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ORIGINAL ARTICLE

Changes in Oregon white oak (*Quercus garryana* Dougl. ex Hook.) following release from overtopping conifers

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Abstract Oregon white oak or Garry oak (*Quercus garryana* Dougl. ex Hook.) is a shade-intolerant, deciduous species that has been overtopped by conifers during the past century in parts of its range due to an altered disturbance regime. We examined the response of suppressed Oregon white oak trees in western Washington, USA, to three levels of release from overtopping Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). We treated individual oak trees with either full release from competition, partial ("half") release from competition, or a stand-level thinning of Douglas-fir not directed toward release (control). Five years after treatment, oak trees had suffered no mortality or windthrow. Stem diameter growth was 194% greater in the full-release treatment relative to the control. Acorn production varied widely by year, but in years of higher production, acorn production was significantly greater in both release treatments than in the control. Frequency of epicormic branch formation was significantly increased for years 1 and 2 by the full release; the greatest response occurred between 2 and 6 m above ground level. The greatest number of epicormic branches formed on trees on which the majority of original limbs had died back prior to treatment. Trees with relatively less crown dieback at the time of treatment generally had greater stem growth and acorn production responses to release treatments. Our findings indicate that these released Oregon white oak trees are beginning to recover after an extended period of suppression.

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Introduction

Oregon white oak (*Quercus garryana* Dougl. ex Hook.) occurs in the inland coastal region of western North America from latitudes of approximately 34 to 50°N (Stein 1990). However, in the northern portion of its range, many Oregon white oak woodland and savanna stands have succeeded to conifer forests during the past century (Sprague and Hansen 1946; Habeck 1962; Thilenius 1968). Prior to European settlement in the mid-1800s, frequent, low-intensity burning by Native Americans limited the extent of coniferous forests, sustaining fire-tolerant oak stands (Agee 1993). Post-settlement fire suppression allowed conifers, primarily Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), to invade oak stands where it rapidly overtopped and suppressed oak trees due to greater annual height growth and greater maximum height. During this period of encroachment, stand structure transitioned from a more open, single-storied oak canopy to a relatively dense conifer overstory with an oak midstory. The result of this suppression has been crown dieback and eventual mortality of the shade-intolerant oak (Stein 1990).

Rapid proliferation of conifers following the alteration of a disturbance regime has been reported for sites throughout western North America (Gallant et al. 2003; Heyerdahl et al. 2006). Restoring native plant communities to such sites is a complex process involving control of invasive species, promotion of native species, and a return to historical disturbance intervals (MacDougall et al. 2004; Monsen et al. 2004). In restoration of Oregon white oak ecosystems, preservation of oak trees is a priority, as they are a valuable structural component that, if extirpated, would require many decades to replace. Restoration of Oregon white oak savanna and woodland stands to their historical condition entails removal of nearly all conifers, followed by repeated understory treatments such as prescribed fire to control conifer regeneration. While Oregon white oak is not a major timber species, oak woodlands, savannas, and associated prairies are a legacy of past cultural practices and provide unique habitats in a landscape dominated by conifers.

In this study we examine how release from overtopping Douglas-fir affects Oregon white oak trees, specifically, stem growth, acorn production, and formation of epicormic branches. The response of suppressed Oregon white oak trees to release has not been studied, nor has epicormic branching of this species. Because relatively few studies have addressed Oregon white oak, we reference other species, particularly white oak (*Q. alba* L.), which is closely related.

For several hardwood species, the rate of stem growth after release from suppression has been shown to depend on the period of time since release as well as the period of suppression (Wright et al. 2000). Stem growth of young ($\leq$50-year-old) oak (*Quercus* spp.) trees increases rapidly following reductions in inter- and intra-specific competition (Hilt 1979; Dale and Sonderman 1984; McGee and Bivens 1984; Graney 1987; Lamson et al. 1990). Significant growth responses to increased resource availability also have been reported for older (50- to 100-year-old) oak trees after removal of adjacent canopy trees (Hilt 1979; Smith and Miller 1991).

Acorn production by individual Oregon white oak trees is inversely related to the level of competition from adjacent trees (Peter and Harrington 2002). Acorn production for several oak species has been positively related to the amount of crown exposed to direct sunlight (Gysel 1956; Post 1998; Peter and Harrington 2002) and to higher positions within the crown (Sharp and Sprague 1967). In young oak stands, release from competition has increased individual-tree acorn production of white oak, chestnut oak (*Q. prinus* L.), and chinkapin oak (*Q. muehlenbergii* Engelm.) (Sharp and Sprague 1967).

Epicormic branches are formed following the release of dormant buds, which may be either proventitious (i.e., formed from original buds) or adventitious, such as buds formed in response to injury (Kramer and Kozlowski 1979). Epicormic branch formation has been linked to numerous variables related to suppression and crown dieback (Crook et al. 2004; Joensson et al. 2005) and to increased light availability (Jemison and Schumacher 1948; Krajicek 1959; Blum 1963; Smith 1966; Trimble and Seegrist 1973; McDonald and Ritchie 1994). Epicormic branches can be an important mechanism for increasing total leaf area and photosynthetic capacity (Remphrey and Davidson 1992), particularly following crown loss due to dieback or damage (Nicolini et al. 2001; Wong et al. 2005).

Our objectives were to quantify the response of Oregon white oak trees to release from long-term conifer suppression. This analysis contains results from the first 5 years post-treatment.

Methods

Study sites

The study is located in four forest stands near Tacoma, Washington, USA, in the Puget Trough physiographic province. The stands, located 10–15 km apart, are named Cherry Hill, Goodacre, Lake Joseph, and Sneesby. Soils, formed in glacial materials, are Typic Melanoxerands and Vitrandic Dystroxerepts (Zulauf 1979; Pringle 1990), mapped as Humic Cambisols by FAO (1995). Soils are sandy to sandy-skeletal in texture and somewhat excessively drained. Elevation is 85–135 m. Mean annual precipitation in Tacoma is 995 mm, although total precipitation from 1 May through 30 September averages only 158 mm (WRCC 2004). For 2001–2005, cumulative precipitation from 1 May through 30 September (majority of growing season) was 215, 85, 51, 240, and 152 mm, respectively. Mean air temperatures in January and July are 5 and 19°C, respectively.

Tree species composition varied somewhat among the four study sites (Table 1), but all sites were characterized by an overstory dominated by Douglas-fir and a midstory of suppressed Oregon white oak. Immediately prior to this study (2000–2001), stand-level commercial thinnings of Douglas-fir took place at all four study sites. Prior to the 2000–2001 thinning operations, one to two other thinnings had been conducted at 10- to 15-year intervals. This is the first generation of Douglas-fir to colonize the sites which were formerly dominated by Oregon white oak woodlands and savannas.

Study installation

Study installation began with the selection of 72 overtopped oak trees, the experimental units, referred to hereafter as “study trees.” Eighteen trees were located at each site, representing a range of sizes and varying degrees of suppression. Selection criteria included a diameter at breast height (DBH) of at least 20.0 cm (one 19.0-cm tree was selected) and a minimum of two overtopping Douglas-fir trees.

Treatments were three levels of release, “full release,” “half release,” and “control,” each randomly assigned to six study trees per site. In the full-release treatment, all Douglas-fir trees greater than or equal to 10.0 cm DBH were removed from around each study tree to a radius equal to the height of that study tree (mean = 16.0 m). In the half-release treat-

Table 1 Pre-treatment composition of forest canopy trees on study plots at four sites

Parameter	Species[a]	Site Cherry Hill	Goodacre	Lake Joseph	Sneesby
Height (m)	Oak	15.5 (3.4)	16.1 (3.3)	16.4 (3.4)	16.1 (2.5)
	Fir	39.4 (8.3)	40.0 (7.7)	44.0 (3.9)	39.0 (5.8)
DBH (cm)	Oak	31.9 (8.7)	29.8 (9.7)	29.8 (7.7)	31.3 (8.3)
	Fir	83.4 (30.2)	81.8 (27.1)	88.5 (17.9)	80.4 (20.3)
Crown diameter (m)	Oak	8.3 (1.8)	8.2 (2.6)	6.0 (2.1)	7.3 (2.2)
Crown depth (m)	Oak	5.6 (3.0)	6.6 (3.0)	4.2 (3.3)	4.9 (2.3)
Live-crown ratio	Oak	0.38 (0.22)	0.41 (0.15)	0.26 (0.17)	0.30 (0.12)
Tree age (years)	Oak	98	130	124	94
	Fir	80	75	75	65
Trees (no. ha^{-1})[b]	Oak	149	57	63	192
	Fir	111	149	215	192
	Other spp	91	27	42	36
BA (m^2 ha^{-1})[b]	Oak	4.8	2.0	4.0	7.8
	Fir	31.6	29.2	46.5	29.7
	Other spp	2.9	0.3	0.9	0.4

Height, DBH, and crown variable means (standard deviations in parentheses) are for Oregon white oak study trees ($n = 18$ per site) and two tallest Douglas-fir per study plot ($n = 36$ per site). BA: basal area.

[a] Oak: Oregon white oak; Fir: Douglas-fir.

[b] Trees $\geq$ 10 cm DBH.

ment, all Douglas-fir trees ($\geq$ 10.0 cm DBH) within a radius of one-half of the study tree's height were removed. On average, 15 and 6 Douglas-fir trees per study tree were removed in the full-release and half-release treatments, respectively. No trees were removed to release the study trees in the control treatment; however, the commercial thinning in 2000–2001 removed an average of two Douglas-fir trees within a tree-height radius of these trees. The full-release treatment was a more intensive treatment than would be applied operationally to individual trees; rather, it was an experimental treatment applied to represent the conditions that would result from a stand-level release of oak from all Douglas-fir competitors. The half-release treatment was similar to individual-tree release treatments that are sometimes applied operationally to release Oregon white oak trees overtopped by conifers. During treatment implementation (April–May 2001), trees were cut with chainsaws and yarded with skidders. Study trees suffered minimal logging damage during the release; several trees had a few broken limbs and two had bark scraped from the bole (Harrington and Kern 2002).

Height and DBH of each study tree and the two tallest Douglas-fir trees overtopping each study tree were measured prior to treatment. Crown diameter of study trees was measured in two directions: at the widest point of the crown and perpendicular to the widest point. Height to live crown base, excluding epicormic branches, was measured. Following the third and fifth growing seasons post-treatment, DBH of study trees was remeasured.

Stand conditions

Prior to treatment, study tree height, DBH, crown diameter, crown depth, and live-crown ratio (LCR; the ratio of live-crown depth to tree height) were generally similar among sites, as were height and diameter of overtopping Douglas-fir trees (Table 1). The study trees ranged in DBH from 19.0 to 53.0 cm and in height from 8.4 to 21.8 m. Mean distance from a study tree to the nearest overtopping Douglas-fir was 4.4 m.

Photosynthetically active radiation (PAR) measurements taken at mid-crown height around nine trees in the control treatment on a sunny day in August 2004 showed that, without release, the Douglas-fir overstory intercepted an average of 87% of potential PAR. After treatment, the amount of direct sunlight reaching each tree was quantified at 2 m above the forest floor by measuring the percentage of the sun's path (at midpoint between summer solstice and fall equinox) above the horizon that was unobstructed by conifers (Harrington et al. 2002). Averages of 23, 14, and 6% of the sun's path were unobstructed in the full-release, half-release, and control treatments, respectively.

Acorn production

Acorn production of the study trees was evaluated during late August or early September in years 1–5 post-treatment. In year 1, a randomly selected subset of trees was surveyed ($n = 38$); in subsequent years all trees were surveyed. In these surveys, crowns of trees were examined from multiple angles from the ground using 10 × 42 power binoculars. The level of acorn production for each tree was visually classified following the method described by Graves (1980). Classes were no acorns (class 1), acorns visible after very close examination (class 2), acorns readily visible (class 3), and acorns readily visible and covering entire tree (class 4). This method has been used successfully and is repeatable for Oregon white oak in the Puget Trough (Peter and Harrington 2002). In years 3 through 5, 60-s acorn tallies were made in addition to Grave's (1980) classification. In the 60-s acorn tally, the observer scans the crown of the tree until the first acorn is sighted, at which point a 60-s period begins during which the observer tallies 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.

Epicormic branching

Following treatment in 2001, study trees were photographed to document the presence of epicormic branches that existed prior to treatment. In October of years 2 through 5 post-treatment, new (i.e., current-year) epicormic branches were tallied on the stem and first-order limbs below the live crown base (as defined by USDA Forest Service 2002). Epicormic branches above the live crown base were excluded due to limited visibility. Tallies were made by viewing trees from multiple locations on the ground with 10 × 42 power binoculars. In year 3, the number of epicormic branches on each study tree was tallied for each 2-m stem segment beginning at ground level, using a telescoping height pole for reference. Each branch was classified according to visually estimated length (<10, 10–19, 20–29, 30–39, 40–49, 50–99, 100–199, 200–299, 300–399 cm), whether it was living or dead, and year of origin as indicated by the number of bud scars (pre-treatment, years 1–2, or year 3). Branches originating prior to treatment (2000 or earlier) are hereafter referred to as “pre-treatment epicormic branches,” while those originating in year 1 (2001) or later are referred to as “post-treatment epicormic branches.” Each tree was assigned a crown dieback class according to the degree of dieback in the original, non-epicormic crown (i.e., sequential branches; Nicolini et al. 2001). Classes were (i) no dieback, (ii) at least one, but $<50\%$ of all major limbs dead, (iii) $\geq 50\%$, but not all, major limbs dead, and (iv) all major limbs dead; epicormic branches only.

Statistical analyses

Analyses of DBH growth, acorn production, and epicormic branch formation were performed with a generalized, randomized complete-block design analysis of variance (ANOVA) model (Hinkelmann and Kempthorne 1994) using Proc GLM in SAS (SAS Institute Inc. 2000). Randomized replication within each site allowed testing of interactions between site (a random effect) and treatment. Because acorn production was recorded in each year, it was analyzed with a repeated-measures model. Live-crown ratio, crown volume index (widest crown diameter × perpendicular crown diameter × crown depth), DBH, and height prior to treatment were tested in the ANOVA models as covariates and included if significant ($P<0.05$) and if there was no covariate × treatment interaction. When necessary, a $\log(x+1)$ transformation was used to achieve normal distribution of data (Snedecor and Cochran 1967). Protected mean separations were performed using Fisher’s LSD test or orthogonal contrasts. Correlation analyses were used to further assess relationships between variables (Proc Corr; SAS Institute Inc. 2000). The level of significance was $P=0.05$.

The 60-s tally was the dependent variable in analysis of acorn production. For years 1 and 2, when production class was recorded rather than a tally, mean tally values that corresponded to each class were used in analysis. Mean tally values were derived from 412 local Oregon white oak trees for which both acorn production classes and 60-s tallies were recorded as part of a range-wide survey (data on file).

In analysis of epicormic branch formation, dependent variables were the numbers of new epicormic branches per tree formed during years 1–2 and years 3–5. A completely randomized design, one-way ANOVA model was used to evaluate differences in the number of pre-treatment and post-treatment epicormic branches per tree among crown dieback classes. Correlation analysis (Proc Corr; SAS Institute Inc. 2000) was used to assess relationships between the number of pre-treatment epicormic branches and height to non-epicormic live crown, DBH, LCR, crown volume index, and number of post-treatment epicormic branches.

Results and discussion

Growth and survival

Three and five years after treatment, DBH growth was significantly increased by release treatments ($P=0.003$ and $P<0.001$, respectively; Fig. 1). After 3 years, DBH growth of trees in the full-release (0.7 ± 0.1 cm) and half-release treatments (0.5 ± 0.1 cm) was greater than that of trees in

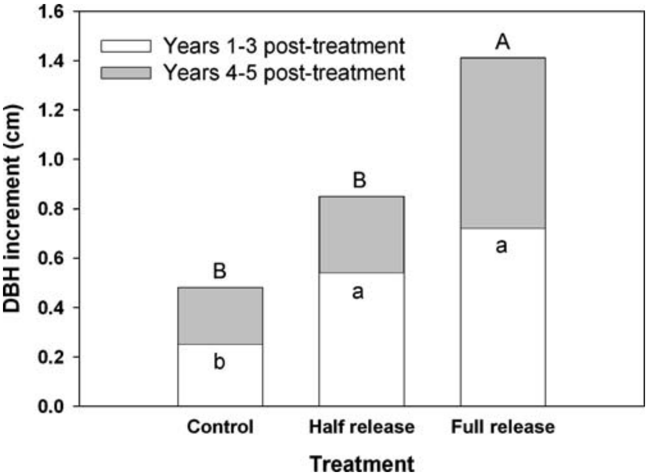


Fig. 1 Diameter at breast height (DBH) growth increment after three release treatments. Same lowercase letters denote no difference ($P \geq 0.05$) in response for years 1–3 only; same uppercase letters denote no difference ($P \geq 0.05$) in response for years 1–5

the control treatment (0.3 ± 0.1 cm). After 5 years, DBH growth of trees in the full-release treatment (1.4 ± 0.1 cm) was greater than that of trees in the half-release and control treatments (0.9 ± 0.1 cm and 0.5 ± 0.1 cm, respectively).

The prompt growth response of Oregon white oak trees to release after an extended period of suppression contrasts with delayed responses to release reported elsewhere for mature conifers (Latham and Tappeiner 2002; Bebber et al. 2004). Presumably, the evergreen conifers required greater time to acclimate to the increased light and the altered microclimate compared to the deciduous oak trees in the present study (Bebber et al. 2004).

Live-crown ratio was a significant variable in the 3- and 5-year growth models ($P = 0.010$ and $P = 0.015$, respectively) and was positively correlated with DBH growth in the half- and full-release treatments (Fig. 2). There were no interactions between LCR and treatment or site and treatment. Pre-treatment DBH and height were not significant predictors of treatment response. In the control treatment, tree age was correlated with pre-treatment DBH ($r = 0.56$; $P = 0.047$), but tree age was not correlated with DBH growth.

The relationship between LCR and DBH growth was not surprising as trees with the largest crowns have the greatest photosynthetic capability and are able to allocate more photosynthates to structural growth. Our findings agree with those of McGee and Bivens (1984), who reported that for overtopped white oak, trees with large crowns had a relatively large growth response to release, while trees with small or poorly formed crowns had a smaller, more variable growth response.

No trees died or were wind-thrown during the 5-year period after treatment implementation.

Acorn production

There was a significant interaction between year and treatment ($P<0.001$) affecting acorn production. In years 2 and 4, when overall acorn production in this study (and regional acorn production) was higher than in other years, production in the full- and half-release treatments was significantly ($P<0.05$) greater than in the control (Fig. 3). In years 1, 3, and 5, there were no differences in acorn production among treatments. For example, in year 3, the mean 60-s acorn tallies in the full-release, half-release, and control treatments were 2.9 ± 0.8, 0.8 ± 0.8, and 1.3 ± 0.8 acorns per tree, respectively. In year 4, when production was highest, mean 60-s acorn tallies in the full-release, half-release, and control treatments were 31.3 ± 4.8, 23.2 ± 5.0, and 9.1 ± 4.9, respectively. In year 5, when production was lowest, the mean 60-s acorn tallies for the same treatments were 0.5 ± 0.2, 0.1 ± 0.2, and 0.2 ± 0.2, respectively.

The causes of inter-annual fluctuations in acorn production are likely complex. These fluctuations have been at-

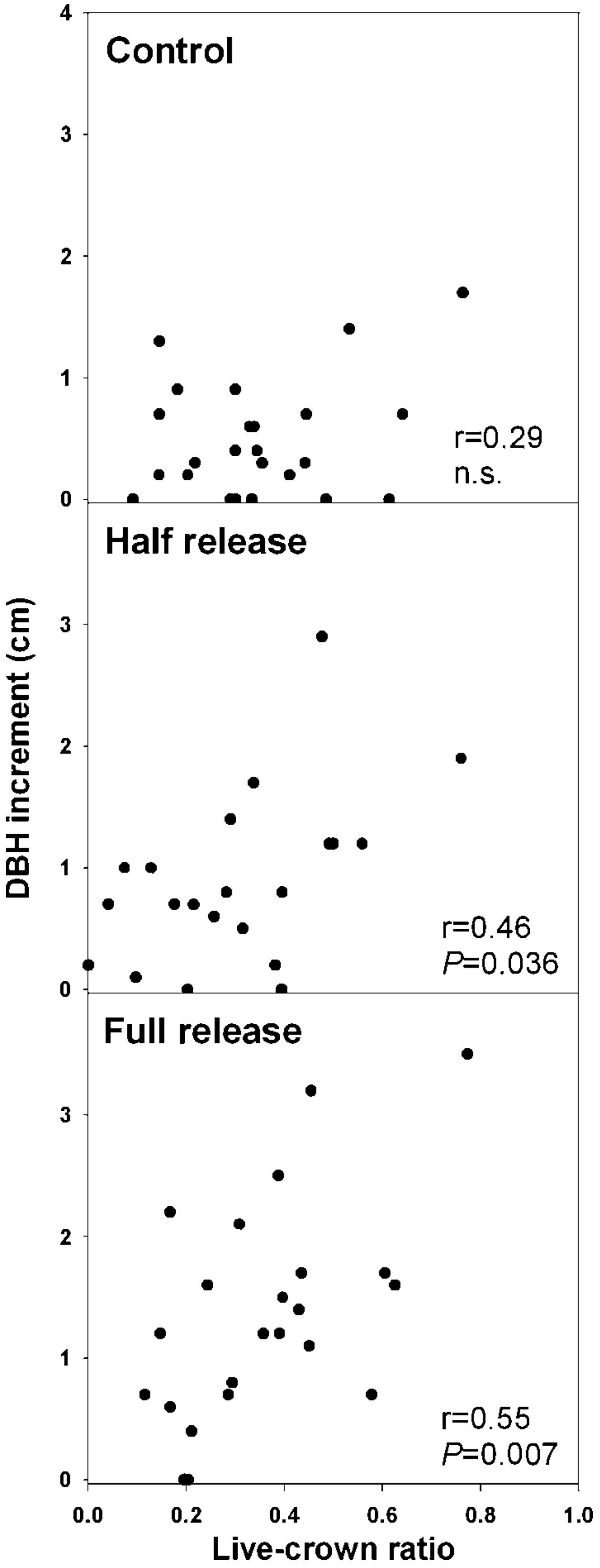
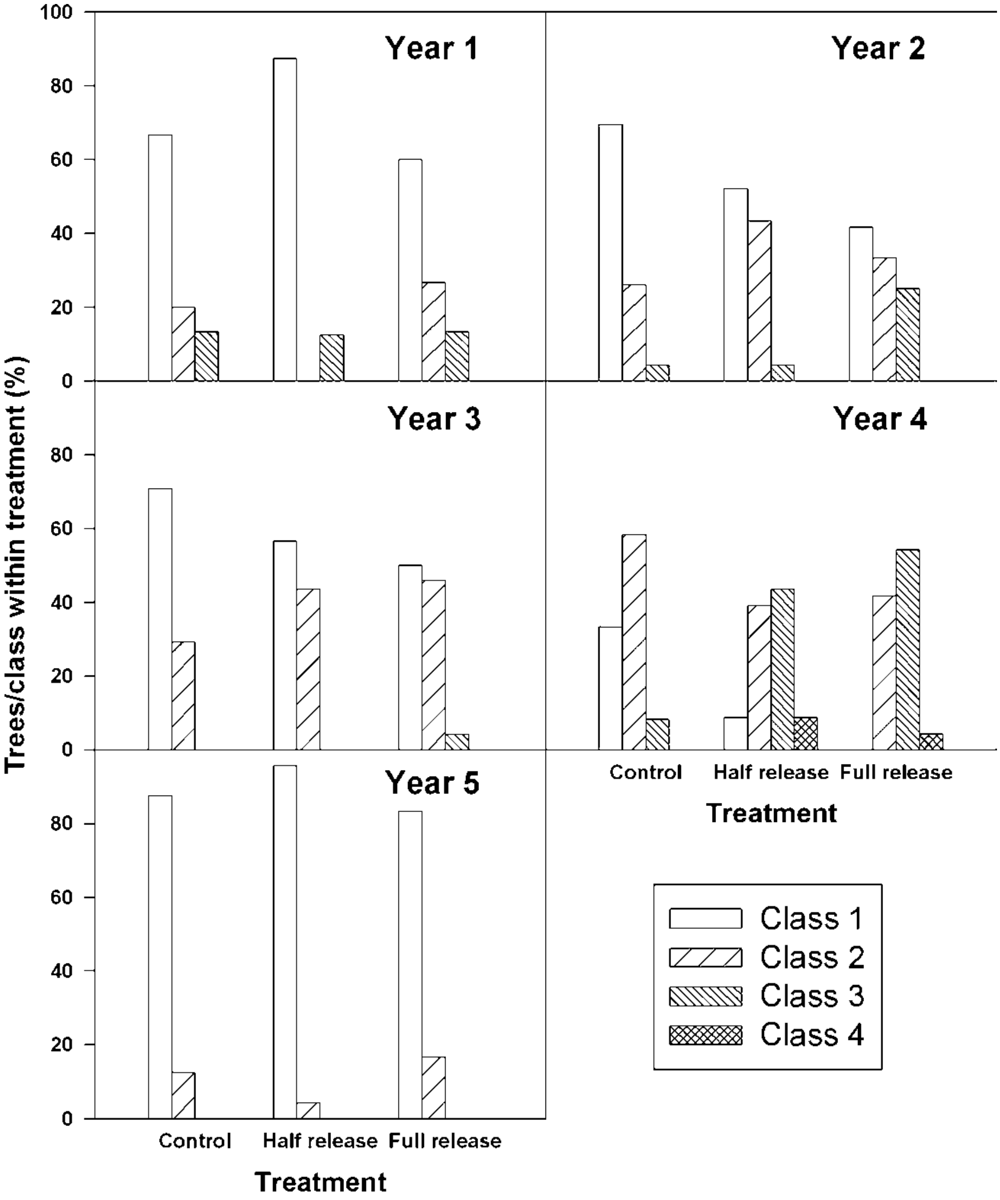


Fig. 2 Correlations between pre-treatment live-crown ratio and 5-year diameter growth increment at breast height (DBH) after three release treatments. A live-crown ratio of 0 indicates all original branches died (only epicormic branches were present)

Fig. 3 Oregon white oak acorn production following three release treatments ($n = 38$ in year 1; $n = 72$ in years 2–5). Class 1: no acorns produced; class 2: acorns visible after very close examination; class 3: acorns readily visible; class 4: acorns readily visible and covering entire tree



tributed to various factors including growing-season precipitation (Rundel 1980), available soil water (Peter and Harrington 2002), weather during pollination (Sharp and Sprague 1967), and inherent masting cycles (Sork et al. 1993; Koenig et al. 1994; Koenig and Knops 2002). However, within the genus *Quercus*, there has been little research to quantify annual levels of biomass allocation between reproductive and vegetative growth (Johnson et al. 2002).

The increased sunlight following release appears to be an important factor in determining acorn production. We observed that portions of the crown receiving direct sunlight bore the greatest numbers of acorns, a phenomenon that has been reported for other oak species (Verme 1953; Sharp and Sprague 1967; Post 1998). We also observed that 5-year-old epicormic branches receiving direct sunlight were producing acorns. In the few studies that have examined acorn production after release from competition, responses were positive but varied by individual tree and crown class (e.g., Sharp and Sprague 1967; Healy et al. 1999).

Crown size, quantified by crown volume index, was a significant covariate ($P<0.001$) in the model of acorn production and was positively related to production in all treatments. The individual trees with greatest acorn production were released trees with relatively large crowns. For most trees, crown size appeared to be a function of the severity of past suppression and related dieback. Similarly, individual Oregon white oak trees that were classified as unhealthy in a visual assessment (including dead and broken limbs, rot, and crown density) produced significantly fewer acorns than did

Table 2 Percent of Oregon white oak study trees with pre- and post-treatment epicormic branches among four sites and three release treatments

Group	Pre-treatment epicormic branches	Post-treatment epicormic branches
Site		
All sites	89	49
Cherry Hill	78	61
Goodacre	89	22
Lake Joseph	89	33
Sneesby	100	78
Treatment		
Control	88	38
Half release	87	43
Full release	92	67

Pre-treatment epicormic branches formed any time prior to treatment; post-treatment branches formed during years 1–5.

trees that were classified as moderately healthy to healthy (Peter and Harrington 2002).

Epicormic branches

We recorded 464 post-treatment and 1,011 pre-treatment epicormic branches. The percentage of trees with epicormic branches is shown by site and treatment in Table 2. The number of new epicormic branches formed per tree during years 1–2 post-treatment differed significantly by treatment ($P = 0.035$; Fig. 4). In years 1–2, 9.3 ± 3.1, 7.1 ± 3.2, and 1.2 ± 3.1 new branches were formed in the full-release, half-release, and control treatments, respectively. In years 3–5, 1.4 ± 0.2, 0.3 ± 0.2, and 0.8 ± 0.2 new branches were formed in the same treatments, respectively, but the treatment effect was not significant. There were no site × treatment interactions or significant covariates.

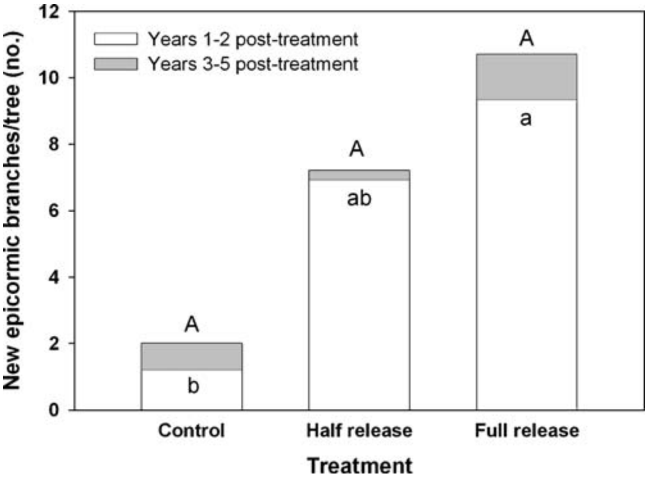


Fig. 4 Number of new epicormic branches per tree formed during the first 5 years after three release treatments. Same lowercase letters denote no difference ($P \geq 0.05$) in response for years 1–2; same uppercase letters denote no difference ($P \geq 0.05$) in response for years 3–5

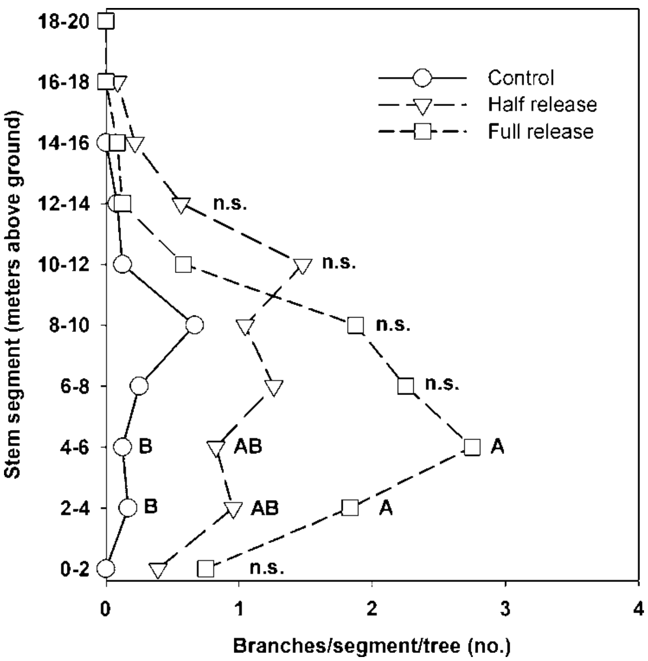


Fig. 5 Number of epicormic branches per stem segment per tree formed during the first 3 years (2001–2003) after three release treatments. Same letters within each stem segment denote no significant difference ($P \geq 0.05$)

The branches formed in years 1–2 comprised 92% of all post-treatment epicormic branches observed in the 5-year study. A preliminary survey found no post-treatment epicormic shoots by July of year 1; thus, most post-treatment epicormic branches were formed in the latter part of the first growing season or in the second growing season after treatment.

The number of post-treatment epicormic branches was greatest in the full-release treatment for stem segments 2–6 m above ground level (Fig. 5). For the 2- to 4-m stem segment, the numbers of post-treatment epicormic branches in the full-release, half-release, and control treatments were 1.8 ± 0.4, 1.0 ± 0.4, and 0.2 ± 0.4, respectively. For the 4- to 6-m stem segment, the numbers of post-treatment epicormic branches in the same treatments were 2.8 ± 0.7, 0.8 ± 0.7, and 0.1 ± 0.7, respectively. Of the pre-treatment epicormic branches, 57% of living branches, but only 29% of dead branches, were greater than 100 cm in length (Fig. 6a). In the smaller length classes, numbers of living and dead pre-treatment epicormic branches were similar. Three years after treatment, the greatest number of post-treatment epicormic branches in the full- and half-release treatments were in length classes between 30 and 99 cm (Fig. 6b).

Crown dieback was prevalent among trees at the beginning of the study. More than one-third of the trees exhibited at least 50% dieback of major limbs and only 17%

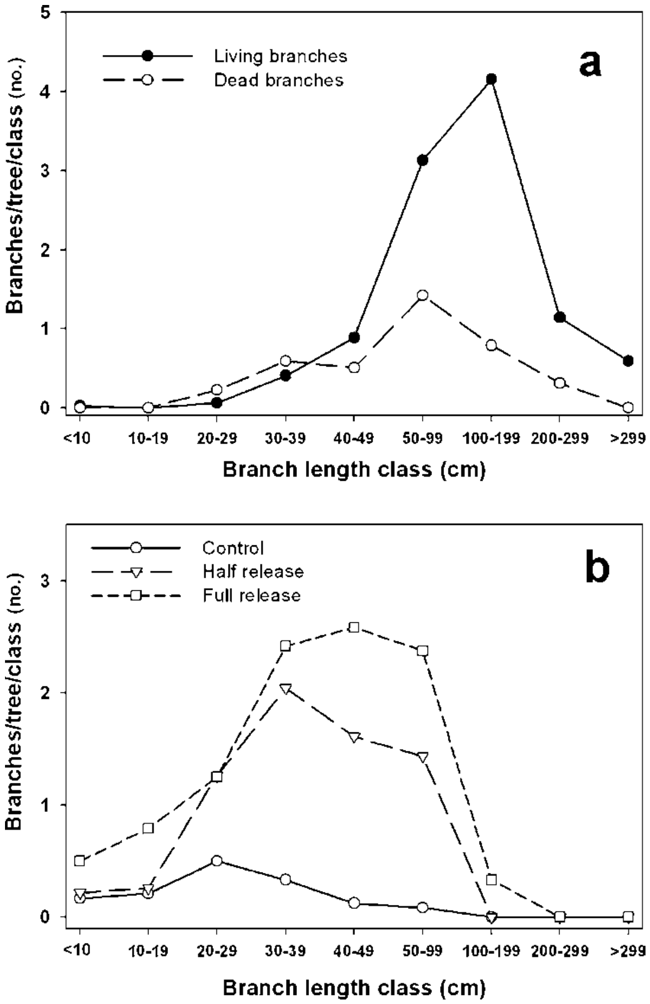


Fig. 6 Number of epicormic branches per tree originating prior to treatment **a** and during the first 3 years after treatment **b** by estimated length class

of the study trees had no dieback of major limbs. Trees with greater crown dieback had a larger number of pre-treatment epicormic branches (Table 3). The number of pre-treatment epicormic branches was positively correlated with height to non-epicormic live crown ($r = 0.41$; $P < 0.001$) and negatively correlated with LCR ($r = -0.36$; $P = 0.002$) and crown volume index ($r = -0.35$; $P = 0.003$). Crown dieback and crown size were not related to the number of post-treatment epicormic branches.

Oregon white oak appears to be similar to white oak in its propensity for epicormic branching (Roth 1948; Krajicek 1959; Smith 1966; McGee and Bivens 1984). Branch formation in this study was associated with both release from competition and crown dieback. Release increases the exposure to direct sunlight which influences auxin concentrations that, in turn, may result in release of dormant buds on the bole of the tree (Kramer and Kozlowski 1979). The observed association between increased crown dieback and greater numbers of pre-treatment epicormic branches is likely a result of disruption of auxin production which otherwise inhibits the sprouting of dormant buds (Bowersox and Ward 1968).

The profusion of epicormic branches following release from competition may provide a temporary increase in leaf area until the crown expands in response to the increase in sunlight (McDonald and Ritchie 1994). However, we observed well-developed epicormic branches, greater than 3 m in length, suggesting some of these branches eventually become permanent components of the crown (Roth 1948; Krajicek 1959; Dale and Sonderman 1984). Measurements of 11 three-year-old epicormic branches in the full-release treatment showed that the mean growth rate was increasing over time (annual length growth = 20, 28, and 36 cm for years 2–4, respectively). Oregon white oak is a long-lived species (Stein 1990), and if these branches continue to develop they may eventually make a substantial contribution to the remaining sequential crown as in the case of older Douglas-fir (Ishii and Wilson 2001).

Implications

Although shade-intolerant, Oregon white oak in this study survived many years of suppression and responded promptly to release from overtopping Douglas-fir. Positive relationships between crown size and both stem growth and acorn production indicate that trees with larger intact crowns (i.e., less crown dieback) are recovering more quickly follow-

Table 3 Mean number of pre- and post-treatment epicormic branches per tree among four crown dieback classes for Oregon white oak

Origin[a]	Group	Crown dieback class			
		No major limbs dead	<50% of limbs dead	$\geq$ 50% of limbs dead	All major limbs dead
Pre-treatment	All sites	4.3 c[b]	11.6 b	18.9 ab	38.6 a
Post-treatment	Control	0.4 (0.5)	4.1 (3.5)	0.1 (0.4)	0 (–)
	Half release	0.3 (0.5)	12.4 (24.7)	0 (0)	6.7 (7.0)
	Full release	6.7 (11.5)	3.5 (4.6)	26.9 (37.5)	2.0 (–)

Statistical analysis of post-treatment data was not conducted due to insufficient replication in some treatment/crown dieback class combinations; standard deviations are shown in parentheses for these combinations where $n > 2$.

[a] Pre-treatment epicormic branches formed any time prior to treatment; post-treatment branches formed during years 1–3.

[b] Same letter denotes no difference ($P \geq 0.05$).

ing release than those with smaller crowns. The study trees responded to both levels of experimental release, but the response to full release was greater in magnitude than the response to half release. Furthermore, the response of trees to the smaller canopy gaps of the half-release treatment will likely be of shorter duration than the response to the full-release treatment as crowns of adjacent conifers expand into the gaps (Wardman and Schmidt 1998), necessitating subsequent release treatments. Partial or incremental releases of heavily suppressed oak trees, similar to our half-release treatment, have been justified in the past due to perceived risks of "shocking" fully released trees through sunscald or windthrow, but these types of damage were not observed in this study. In practice, single-tree release treatments may not be economically feasible, as the volume of timber removed from the stand is relatively small. The primary advantage of single-tree release is the ability to maintain timber production by the dominant species while gaining at least short-term preservation of the suppressed species. The efficacy of our full-release treatment suggests that, for suppressed Oregon white oak, a stand-level release from competition would provide greater benefit to the trees than would single-tree release. Furthermore, a stand-level release would allow understory management through treatments such as prescribed burning.

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