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# Restoration release of overtopped Oregon white oak increases 10-year growth and acorn production

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ABSTRACT

In the Willamette Valley–Puget Trough–Georgia Basin ecoregion of the North American Pacific Northwest, there has been widespread encroachment of Douglas-fir (*Pseudotsuga menziesii*) upon Oregon white oak (*Quercus garryana*) savanna and woodland stands that were historically maintained by frequent anthropogenic fire. Restoration of these stands requires removal of the Douglas-fir overstory, although there is little information on how oak trees that have been suppressed for decades respond to release. Our objective was to evaluate the 10-year response of oak trees to three release treatments from overtopping Douglas-fir in a study replicated at four western Washington sites. Treatments were: full release (removal of all Douglas-fir within a radius equal to the oak's height), half release (removal of Douglas-fir within a half-height radius), and thin only (stand-level commercial thinning of the Douglas-fir overstory; oaks not targeted for release). Periodic diameter growth of oak trees in the full-release treatment was significantly greater (by as much as 243%) than that in the other treatments and increased with time since treatment. Oak height and crown area growth rates were not influenced by treatment, but larger pre-treatment crown size was associated with greater post-treatment diameter growth and acorn production. Full release increased acorn production compared to thin only in years when region-wide production was moderate to high (5 of 9 years); half release increased production relative to thin only in 2 of 9 years, but to a lesser degree. Height growth of residual Douglas-fir trees was greater than that of oak trees in all treatments. The increasing post-treatment growth rate of the fully released oak trees and their increased acorn production indicate the capacity of long-suppressed Oregon white oak to rapidly recover following complete removal of a conifer overstory. The oak trees showed no negative effects following the dramatic change in environment associated with this treatment. Thus, a single-entry, complete release from overtopping conifers was effective in restoring overstory structure and composition, which is an initial step in restoration of invaded oak woodland or savanna.



## 1. Introduction

Encroachment of woody plants into savanna ecosystems during the past century has been widely documented in Africa, North America, South America, and Australia (San José and Fariñas, 1983; Archer, 1994; Fensham et al., 2005; Smit, 2004; Staver et al., 2011). Climate, fire regime, soils, and grazing are important determinants of savanna distribution at a global scale (Staver et al., 2011). Prior to European settlement, oak savannas and woodlands occupied substantial portions of North America (McPherson, 1997). Major regions of oak savanna were the Midwest, between the tallgrass prairies and the eastern deciduous forest (Anderson, 1998); the Southwest, in New Mexico, Arizona, and northern Mexico (McClaran and McPherson, 1999); and a region near the Pacific Coast stretching from southern British Columbia to Mexico (Allen-Diaz et al., 1999). Historically, the vegetative structure and composition of North American oak savannas were maintained by various combinations of fire, drought, herbivory, or in rare instances, flooding (McPherson, 1997; Anderson, 1998). Since European settlement, the structure and ecological processes of many oak savannas have been substantially altered by a reduction in fire frequency, introduction of exotic species, grazing of livestock and other agricultural uses, and development (Agee, 1993; McPherson, 1997; Anderson et al., 1999; Lea, 2006; Dunwiddie et al., 2011).

Savannas encroached upon by trees and shrubs undergo altered soil water availability (Asbjornsen et al., 2007; Devine and Harrington, 2007), changes in nutrient cycling (Archer et al., 2001; Hibbard et al., 2001), and a dramatic shift in the understory environment that leads to changes in understory plant composition (Thysell

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and Carey, 2001; Devine et al., 2007; Brudvig and Asbjornsen, 2009). After invasion, low-intensity fire, an ideal tool for restoring savannas and woodlands (Hamman et al., 2011), may become infeasible owing to a reduction in herbaceous biomass and an increase in woody fuels and fuel moisture levels (Engber et al., 2011). The invading woody species also compete with relic oak trees, crowding them, and in some cases overtopping them. Mortality of the relic oak trees represents a significant loss to the structure of the ecosystem; these trees require many decades to centuries to replace. Although oak trees are only one component of an oak savanna or woodland, they are a critical structural element for habitat, provide food for wildlife, and have cultural significance.

Recently, researchers have begun to address the issue of restoring oak savanna or woodland structure by removing the invading trees or shrubs while retaining the relic oak trees. In a white oak (*Quercus alba*) savanna in central Iowa, USA, relic oak trees were released from invading trees after more than 40 years of encroachment; diameter growth of released trees was significantly greater in the 7 years post-release compared to unreleased trees (Brudvig et al., 2011). Although thinning and release treatments have long been conducted in young hardwood stands to promote growth of oak (*Quercus* spp.) crop trees for timber production (McGee and Bivens, 1984; Lamson et al., 1990), the stand conditions, prescriptions, and long-term objectives of that type of release treatment differ from those of restoration treatments. For example, in oak woodland restoration, the trees selected for release are often much older than the removed trees, are frequently lower in vigor at the time of release, and are chosen for non-timber attributes.

The present study took place in the Puget Trough of western Washington, where frequent anthropogenic fire maintained prairies and Oregon white oak (*Quercus garryana*) savannas and woodlands prior to European settlement (Crawford and Hall, 1997). During the past century, Douglas-fir (*Pseudotsuga menziesii*) has regenerated throughout the North American Pacific Northwest prairie and oak ecosystems in the absence of fire (Crawford and Hall, 1997; Thysell and Carey, 2001; Lea, 2006; Dunwiddie et al., 2011). Owing to its rapid growth and large size ($\geqslant$40 m height after 75 years), the encroaching Douglas-fir has overtopped and suppressed the shade-intolerant oak; many of these remaining oak trees are now in poor condition with significant crown dieback. This encroachment has transformed oak savannas and woodlands into conifer forests with some relic structure and species retained from the previous ecosystem (Devine and Harrington, 2006; Gould and Harrington, 2008). This study evaluates, as a restoration tool, the mechanical removal of encroaching trees, which is an initial step in restoring an invaded oak savanna ecosystem (Peterson and Reich, 2001; Brudvig et al., 2011). Specifically, the analysis focuses on the effects of overstory Douglas-fir removal on residual oak trees. We evaluated three different levels of removal, ranging from full release of oak trees (representing a restoration treatment) to a stand-level commercial thinning of the Douglas-fir overstory (representing management with a timber production objective). Five-year results from this study showed that overtopped Oregon white oak trees released from encroaching Douglas-fir responded by increasing diameter growth and acorn production and by forming epicormic branches (Devine and Harrington, 2006). In the present study, the primary objective was to assess the 10-year effects of release treatments on oak trees to determine whether early responses to release have faded or are increasing. In addition to remeasuring the same oak trees evaluated at year 5, the 10-year response of all other oak and residual Douglas-fir trees in the treatment areas was assessed to provide information on relative treatment responses of the two species which may indicate treatment effects on future stand structure.

## 2. Methods

### 2.1. Study sites

The study is located on Joint Base Lewis-McChord, in the Puget Trough physiographic province of western Washington, USA. The study took place in four forest stands, located 10–15 km apart; elevations ranged from 85 to 135 m above mean sea level. These stands were former oak savannas and woodlands that were colonized by Douglas-fir during the early to mid-20th century. They are characterized by an overstory dominated by Douglas-fir and a mid-story containing Oregon white oak under varying degrees of suppression (Table 1). The Douglas-fir canopy intercepted an average of 87% of potential photosynthetically actively radiation (Devine and Harrington, 2006). The Douglas-fir overstory in all four stands had been commercially thinned two to three times prior to this study at 10- to 15-year intervals; the most recent thinning occurred in conjunction with study installation (2000–2001).

The soils of the study area are formed in glacial materials; they are classified as Typic Melanoxerands and Vitrandic Dystroxerepts (Zulauf, 1979; Pringle, 1990) and are mapped as Humic Cambisols by FAO (1995). These soils are sandy to sandy-skeletal in texture and are somewhat excessively drained. The climate has a maritime influence with warm, dry summers and mild, wet winters. Mean annual precipitation in Tacoma, WA (15–25 km from study sites) is 1008 mm, although total precipitation from 1 May through 30 September averages only 166 mm (WRCC, 2012). Mean air temperatures in January and July are 4 and 18 °C, respectively.

### 2.2. Study installation

The study began in late 2000 with the selection of 72 overtopped oak trees (18 per site) representing a range of sizes (diameter at breast height (DBH) = 19.0–53.0 cm; height = 8.4–21.8 m) and varying degrees of suppression (i.e., crowns partially to completely overtopped by Douglas-fir). The selected oak trees had crowns that were overtopped by a minimum of two Douglas-fir trees (Table 1). Among sites, mean age of selected oak trees ranged from 94 to 130 years; mean age of dominant/co-dominant Douglas-fir ranged from 65 to 80 years. Although density of both species varied among sites, the vertical structure was consistent: mean height of dominant/co-dominant Douglas-fir ranged from 39.0 to 44.0 m and that of oak ranged from 15.5 to 16.4 m. The mean distance from the bole of a study tree to the bole of the nearest overtopping Douglas-fir was 4.4 m.

Centered on each of these selected oak trees, a study plot was established with a radius equal to the tree's height (mean height = 16.0 m); the selected oak trees are hereafter termed "center trees". All of the other trees occurring on the study plots are termed "plot trees". Center trees were randomly assigned one of three release treatments (six replications per site):

Thin only: no Douglas-fir trees were removed specifically to release the center trees; however, the stand-level commercial thinning in 2000–2001 removed an average of two Douglas-fir trees per plot.

Half release: in addition to the commercial thinning, all Douglas-fir trees ($\geqslant$10.0 cm DBH) within a radius of one-half of the center tree's height were removed. This treatment removed an average of 6 Douglas-fir trees per plot.

Full release: in addition to the commercial thinning, all Douglas-fir trees ($\geqslant$10.0 cm DBH) were removed from the plot. This treatment removed an average of 15 Douglas-fir trees per plot.

The thin-only treatment was a low-intensity, commercial thinning of the Douglas-fir overstory; oak trees were not specifically targeted for release but were always retained. The half-release treatment was similar to individual-tree release treatments that have been applied operationally to Oregon white oak trees in the

**Table 1**
Pre-treatment study plot and tree attributes at four study sites on Joint Base Lewis-McChord, western Washington. Means are shown, with standard deviation in parentheses for individual-tree measurements (tree ages were not available for some trees owing to rot).

| Parameter | Species | Site | | | |
|---|---|---|---|---|---|
| | | Cherry hill | Goodacre | Lake Joseph | Sneesby |
| *Study plot composition*[a] | | | | | |
| Trees (no. $ha^{-1}$) | Oak[b] | 149 | 57 | 63 | 192 |
| | Douglas-fir | 111 | 149 | 215 | 192 |
| | Other spp[b] | 91 | 27 | 42 | 36 |
| BA ($m^2$ $ha^{-1}$) | Oak | 4.8 | 2.0 | 4.0 | 7.8 |
| | Douglas-fir | 31.6 | 29.2 | 46.5 | 29.7 |
| | Other spp | 2.9 | 0.3 | 0.9 | 0.4 |
| *Oak center trees* | | | | | |
| DBH (cm) | | 31.9 (8.7) | 29.8 (9.7) | 29.8 (7.7) | 31.3 (8.3) |
| Height (m) | | 15.5 (3.4) | 16.1 (3.3) | 16.4 (3.4) | 16.1 (2.5) |
| Crown area index ($m^2$)[c] | | 53.8 (22.1) | 49.2 (24.5) | 22.7 (21.3) | 38.8 (27.4) |
| Live-crown ratio[d] | | 0.38 (0.22) | 0.41 (0.15) | 0.26 (0.17) | 0.30 (0.12) |
| Tree age at study installation (year) | | 98 | 130 | 124 | 94 |
| *Two tallest Douglas-fir per plot* | | | | | |
| DBH (cm) | | 83.4 (30.2) | 81.8 (27.1) | 88.5 (17.9) | 80.4 (20.3) |
| Height (m) | | 39.4 (8.3) | 40.0 (7.7) | 44.0 (3.9) | 39.0 (5.8) |
| Tree age at study installation (year) | | 80 | 75 | 75 | 65 |

[a] Trees ⩾ 10 cm DBH.
[b] Oak = Oregon white oak; other species that were most prevalent were bigleaf maple (*Acer macrophyllum*), Oregon ash (*Fraxinus latifolia*), and bitter cherry (*Prunus emarginata*).
[c] Crown area index = crown diameter × crown diameter measured in a perpendicular direction.
[d] Live-crown ratio = (total height − height to crown base)/total height.

region to temporarily reduce competition and prevent mortality until subsequent management actions are taken. The full-release treatment was designed to represent the conditions that result from a stand-level release of oak from all Douglas-fir competitors. Full release restoration treatments have been applied to Oregon white oak in some locations, but with the exception of this study, few data exist to show trees' responses.

The half- and full-release treatments were applied in April–May 2001; trees were cut with chainsaws and yarded with skidders. Minimal logging damage occurred during the release; several center oak trees had a small number of broken limbs and two had bark scraped from the bole (Harrington and Kern, 2002).

### 2.3. Data collection

The 72 center trees were measured for DBH (nearest mm), height (nearest 0.1 m), height to base of live crown (nearest 0.1 m; excluding epicormic branches), and crown diameter (in two perpendicular directions; nearest 0.1 m) prior to treatment and after the 3rd, 5th, and 10th years post-treatment. Height and DBH of the two tallest Douglas-fir trees per plot ($n = 144$ trees), and of all plot oak trees ($n = 875$) were measured pre-treatment and after years 5 and 10 post-treatment. At the same interval, DBH was measured for all non-oak plot trees, which were primarily Douglas-fir ($n = 899$).

Acorn production of the center oak trees was evaluated annually during late August or early September in years 3 through 11 post-treatment. For each tree, a 60-second tally (Devine and Harrington, 2006) of mature acorns was made by examining crowns from the ground using 10 × 42 power binoculars. In the 60-second acorn tally, the observer scanned the crown of a tree until the first acorn was sighted, at which point a 60-second period began during which the observer tallied every mature acorn seen. Prior to data collection, the two observers making tallies successfully verified the repeatability of this method (counts consistently within 20%) on 50 trees.

### 2.4. Data analyses

Analyses of tree growth and acorn production were performed with a generalized, randomized complete-block design analysis of variance (ANOVA) model (Hinkelmann and Kempthorne, 1994) using Proc Mixed in SAS (SAS Institute, 2008). Site (i.e., block) was treated as a random effect; the three treatments were replicated six times per block. The experimental unit was the center oak or, in the analysis of plots trees, the study plot. Repeated-measures ANOVA was used for growth variables that had multiple measurement periods ($n = 2$ or 3, depending on variable) and for annual acorn production ($n = 9$ years).

Crown area index was calculated by multiplying the two crown diameter measurements. Crown depth was defined as the difference between tree height and height to base of live crown. A crown volume index was calculated by multiplying crown area index by crown depth. Live-crown ratio was defined as the ratio of crown depth to tree height. Pre-treatment values for tree height, DBH, crown depth, live-crown ratio, crown area index, and crown volume index were tested as potential covariates in all analyses of center oak tree growth and acorn production; pre-treatment values for tree height and DBH were tested as potential covariates in analyses of plot trees. Covariates were included in the final model if significant. Crown area index was analyzed as a dependent variable, but dependent variables based on crown depth (e.g., crown volume index) are not presented because that parameter did not change significantly over time. A $\log(x + 1)$ transformation was used to achieve normal distribution of acorn production data (Hinkelmann and Kempthorne, 1994). Individual-tree basal area growth increment (at breast height) was analyzed but results are not presented here because they did not differ appreciably from the results of the DBH analysis. Mean separations were performed using Tukey's HSD test. Significance was judged at alpha = 0.05 throughout.

## 3. Results

### 3.1. Growth of center oak trees

During each of the three post-treatment time periods, the full-release treatment was consistently associated with the greatest annual DBH growth (Fig. 1; Table 2). Annual DBH growth in the half-release and thin-only treatments did not differ during any time period. The rate of DBH growth in the full-release treatment trended upward over time, in contrast to the other two treatments,

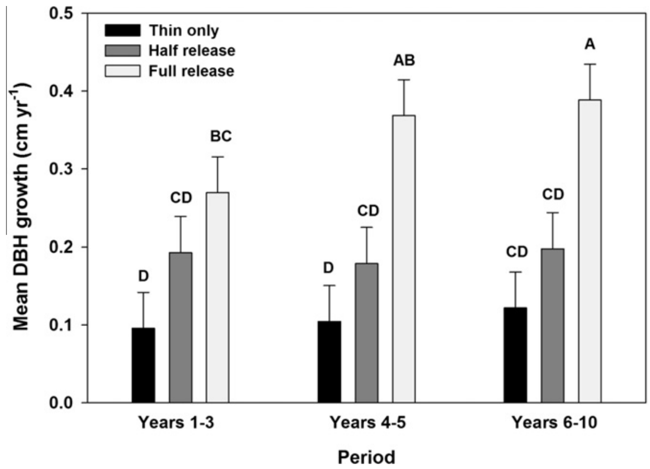


**Fig. 1.** Annual DBH growth (with one standard error) of Oregon white oak center trees in three release treatments during three time periods post-treatment. Bars accompanied by the same letter do not differ (95% confidence level).

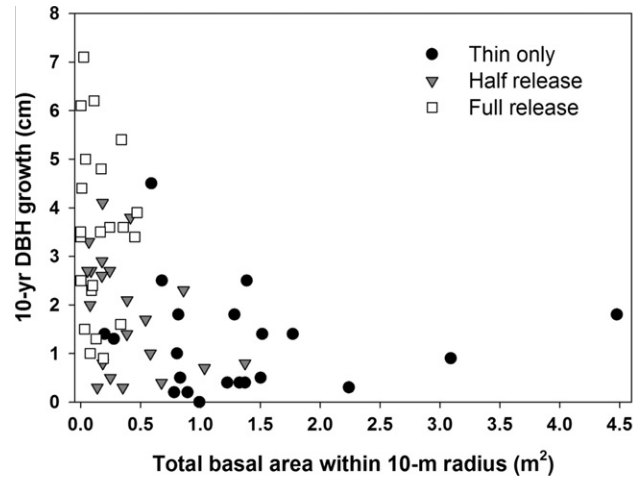


**Fig. 2.** Cumulative 10-year DBH growth for Oregon white oak center trees following three release treatments; data are plotted against the summed basal area, measured immediately after treatment, of all trees growing within a 10-m radius of the center tree. Note that the data point at the far right was influenced by one very large Douglas-fir tree (223 cm DBH; 3.91 $m^2$ basal area).

although the treatment × time period interaction was non-significant. After accounting for the effects of the designed experiment, two covariates described additional variation in annual DBH growth of center oaks: a larger initial DBH was associated with a lower DBH growth rate, whereas a larger initial crown volume index was associated with a greater DBH growth rate (Table 2). The influence of competition on 10-year DBH growth is illustrated by plotting 10-year growth against total basal area of all trees within 10 m of the center oak (Fig. 2); 10-year DBH increment was 2.5 cm or less for all center oaks with competitors totaling more than 0.6 $m^2$ basal area.

Ten-year height growth of center oak trees was not significantly influenced by treatment (Table 2; Fig. 3), but variation in height growth was explained by two covariates: initial DBH (positive association) and pre-treatment height (negative association). Ten-year change in crown area index was not significantly affected by treatment, but variation in crown area index was explained by pre-treatment DBH (positive association), as a covariate (Table 2; Fig. 3).

### 3.2. Acorn production of center oak trees

Acorn production (i.e., 60-s acorn tally) was significantly influenced by treatment, year, and the treatment × year interaction (Table 2). Additional variation in acorn production was explained by a positive effect of initial crown volume index (a covariate). During the 9 years in which acorn production was assessed, there was no treatment effect in the 4 years of very low production (years 3, 5, 10, and 11) (Fig. 4). In the other 5 years, production in the full-release treatment was greater than that in the thin-only treatment each year. In two of those 5 years (years 4 and 7), production in the half-release treatment also was significantly greater than that in the thin-only treatment.

### 3.3. Growth of plot trees

DBH growth of plot oak trees (⩾10 cm DBH) was significantly greater in the full-release treatment than in the other treatments during both 5-year periods (Table 3, Fig. 5a). However, DBH growth also was less in the second period than in the first period ($p < 0.001$). Variation in DBH growth not explained by the designed experiment was explained by a positive influence of initial DBH (a covariate) on post-treatment DBH growth (Table 3).

Height growth of plot oak trees (⩾10 cm DBH) was not significantly influenced by treatment during the two time periods, but

**Table 2**
ANOVA results for growth of Oregon white oak center trees ($n = 72$). For periodic DBH growth rate analysis, the 10-year study was divided into three time periods: year 1–3, year 4–5, and year 6–10.

| Variable | Source | Deg. freedom | | *F* value | Pr > *F* | Covariate effect |
|---|---|---|---|---|---|---|
| | | Num. | Den. | | | |
| Periodic DBH growth rate (cm $year^{-1}$) | Treatment | 2 | 50 | 20.3 | <0.001 | |
| | Time period | 2 | 144 | 2.5 | 0.087 | |
| | Treatment × time | 4 | 144 | 1.6 | 0.169 | |
| | Initial DBH[a] | 1 | 94 | 10.4 | 0.002 | −0.006 |
| | Initial CVI[a] | 1 | 93 | 12.9 | <0.001 | +0.0002 |
| 10-year cumulative height growth (m) | Treatment | 2 | 5 | 5.2 | 0.057 | |
| | Initial DBH[a] | 1 | 52 | 7.4 | 0.009 | +0.094 |
| | Initial height[a] | 1 | 38 | 16.2 | <0.001 | −0.329 |
| 10-year CAI increment ($m^2$) | Treatment | 2 | 43 | 1.7 | 0.261 | |
| | Initial DBH[a] | 1 | 59 | 15.1 | <0.001 | +1.194 |
| Annual acorn count[b] | Treatment | 2 | 48 | 7.3 | 0.002 | |
| | Year | 8 | 548 | 64.2 | <0.001 | |
| | Treatment × year | 16 | 548 | 2.4 | 0.002 | |
| | Initial CVI[a] | 1 | 204 | 7.6 | 0.006 | +0.0007 |

[a] Covariate. DBH = diameter at breast height; CVI = crown volume index; CAI = crown area index.
[b] Analysis performed on log-transformed values.

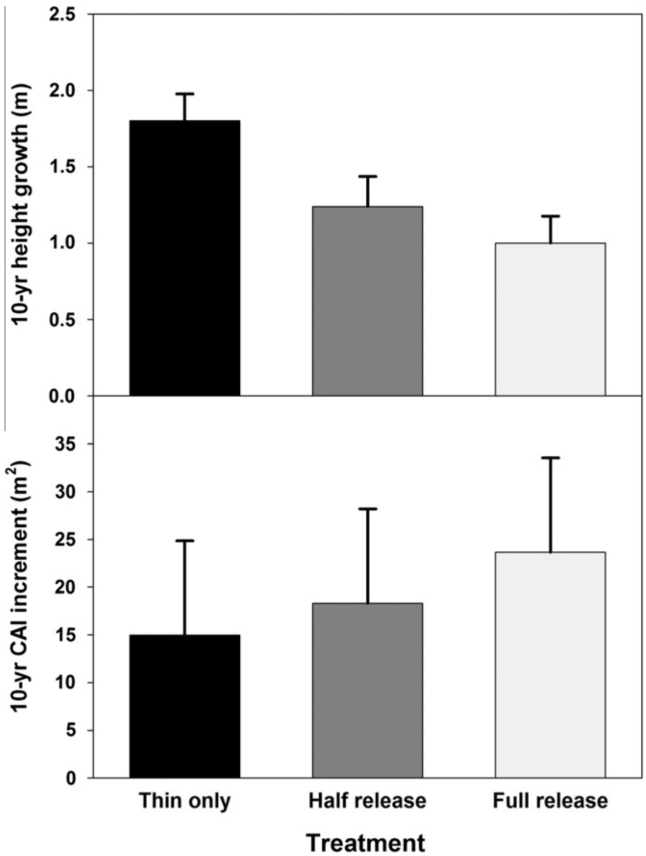


**Fig. 3.** Ten-year post-treatment cumulative height growth and crown area index (CAI) increment (with one standard error) for Oregon white oak center trees in three release treatments. No significant differences occurred among treatment means (95% confidence level).

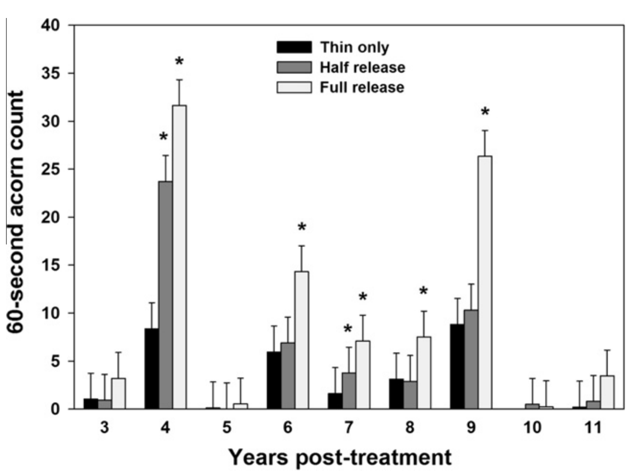


**Fig. 4.** Mean acorn production of Oregon white oak center trees in three release treatments during years 3 through 11 post-treatment (with one standard error). Asterisk indicates that the half- or full-release treatment mean differs from that of the thin-only treatment within a given year (95% confidence level).

height growth was greater in the second than in the first period ($p = 0.007$; Table 3; Fig. 5d). Initial height, as a covariate, was negatively associated with post-treatment height growth (i.e., trees that were initially smaller had greater height growth during the study). Height growth of small oak trees (initially $\leqslant 3.0$ m tall) was not significantly affected by treatment or time period (Table 3; Fig. 5c).

Douglas-fir DBH growth (trees $\geqslant 10$ cm DBH) was not influenced by treatment but was greater in the first than in the second time period across all treatments (Table 3; Fig. 5b). Initial DBH, as a covariate, was positively related to DBH growth during the 10 years post-treatment. Basal area of residual Douglas-fir in the thin-only treatment increased by 19.4% from $33.0 \pm 13.9$ to $39.4 \pm 17.1$ $m^2$ $ha^{-1}$ during the 10-year study. Basal area of residual Douglas-fir in the half-release treatment increased by a similar amount (21.1%), from $24.6 \pm 15.2$ to $29.8 \pm 17.2$ $m^2$ $ha^{-1}$ during the same interval.

Height growth of the two tallest Douglas-fir trees per plot was not significantly affected by treatment ($p = 0.060$), although the growth of trees in the half-release treatment trended greater than that of trees in the thin-only treatment (Fig. 5e). Initial height was negatively associated with 10-year height growth, as a covariate (Table 3).

## 4. Discussion

The growth response of the Oregon white oak center trees indicates that full release not only provides the greatest diameter growth response in the initial years following treatment, but that the diameter growth response in this treatment also increased over time. The positive effect of release on Oregon white oak growth was also demonstrated in a recent operational release at another western Washington location; in that study, DBH growth of fully released trees was greatest while that of trees still receiving competition was strongly correlated with the amount of crown that was free from contact with adjacent Douglas-fir (Gould et al., 2011). Although we did not measure crown contact, we observed a clear relationship between DBH growth and basal area of nearby competitors (Fig. 2). On a Midwest savanna, DBH growth of white oak trees receiving a restoration release from encroaching broadleaf species increased nearly 50% during the first 7 years after release (Brudvig et al., 2011). The greater magnitude of the response to full release in our study (a 243% DBH growth increase compared to thin-only) may have been influenced by the greater level of interspecific competition associated with the coniferous overstory at our sites. Our study did not include a true control treatment (i.e., a treatment with no Douglas-fir removal); thus, it is unclear whether the trees in the thin-only treatment benefitted from the stand-level overstory thinning. If there was a benefit, then our observed treatment responses (i.e., differences in response between full- or half-release treatment compared to thin-only) are smaller than would have occurred using a true control as the reference stand condition.

The fact that diameter growth of fully released center oak trees increased in the second 5-year period – while diameter growth of plot oak trees in all treatments decreased – indicates a growth advantage of the center oaks' plot-center location. Other oak trees located throughout the full-release study plots were closer to the plot edge than the center oaks; these trees would have received less direct sunlight and likely would have experienced greater belowground competition for water and nutrients from roots of the Douglas-fir trees surrounding the plot. Earlier data show that the plot-center location in the full-release treatment received greater direct sunlight than in the other treatments (Devine and Harrington, 2006), and an associated study showed increased soil water content at plot center (Devine and Harrington, 2007). In gaps similar in size to our full-release treatment plots, photosynthetically active radiation and soil water content were highest in the center of the gap and decreased toward the gap edge (Gray et al., 2002). Following overstory density reduction, available soil water in oak stands has been shown to increase for residual trees owing to the combined effects of decreased interception of rainfall and reduced stand-level transpiration (Bréda et al., 1995). Although our study plot size was limited by logistical constraints, these patterns

**Table 3**
ANOVA results for annual growth rate of Oregon white oak and Douglas-fir plot trees (data do not include center oak trees; see Table 2). Annual growth rate was analyzed for two periods post-treatment: year 1–5 and year 6–10. For Douglas-fir height growth analysis, only the two tallest trees per plot (at the time of study installation) were analyzed.

| Variable | Source | Deg. freedom | | *F* value | Pr > *F* | Covar. effect |
|---|---|---|---|---|---|---|
| | | Num. | Den. | | | |
| *Trees with initial DBH ⩾ 10.0 cm* | | | | | | |
| Oak DBH (cm $year^{-1}$) | Treatment | 2 | 38 | 9.8 | <0.001 | |
| | Time period | 1 | 971 | 66.2 | <0.001 | |
| | Treatment × time | 2 | 971 | 0.6 | 0.577 | |
| | Initial DBH[a] | 1 | 1001 | 33.1 | <0.001 | +0.004 |
| Oak height (m $year^{-1}$) | Treatment | 2 | 35 | 0.1 | 0.902 | |
| | Time period | 1 | 192 | 7.5 | 0.007 | |
| | Treatment × time | 2 | 192 | 1.5 | 0.230 | |
| | Initial height[a] | 1 | 171 | 6.8 | 0.010 | −0.008 |
| Douglas-fir DBH (cm $year^{-1}$) | Treatment | 1 | 3 | 0.8 | 0.434 | |
| | Time period | 1 | 767 | 14.8 | <0.001 | |
| | Treatment × time | 1 | 767 | 0.1 | 0.763 | |
| | Initial DBH[a] | 1 | 806 | 117.2 | <0.001 | +0.003 |
| Douglas-fir height (m $year^{-1}$) | Treatment | 1 | 28 | 3.9 | 0.060 | |
| | Time period | 1 | 116 | 0.2 | 0.700 | |
| | Treatment × time | 1 | 116 | 0.2 | 0.669 | |
| | Initial height[a] | 1 | 90 | 14.5 | <0.001 | −0.011 |
| *Trees with initial height ⩽ 3.0 m* | | | | | | |
| Oak height (m $year^{-1}$) | Treatment | 2 | 3 | 3.0 | 0.224 | |
| | Time period | 1 | 104 | 0.0 | 0.964 | |
| | Treatment × time | 2 | 104 | 0.0 | 0.986 | |

[a] Covariate.

support the idea that oak trees would receive the greatest increase in above- and below-ground resources from a release treatment applied to a large area or at the stand level. Release at that scale would also facilitate understory treatments such as prescribed burning or mowing.

Diameter growth of oak and Douglas-fir trees on study plots, across all treatments, decreased from the first to the second 5-year period (Fig. 5a and b). Thus, we can infer that a study-wide phenomenon was influencing tree diameter growth. Because all three treatments received some level of overstory reduction, it is possible that this reduction in competition provided an increase in resource availability that declined by the second 5-year period as the additional resources were more fully exploited by vegetation. For example, uptake of belowground resources could have increased in association with the increase in post-treatment understory growth (Black et al., 1980; Devine et al. 2007). It is also possible that inter-annual differences in climate, most likely summer precipitation, could have contributed to the differences in DBH growth between measurement periods. For oak near the study area, a significant portion of annual diameter growth occurs during June (Gould et al., 2011); during the first 5-year period, June precipitation twice exceeded 10 cm, whereas this only occurred once during the second 5-year period. This would likely not explain the growth trend for Douglas-fir, which typically continue to grow in diameter later in summer and into fall.

The DBH growth rate of the center oak trees in our thin-only treatment was very slow (approximately 1 mm $year^{-1}$) relative to open-grown Oregon white oak trees (3–4 mm $year^{-1}$ for released trees; Gould et al., 2011) and, considering the level of competition at the study sites, suggests a relatively high probability of tree mortality in coming years (Gould et al., 2008, 2011). Dead oak trees have been observed in the vicinity of study plots at all of our study sites. A study of growth rate prior to mortality in southeastern USA hardwood forests found that oak species, when suppressed, suffered a relatively long period of growth decline (12 years or more) prior to mortality (Wyckoff and Clark, 2002). Pedersen (1998) evaluated growth patterns associated with mortality in Midwestern oak trees; trees with reduced diameter growth rates, potentially associated with competition, were susceptible to further growth reductions from environmental stresses such as drought, which increased the likelihood of a tree's death, whereas trees with increasing growth rates were much less likely to suffer mortality. Thus, the dramatic increase in growth rates exhibited by our full-release treatment suggests that a restoration release can likely reduce future mortality rates of Oregon white oak trees.

Two covariates explained variation in center oak DBH growth that was not explained by the designed treatments: initial crown size and initial DBH. Initial crown size was positively associated with post-treatment DBH growth. This positive association occurred across the three treatments but was not interactive with the treatment effect: all center oak trees benefitted from greater initial crown size, and the full-release treatment conferred an added growth benefit. The trees with smaller crowns were typically those that had previously experienced a high level of dieback as a result of competition; across all treatments, 83% of trees had dieback of at least one major limb (Devine and Harrington, 2006). Our finding that DBH growth was positively associated with crown size and initial DBH supports the findings of a study in several southern Appalachian (USA) stands that found individual-tree basal area growth of two oak species (*Quercus rubra* and *Quercus prinus*) was strongly predicted by exposed crown area and initial tree basal area (Wyckoff and Clark, 2005). In that study and in our study, exposure of crown to sunlight explained variation in growth not explained by tree size alone, although in our study, the degree of crown exposure was largely determined by the release treatments (Devine and Harrington, 2006).

The negative association between initial DBH of center oak trees and post-treatment DBH growth (covariate in Table 2) was the opposite of the pattern shown by plot oak trees, which had a positive association between initial DBH and post-treatment DBH growth (covariate in Table 3). However, this pattern may be explained by the fact that the datasets were truncated differently (i.e., ⩾10 cm DBH for plot trees and ⩾19 cm DBH for center trees). When the plot tree dataset was truncated to include the same DBH range as the center tree dataset, the positive covariate association between initial DBH and post-treatment DBH growth no longer ex-

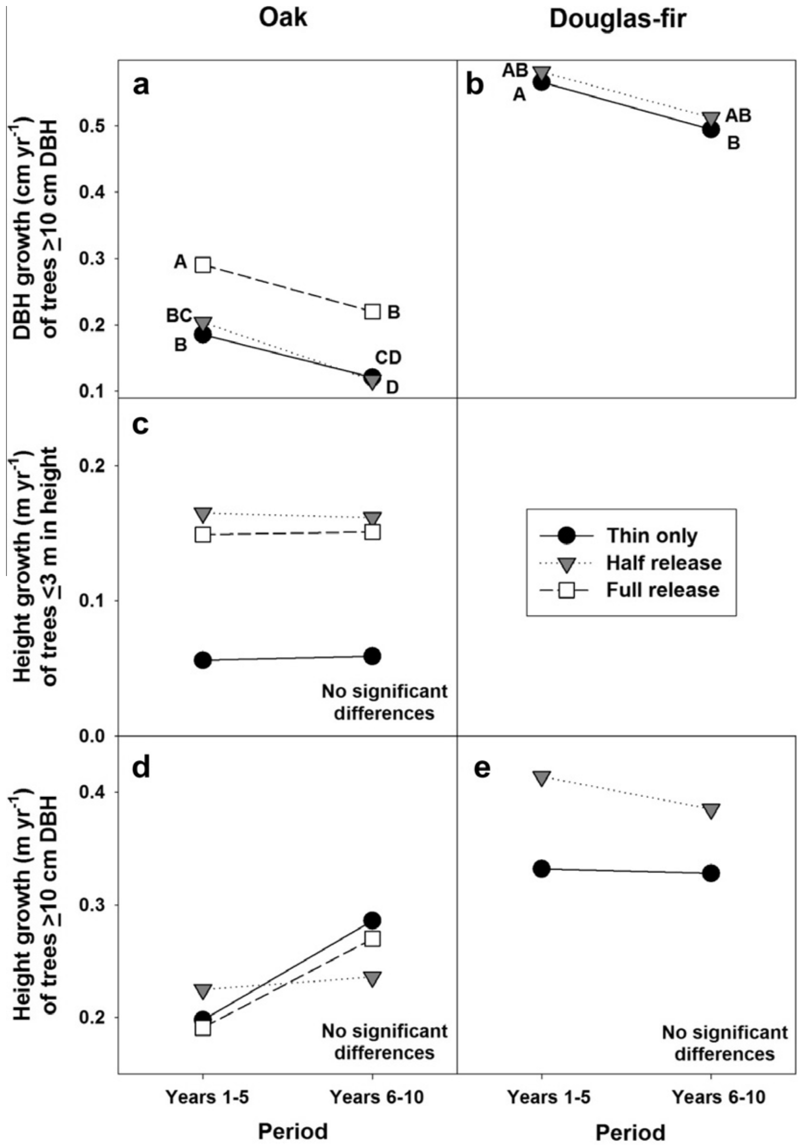


**Fig. 5.** DBH growth rates (a and b) and height growth rates (c–e) of Oregon white oak and Douglas-fir plot trees (data do not include center oak trees) during two periods following release treatments. Douglas-fir height growth is for two tallest trees per plot at study installation. Analysis groups were defined by pre-treatment DBH (⩾10 cm) or height (⩽3 m). Means accompanied by the same letter do not differ (95% confidence level); non-sequential significance patterns (e.g., an intermediate value differs from the smallest value, whereas the largest value does not differ from the smallest) are a result of differences in variation among treatments.

isted. Thus, the smaller-diameter oak trees in this study (i.e., 10–19 cm DBH) were associated with the least post-treatment DBH growth.

Oak height growth was not influenced by release treatments, but pre-treatment height was negatively associated with post-treatment height growth for both center and plot oaks. Assuming that productivity is similar across sites, this trend may be a result of the slowing of oak height growth with age, which is characteristic of many oak species (Carmean, 1972). Similarly, oak crown area index increment was not significantly affected by the treatments, although it is possible that crowns responded to treatments in a way that was not well captured by our measurements. For example, we did not quantify density of foliage within the crown, which is related to tree vigor (Meadows and Stanturf, 1997), or individual-tree leaf area. Crown expansion associated with epicormic branch formation was reported in the year-5 analysis (Devine and Harrington, 2006); at year 10, we observed that the epicormic branches reported at year 5 were still present and continuing to develop. Based on crown development patterns in other species, and observations of the oak trees in our study, it is likely that some of the branches that originated as epicormic sprouts following release will compose a significant and permanent component of the crowns (Bond and Midgley, 2003; Ishii and Wilson, 2001).

Acorn production varied widely among study years; annual levels of acorn production by this species are generally synchronous within the Puget-Willamette Trough but are influenced by multiple climatic factors (Peter and Harrington, 2009). The greater acorn production of trees in the full-release treatment was likely affected by the increased exposure of crowns to direct sunlight (Sharp and Sprague, 1967; Post, 1998; Peter and Harrington, 2002). Initial crown area also was positively correlated with production, likely because trees with larger pre-treatment crowns had less dieback prior to treatment and an overall higher level of vigor (Devine and Harrington, 2006). The relationship between vigor and acorn production is evident in the fact that 10-year DBH growth was positively correlated with acorn production in the years when overall production was high (e.g., $r = 0.43$; $p = 0.0002$ in 2004). The patterns in relative acorn production associated with the three treatments were similar to patterns reported for trees classified as good, moderate, and poor acorn producers in a study of five oak species in the southeastern USA (Greenberg, 2000). In that study, differences in production among the three classes of trees were most apparent in years of high production, when the good producers produced a substantially higher number of acorns than the other two classes of trees.

Height growth of Douglas-fir was marginally greater ($p = 0.060$) in the half-release treatment than in the thin-only treatment, likely because the residual Douglas-fir on the study plots bordered the opening that was created around the center oak trees. This gap would have increased the amount of light reaching the crowns of the bordering Douglas-fir trees and may have also reduced competition for belowground resources. Based on the diameter growth rates of the residual Douglas-fir trees, which were substantially greater than those of oak trees, the residual Douglas-fir will likely provide an ever-increasing level of competition for the oak in the future. This also is evidenced by the approximate 20% increase in Douglas-fir basal area on the thin-only and half-release treatment plots during the 10-year study. Given that mortality has already been observed among the oak trees, there is a limited window of opportunity remaining for releasing oak in encroached stands such as these, which are prevalent in much of the Pacific Northwest range of Oregon white oak.

Our year-10 findings indicate that a single-entry, complete release of suppressed Oregon white oak from conifers is biologically feasible for the oak trees. In addition to the diameter growth and acorn production responses, we observed no significant negative impacts of the release treatments on the condition of oak trees: no windthrow, minimal damage during logging, and no evidence of the "thinning shock" that has been observed in other species such as Douglas-fir (Harrington and Reukema, 1983). The responses of oak trees to the half-release treatment were small: the growth response was not significant, and it is unclear for how long the acorn production response will persist. Throughout this 10-year period, oak trees clearly benefitted more from the full release. Additionally, managers must consider whether the smaller magnitude of the half-release responses warrants the operational costs of applying that type of treatment (i.e., the costs associated with multiple stand entries, because the half-release would require additional follow-up release treatments). Restoration of overstory structure, as demonstrated here through the full release from overtopping trees, represents the initial step in restoration of an encroached oak savanna (Brudvig et al., 2011). Although our study was based on treatment plots within larger stands, an operational release at the stand level would not only ensure a long-term control of overstory conifer competition, it would facilitate application of understory restoration treatments on an ecologically meaningful scale. Understory restoration treatments, using prescribed fire (Hamman et al., 2011), mechanical, or chemical approaches, are typically required to manage understory species composition and structure but will also be vital in preventing conifers from regenerating and again overtopping the oak trees. If an oak release treatment is designed to leave a residual conifer component (e.g., for wildlife habitat), the proximity of the residual conifers to the oak trees is an important consideration, as nearby conifers will influence the growth of the oaks, as indicated by the difference between oak growth in our half- and full-release treatments.

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