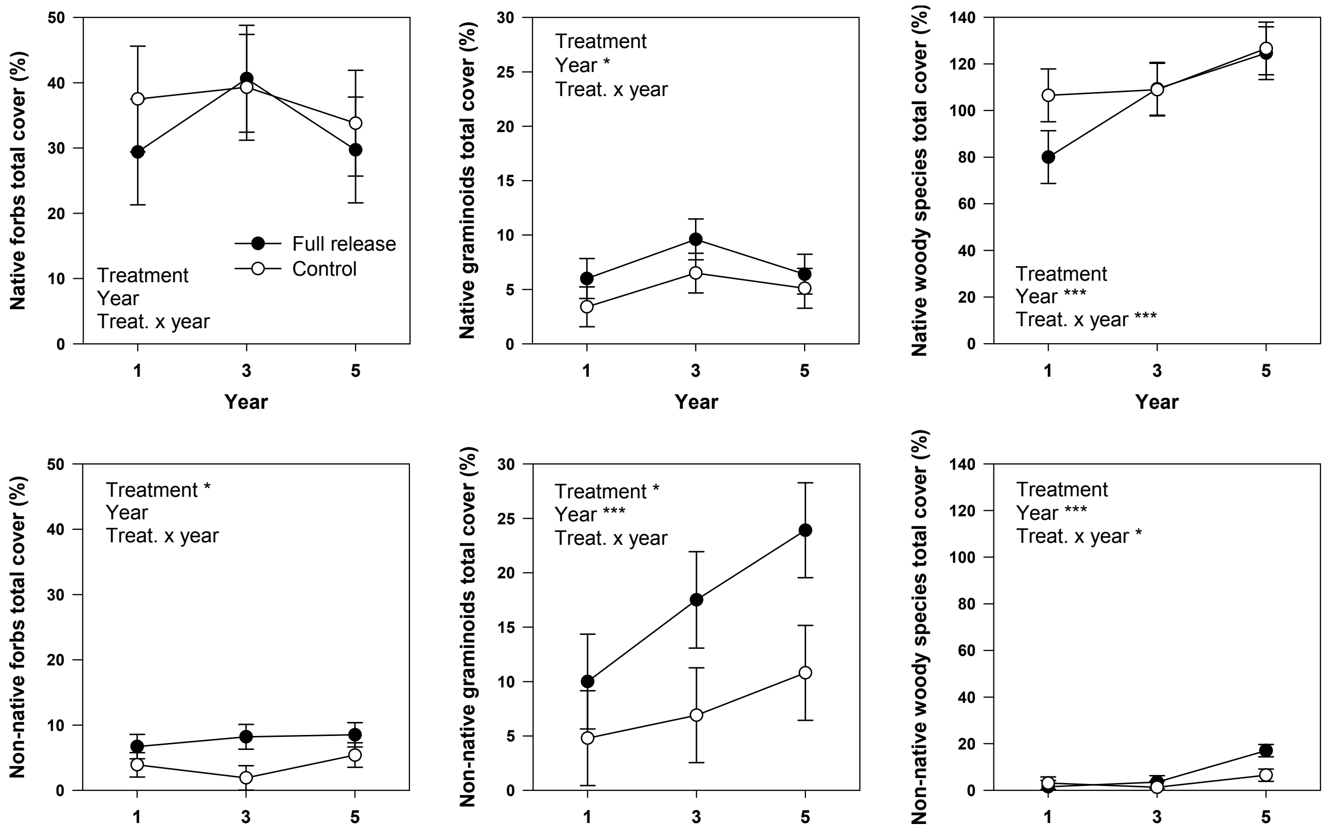

Figure 3. Total cover (± SE) of native and non-native forbs, grasses, and woody understory species for two treatments and three sampling periods. Significance of fixed effects at *p*-values of 0.05 and 0.001 is denoted by * and *, respectively.**

under unobstructed sunlight (Devine and Harrington 2006).

Our microclimate findings are in agreement with other studies that found greater diurnal fluctuation in air temperature and greater VPD in openings relative to a closed-canopy forest (Carlson and Groot 1997, Gray et al. 2002, Ritter et al. 2005). The increases in near-ground maximum air temperature, VPD, and solar radiation, resulting from removal of the conifer overstory, created an understory microclimate that is likely more similar to that of historical conditions. The return of a warmer, drier understory with greater solar radiation is important not only for reestablishing native plant species that formerly existed in that environment, but also for reducing the moisture content of fuels and thus creating conditions that will facilitate a prescribed burning regime similar to that which existed historically (Agee 1993, Tveten and Fonda 1999).

Native and non-native understory cover

Cover of native and non-native vegetation followed different trends after treatment. Cover of native forbs and grasses was not significantly changed by the full-release treatment compared to the control, but cover of non-native grasses, and, to a lesser extent, non-native forbs, was increased by the full-release treatment (Figure 3, Table 1). Non-native grass cover also increased substantially over time from year one to year five. Cover of native woody species was reduced in the full-release treatment compared to the control in year one, likely due to disturbance during the release operation. Cover of non-native woody species (predominantly Scotch broom) increased over time, and in year five was significantly greater in the full-release treatment than in the control.

The release operation used ground-based harvesting equipment that inevitably disturbed the forest floor. This resulted in a temporary but significant reduction in understory cover and an increase in exposed soil (Figure 4). Soil seed banks in 40- to 60-year-old conifer forests in the Pacific Northwest have been found to contain a significant fraction of non-native grasses and forbs, and disturbance may favor establishment of these non-native species in the understory (Halpern et al. 1999). Because the understory disturbance and the removal of the Douglas-fir overstory in our study appear to have created an environment favorable to non-native, ruderal species (i.e., those common to disturbed areas), a strategy to control undesirable plant species may be most effective if initiated prior to the release operation (Hanna and Dunn 1997). On particularly sensitive sites, aerial harvesting systems may reduce forest floor disturbance, although costs are much greater than those associated with ground-based systems (Stokes and Schilling 1997).

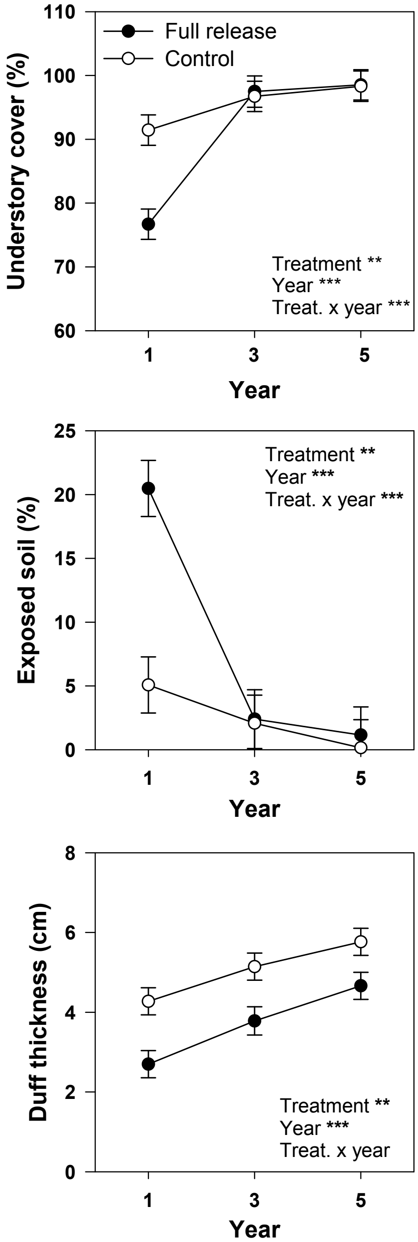

Figure 4. Total percent cover (± SE) of understory, exposed soil, and duff layer thickness for two treatments and three sampling periods. Significance of fixed effects at *p*-values of 0.01 and 0.001 is denoted by ** and *, respectively.**

Mean duff layer thickness increased over time in the full-release and control treatments, but was consistently greater in the control treatment (Figure 4). These patterns in duff layer thickness were clearly influenced by needle litter from overstory Douglas-fir. The increase over time in duff layer thickness in the full-release treatment was apparently due to litter from Douglas-fir trees at the edge of the release area as well as litter from the understory. The current accumulation of duff is certainly much greater than the organic layer that was present prior to settlement, under a regime of frequent, low-intensity fire. Thus, this duff layer presents different seedbed and fuel conditions (Tveten and Fonda 1999).

A site may become susceptible to invasion by non-native species when unused resources increase (Tilman 1985 Davis et al. 2000). In this study, removal of overstory Douglas-fir caused a rapid increase of several resources in the understory: direct sunlight, growing space, soil water, and possibly soil N (Devine and Harrington 2006, 2007). Among the three understory growth forms, the non-native grasses appeared to increase most rapidly in response to the increased resource availability (Figure 3). Coverage of both colonial bentgrass (*Agrostis capillaris*) and common velvetgrass (*Holcus lanatus*) increased significantly over time in the full-release treatment, but not in the control (Table 1). The moderate increase in non-native grass cover in the control treatment may have been associated with the commercial thinning that removed scattered Douglas-fir trees prior to the study. In southwestern British Columbia, disturbance of the understory in Oregon white oak savannas led to overall increases in invasive species and shifts in abundance of native and non-native grasses as different competitive strategies were favored (MacDougall 2002, MacDougall and Turkington 2004). Following removal of Douglas-fir from an Oregon white oak savanna in Oregon's Willamette Valley, there was a rapid increase in abundance of non-native forb and grass species, although the fraction of non-native species had begun to decline slightly by the fourth year after treatment (Vance et al. 2006).

Scotch broom, although removed from around the study trees soon after release in year one, comprised 95% of the cover of non-native woody species in the full-release treatment in year five. Scotch broom is an invasive species of particular concern in restoration of the region's prairies and savannas as it establishes and spreads rapidly and dramatically changes the understory structure (Parker et al. 1997, Parker 2000). Repeated control treatments (e.g., burning or pulling) offer the best chance to reduce Scotch broom populations, although its seed bank may endure for decades (Alexander and D'Antonio 2003). In our study, proximity to seed source influenced the spread of Scotch broom after Douglas-fir removal. For example, where Scotch broom plants occurred along forest roads in the vicinity of released trees, there appeared to be a greater likelihood of the species' encroachment upon those trees.

Oak and Douglas-fir regeneration

During the five years following treatment, growth of oak saplings increased in the full-release treatment relative to the control, while growth in the half-release treatment remained intermediate (Figure 5). Growth of oak across all treatments was significantly affected by the level of understory competition (Figure 6). Overtopped saplings grew significantly less than those that had more direct sunlight. Establishment and vigor of oak can be increased by removing understory and midstory vegetation to provide greater access to sunlight and soil water (Janzen and Hodges 1985, Davis et al. 1998, Rey-Benayas et al. 2005). On similar sites, height and diameter growth of planted Oregon white oak seedlings was increased by controlling competing vegetation using plastic mulch within a 60-cm radius of seedlings (Devine et al. 2007).

Post-treatment growth of oak saplings was significantly affected by crown shape. Across all three treatments, annual growth of flat-topped oak saplings was significantly less (5.9 ± 1.0 cm) than saplings with one leader (12.1 ± 1.3 cm) or saplings with multiple leaders (12.9 ± 1.0 cm). Similarly, oak saplings with

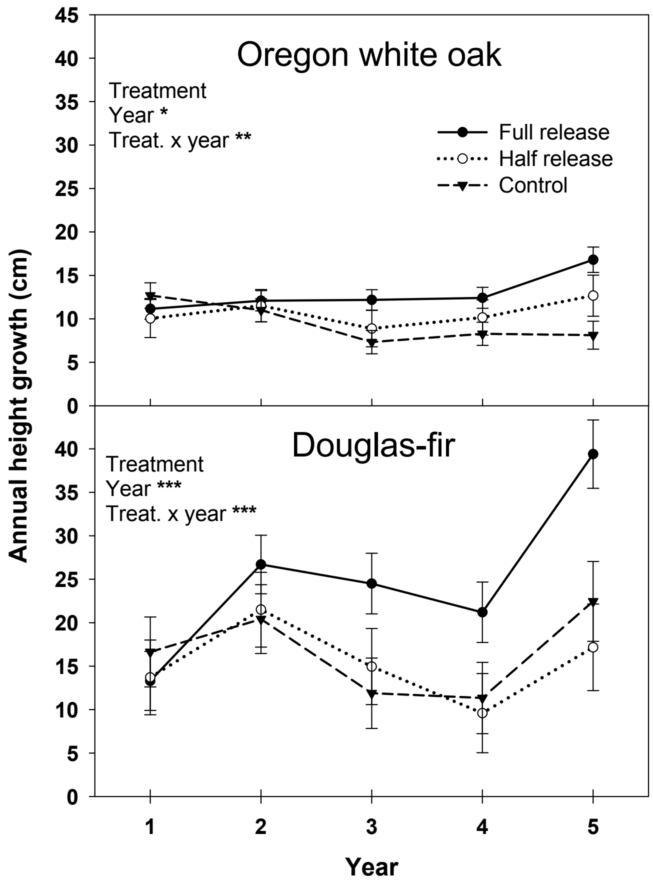

Figure 5. Annual height growth (± SE) for Oregon white oak and Douglas-fir saplings in three treatments. Significance of fixed effects at *p*-values of 0.05, 0.01, and 0.001 is denoted by *, **, and *, respectively.**

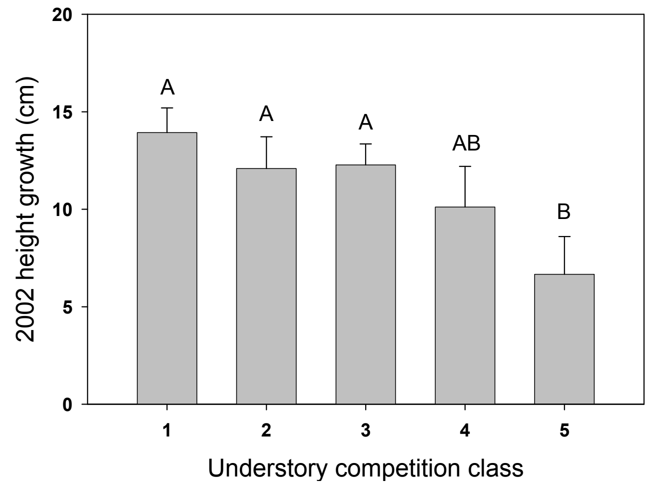

Figure 6. Height growth increment (± SE) in 2002 for Oregon white oak (*Quercus garryana*) saplings in five understory competition classes: 1) no competition near sapling crown, 2) sapling has three or more years of growth above competition, 3) sapling has one or two years of growth above competition, 4) sapling overtopped; some direct sunlight, and 5) sapling overtopped; little direct sunlight. Same letter denotes no difference at *p* = 0.05.

flat-topped crowns (white oak (*Q. alba*), northern red oak (*Q. rubra*) and chestnut oak (*Q. montana*)) in West Virginia responded slowly after partial canopy removal, although half had formed a dominant leader four years post-treatment (Carvell 1967). In our study, the growth rate of saplings with flat-topped crowns had not improved by year five in any of the treatments. Saplings that exhibited apical dominance (i.e., a dominant terminal shoot suppressing other shoots via hormone production) responded to release with greater height growth throughout the five-year period. In a related study, we improved growth rates of flat-crowned oak saplings and oak saplings damaged during a release operation by cutting saplings near the base and allowing the stump to sprout. Three-year sprout growth averaged 86 ± 34 cm, while growth of untreated saplings averaged 25 ± 15 cm.

The increase in the rate of oak growth in response to release, although statistically significant, was relatively small in magnitude, especially during the first few years after treatment. The same was true for Douglas-fir. These trends may be indications of low root to shoot ratios of these saplings prior to release. Although both of these species grow best in full sunlight, as saplings they may survive for many years beneath a Douglas-fir canopy. Growth under such conditions generally favors stem and foliar development, rather than roots, as a response to the limited light availability (Hodges and Gardiner 1992). Thus, during the initial years after release, stem growth may have been negatively affected as resources were instead allocated to root development in response to the increased light (Beon and Bartsch 2003).

Annual growth of Douglas-fir in the full-release treatment increased over time relative to growth of the conifers in the control and half-release treatments. By year five, Douglas-fir in the full-release treatment was growing at more than twice the rate of oak in the same treatment. This difference in growth rate is typical for these species when they are exposed to full sunlight, and, assuming it persists, the Douglas-fir will eventually overtop and shade the released oak trees. A restoration effort that includes removal of undesired overstory trees also must include control of young trees, and if a seed source remains on or near the site, repeated treatments will be necessary.

Implications for Practice

Removal of invading conifers is a necessary early step in restoring native oak woodlands and savannas because of the conifers' substantial effect on the understory microclimate and species composition. However, removal of overstory trees will abruptly change the microclimate and forest floor condition, making the site susceptible to colonization by invasive species. Control of particularly undesired species may be best initiated prior to the overstory treatment because heavy machinery will likely expose soil, creating a seedbed prone to colonization. Dispersal of seed via logging machinery and vehicular traffic may be reduced by cleaning vehicles and equipment before entering a site (Dalsimer 2002).

Changes in the plant understory five years after release from Douglas-fir indicate that post-release treatments will be necessary to control undesirable plant species and favor the native plant community. While prescribed burning is the traditional method of maintaining savannas and prairies in the Pacific Northwest, it is a logistical challenge to implement with regularity or on a large scale. Alternative tools for restoring native vegetation include mowing, tilling, and applying herbicide to undesirable species (Schuller 1997, Tveten and Fonda 1999, Ewing 2002, MacDougall et al. 2004). Four-year results from a restoration study show that native grasses and forbs may be established by sowing and planting, respectively, following overstory conifer removal from an oak savanna (Vance et al. 2006).

The growth of oak saplings after overstory Douglas-fir removal was affected by competition from the understory and by sapling crown shape. Oak saplings would probably benefit from control of adjacent understory competitors until the oak grows above the understory. Oak saplings with dominant leaders are likely to grow above understory competitors more quickly than saplings with flat-topped crowns. Because Douglas-fir grows rapidly following overstory removal, continuing efforts to control this species must take place to prevent it from regaining dominance of the site. Control of this regeneration is most easily implemented and least expensive when these trees are still small.

Acknowledgments

We thank the Fort Lewis Forestry Program for financial and logistical support for this project, particularly Gary McCausland and Jim Rohde (both retired) for their work in installing the study. We thank members of the Silviculture and Forest Models Team for their assistance with field and office work and Christel Kern for her work in the establishment of this study. We thank Jeffrey Foster, Roberta Davenport, and Peter Gould for reviewing a draft manuscript.

References

Agee, J.K. 1993. *Fire Ecology of Pacific Northwest Forests.* Washington, DC: Island Press.

Alexander, J.M. and C.M. D'Antonio. 2003. Control methods for the removal of French and Scotch broom tested in coastal California. *Ecological Restoration* 21:191–198.

Beon, M.S. and N. Bartsch. 2003. Early seedling growth of pine (*Pinus densiflora*) and oaks (*Quercus serrata*, *Q. mongolica*, *Q. variabilis*) in response to light intensity and soil moisture. *Plant Ecology* 167:97–105.

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.

Carvell, K.L. 1967. The response of understory oak seedlings to release after partial cutting. Agricultural Experiment Station Bulletin 553. Morgantown: University of West Virginia.

Chappell, C.B. and R.C. Crawford. 1997. Native vegetation of the South Puget Sound prairie landscape. Pages 107–122 *in* P. Dunn and K. Ewing (eds.), *Ecology and Conservation of the South Puget Sound Prairie Landscape*. Seattle, WA: The Nature Conservancy of Washington.

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

Dalsimer, A. 2002. Why DOD is interested in invasive species. *Federal Facilities Environmental Journal* 13:41–54.

Davis, M.A., J.P. Grime and K. Thompson. 2000. Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology* 88:528–534.

Davis, M.A., K.J. Wrage and P.B. Reich. 1998. Competition between tree seedlings and herbaceous vegetation: Support for a theory of resource supply and demand. *Journal of Ecology* 86:652–661.

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.

_____. 2007. Release of Oregon white oak from overtopping Douglas-fir: Effects on soil water and microclimate. *Northwest Science* 81:112–124.

Devine, W.D., C.A. Harrington and L.P. Leonard. 2007. Post-planting treatments increase growth of Oregon white oak (*Quercus garryana* Dougl. ex Hook.) seedlings. *Restoration Ecology* 15:212–222.

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.

Ewing, K. 2002. Effects of initial site treatments on early growth and three-year survival of Idaho fescue. *Restoration Ecology* 10:282–288.

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.

Halpern, C.B., S.A. Evans and S. Nielson. 1999. Soil seed banks in young, closed-canopy forests of the Olympia Peninsula, Washington: Potential contributions to understory reinitiation. *Canadian Journal of Botany* 77:922–935.

Hanna, I. and P. Dunn. 1997. Restoration goals for Oregon white oak habitats in the south Puget Sound region. Pages 231–246 *in* P. Dunn and K. Ewing (eds.), *Ecology and Conservation of the South Puget Sound Prairie Landscape*. Seattle, WA: The Nature Conservancy of Washington.

Harrington, C.A. and W.D. Devine. 2006. A practical guide to oak release. USDA Forest Service General Technical Report PNW-666.

Hodges, J.D. and E.S. Gardiner. 1992. Ecology and physiology of oak regeneration. Pages 54–65 *in* D. Loftis and C. McGee (eds.), Oak regeneration: Serious problems, practical recommendations. USDA Forest Service General Technical Report SE-84.

Janzen, G.C. and J.D. Hodges. 1985. Influence of midstory and understory vegetation removal on the establishment and development of oak regeneration. Pages 273–278 *in* E. Shoulders (ed.),

Proceedings of the 3rd Biennial Southern Silvicultural Research Conference. USDA Forest Service General Technical Report SO-54.
Lea, T. 2006. Historical Garry Oak ecosystems of Vancouver Island, British Columbia, pre-European contact to the present. *Davidsonia* 17:34–50.
Lee, R. 1978. *Forest Microclimatology.* New York: Columbia University Press.
MacDougall, A.S. 2002. Invasive perennial grasses in *Quercus garryana* meadows of southwestern British Columbia: Prospects for restoration. Pages 159–168 *in* R.B. Standiford, D. McCreary and K.L. Purcell (tech. coords.), Proceedings of the 5th symposium on oak woodlands: Oaks in California's changing landscape. USDA Forest Service General Technical Report PSW-184.
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.
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.
Parker, I.M. 2000. Invasion dynamics of *Cytisus scoparius*: A matrix model approach. *Ecological Applications* 10:726–743.
Parker, I.M., W. Harpole and D. Dionne. 1997. Plant community diversity and invasion of the exotic shrub *Cytisus scoparius*: Testing hypotheses of invasibility and impact. Pages 149–162 *in* P. Dunn and K. Ewing (eds.), *Ecology and Conservation of the South Puget Sound Prairie Landscape*. Seattle, WA: The Nature Conservancy of Washington.
Rey-Benayas, J.M., J. Navarro, T. Espigares, J.M. Nicolau and M.A. Zavala. 2005. Effects of artificial shading and weed mowing in reforestation of Mediterranean abandoned cropland with contrasting *Quercus* species. *Forest Ecology and Management* 212:302–314.
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.
Schuller, R. 1997. Vegetation response to fall prescribed burning within *Festuca idahoensis*-dominated prairie, Mima Mounds Natural Area Preserve, Washington 1985–1992. Pages 207–216 *in* P. Dunn and K. Ewing (eds.), *Ecology and Conservation of the South Puget Sound Prairie Landscape*. Seattle: The Nature Conservancy of Washington.
Singsaas, E.L., D.R. Ort and E.H. DeLucia. 2000. Diurnal regulation of photosynthesis in understory saplings. *New Phytologist* 145:39–49.
Stein, W.I. 1990. Oregon white oak. Pages 650–660 *in* R.M. Burns and B.H. Honkala (tech. coords.), Silvics of North America: Hardwoods. USDA Agricultural Handbook Number 654.
Stokes, B.J. and A. Schilling. 1997. Improved harvesting systems for wet sites. *Forest Ecology and Management* 90:155–160.
Thysell, D.R. and A.B. Carey. 2001. *Quercus garryana* communities in the Puget Trough, Washington. *Northwest Science* 75:219–235.
Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *American Naturalist* 125:827–852.
Tveten, R.K. and R.W. Fonda. 1999. Fire effects on prairies and oak woodlands on Fort Lewis, Washington. *Northwest Science* 73:145–158.
Vance, N., A. Neill and F. Morton. 2006. Native grass seeding and forb planting establishment in a degraded oak savanna plant community in the Coast Range foothills of western Oregon. *Native Plants Journal* 7:35–46.
Western Regional Climate Center (WRCC). 2005. Washington climate summaries. www.wrcc.dri.edu/summary/climsmwa.html.

Warren D. Devine, Research Forester, USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3625 93rd Ave SW, Olympia, Washington 98512, 360/753-7675, email wdevine@fs.fed.us

Constance A. Harrington, Research Forester, USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3625 93rd Ave SW, Olympia, Washington 98512

David H. Peter, Ecologist, USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3625 93rd Ave SW, Olympia, Washington 98512
