

Techniques to Promote Garry Oak Seedling Growth and Survival in Areas with High Levels of Herbivory and Competition

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Source: Northwest Science, 85(2): 172-181

Published By: Northwest Scientific Association

URL: https://doi.org/10.3955/046.085.0208

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Abstract

Though regeneration of Garry oak (*Quercus garryana*) seedlings within Garry oak ecosystems is important to maintain this threatened habitat, seedling regeneration is often poor. Two independent studies were initiated in the early 2000s to examine questions surrounding Garry oak recruitment: one at the Crow's Nest Ecological Research Area (CNERA) on Salt Spring Island, BC, and another at the Pacific Rim Institute for Environmental Stewardship (PRI) on Whidbey Island, WA. In both areas, Garry oak seedlings were caged and monitored for growth and relative health. Over 8 years at CNERA, growth of caged plants outpaced growth of controls, which was indicative of high browsing pressure and relatively high palatability of Garry oak seedlings to black-tailed deer and feral sheep. The PRI oaks grew more slowly and at four PRI sites survival was 30-50% over 5-6 years as compared to 90% survival at CNERA over 8 years. The mortality at PRI was likely due to a combination of dry summer conditions and large numbers of voles, which took advantage of the cages for protection from predators; furthermore, lack of mycorrhizal hosts could have inhibited seedling establishment. Weed block inside exclosure cages provided ideal nesting conditions for voles. This study demonstrated that the caging of Garry oak seedlings, although labor-intensive and requiring frequent maintenance, provides valuable protection from large ungulate browsers and can be maintained as a relatively long-term measure, but vigilance is required to protect young seedlings from other threats such as voles or competing vegetation.

Introduction

In the Pacific Northwest, Garry oak (*Quercus garryana*), also known as Oregon white oak, represents a foundation species in various savanna and woodland community types that occur from northern California to southern British Columbia, wherever rainfall is relatively low, and often in areas with a strong rain shadow effect (Stein 1990, Gonzales and Clements 2010). In British Columbia annual precipitation in Garry oak habitats ranges from ca. 60–120 cm (Roemer 1993). The existence of relatively high populations of Garry oaks in some areas is attributed to anthropogenic influences. Large areas of the relatively open, savanna and prairie-like ecosystems where Garry oak trees thrive are thought to have been maintained since the last glacial period

by aboriginal peoples, who used fire to enhance the habitat and productivity of plants with edible bulbs such as common camas (*Camassia quamash*), particularly in the northern range of *Q. garryana* (Turner 1999).

Euro-American settlement in the Pacific Northwest impacted Garry oak populations and associated ecosystems through a reduction in fire frequency, invasion by non-native vascular plants, and increased deer populations (Pellatt et al. 2001, MacDougall et al. 2004, Lea 2006, Gonzales and Clements 2010). Evidence suggests that in many areas, a new cohort of Garry oak trees was recruited around the time of Euro-American settlement, with very little subsequent recruitment (Thilenius 1968, Dunwiddie et al. 2011, Gilligan and Muir 2011).

In light of the vulnerability of Garry oak ecosystems in the Pacific Northwest, recruitment of new oak trees is a significant issue. Challenges to regeneration may be

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grouped by life history stages, e.g.: acorn production, acorn predation and viability, seedling establishment, and sapling growth and survival.

A survey of acorn production conducted from Whidbey Island, WA to Roseburg, OR identified a number of key factors influencing number of acorns, with the openness of the habitat and nature of the understory playing important roles (Peter and Harrington 2002). Open grown oaks produced much larger acorn crops, and oaks growing in areas where the understory had recently been burned also tended to produce more fruit. Garry oak ecosystems are increasingly fragmented by urban and agricultural development (Lilley and Vellend 2009), reducing potential oak seedling recruitment. In such cases, planting oaks becomes an important tool in restoration (Devine et al. 2007a).

A Vancouver Island study found that the fate of acorns was highly dependent on acorn burial by soil or litter (Fuchs et al. 2000). They found that the portion of acorns remaining on the ground surface taken by vertebrates was more than 53%, while declining to 7-48% when concealed in soil or litter. Burial of acorns also reduced acorn mortality caused by insect predation or desiccation. Two key insect acorn predators are the filbert weevil (Curculio occidentis) and the filbertworm (Cydia latiferreana), with 51-81% acorn infestation recorded in one British Columbia study (Rohlfs 1999).

Fuchs et al. (2000) found that seedling oaks were able to establish equally well in open or shaded environments. As a result, regeneration tends to be more prevalent in shade, potentially due to proximity to adult trees or seed hoarding by animals in more shady sites (Fuchs et al. 2000, Regan 2001). Michalak (2011) likewise observed higher abundance of oak seedlings under mature oaks and other canopies, but this relationship was less pronounced among older seedlings. In areas of Oregon where oaks form the dominant cover, Gilligan and Muir (2011) observed relatively high seedling recruitment in some areas but low recruitment in other areas, depending on acorn production and other sitespecific factors. Proximity to mature trees may also be a critical factor in ensuring there is sufficient inoculum for oak mycorrhizae (Frank et al. 2009). Additionally, Fuchs et al. (2000) found that seedlings growing on open slopes with a southern aspect were vulnerable to desiccation during hot, dry weather. In areas where browsing vertebrates are abundant, regeneration tends to occur under shrubs or within inaccessible topographical microsites (Williams et al. 2006, Clements, pers. obs.).

Once Garry oak seedlings are established, the relatively slow growth of juvenile oak trees leaves them

vulnerable to browsing by both vertebrates and invertebrates, and to overgrowth by competing vegetation. Gonzales and Clements (2010) found that peak levels of browsing by black-tailed deer (Odocoileus hemionus columbianus) in Garry oak meadows occurred during the spring months, and corresponded with the time when young oak seedlings are putting the most energy into leaf production, and thus are most vulnerable. Garry oaks are known to sprout in response to browsing (Hibbs and Yoder 1993), producing new shoots from dormant buds on the root collar. Thus, survival of browsed seedlings may depend on the amount of reserves held by seedling oaks, which in turn depends on site conditions and cumulative growth of roots and other plant parts (Shaw 1974, Crow 1988). Given high ungulate pressure in many areas where Garry oaks occur, treatments that protect young oak seedlings may be necessary to enable them to attain a height at which shoots are no longer vulnerable to browsing (Potter 1988, McCreary and Tecklin 2001, Devine et al. 2007a). Devine et al. (2007a) observed that for Garry oak trees planted at a variety of sites near Olympia, WA, shelters provided young trees with essential protection until they reached a less vulnerable size.

In addition to herbivory, competition from other plants can impede growth of newly established oak seedlings, and tree shelters also provide some protection (Devine et al. 2007a). Oaks are vulnerable to competing vegetation, as evidenced by increased growth following removal of competing conifers (Devine et al. 2007b). Other potential measures to protect seedlings from competing vegetation tested by Devine et al. (2007a) were the use of weed block fabric (also known as brush blankets), designed to inhibit vegetation around tree bases, and one-time manual removal of the sod layer. The presence of mulch significantly increased oak seedling growth over 4 years (Devine et al. 2007a). Weed block had the added benefit of increasing soil moisture. Likewise, tree shelters improved the microhabitat for seedling growth, although solid-walled shelters tended to produce seedlings with unusually narrow architecture (Devine et al. 2007a). Garry oak trees did grow more rapidly in solid-walled shelters than wire cage shelters in the first few years (Devine et al. 2007a), but this advantage may be nullified in the long-term since wire cages can be modified over time to accommodate seedling growth.

Relatively little work had been done on Garry oak seedling growth enhancement prior to studies by Devine et al. (2007a), but there is an urgent need to further develop methods of Garry oak recruitment. Current pressures on Garry oak regeneration include high rates

of browsing due to increased herbivore populations (Gonzales and Arcese 2008), increased competition due to invasive species and in particular invasive alien grass species (MacDougall et al. 2004), and potential climate change requiring relatively rapid responses by Garry oak trees (Schafer et al. 2001, Scott et al. 2001).

Our objective was to evaluate chicken wire caging, weed block, and vole tubes designed to protect Garry oak seedlings under pressure from abundant herbivores and competing vegetation. Although detailed information is available on some types of Garry oak seedling protection (Devine et al. 2007a), our study addressed seedling protection in more northerly locations and provided a more in-depth comparison of three protection methods.

Study Sites

Crow's Nest Ecological Research Area (CNERA) on Salt Spring Island (48°46′ N, 123°27′ W) is 200 m above sea level with a southeast aspect (Figure 1). The sub-Mediterranean climate is mild and wet from November to April (monthly mean air temperature and precipitation values 5 °C and 128 mm, respectively) and moderate and drier from May to October (monthly mean air temperature and precipitation values 13 °C and 43 mm, respectively). Soils are shallow and interspersed with exposed bedrock. The 30 ha research area is comprised of two plant communities; 1.4 ha are open Garry oak meadows with rocky outcrops, and the remainder is Douglas-fir (Pseudotsuga menziesii)-dominated forest with some oaks persisting among the firs. Non-native grasses are abundant and high levels of herbivory are indicated by the modified architecture of shrubs and trees. Abundant native black-tailed deer and a small flock of feral sheep are present at CNERA. Garry oak trees are abundant on the site, but the populations are bimodally distributed and skewed to older age classes. There are two distinct cohorts, 55 and 150 years in age, respectively (Jordan 2007).

Pacific Rim Institute for Environmental Stewardship (PRI) on Whidbey Island (48°12′ N, 122°38′ W) is 65 m above sea level on a historical prairie known as Smith Prairie (Figure 1). The sub-Mediterranean climate is mild and somewhat drier than CNERA, mild and moist from November to April (monthly mean air temperature and precipitation values 6°C and 54 mm, respectively) and moderate and drier from May to October (monthly mean air temperature and precipitation values 14 °C and 31 mm, respectively). The site is fairly flat (< 2% slope) with relatively small changes in elevation. Soils are classified as sandy loam and consist

primarily of sand, gravel, and sandy-gravel mixtures with minor interlayered silt and silty sand. Topsoil depth varies significantly within the area and is well drained. The 70.8 ha research area is comprised of a variety of plant communities, mainly associated with old field agricultural species and glacial outwash prairie forbs and grasses. Non-native grasses are abundant and high levels of herbivory are indicated by the modified architecture of shrubs and trees.

Relatively heavy populations of native black-tailed deer occur throughout Whidbey Island. Populations of Townsend's voles (*Microtus townsendii*) on the site go through periodic fluctuations. During this study, populations reached peak densities in 2004 and 2008, followed by marked declines in subsequent years (R. Van Dragt, personal observations). Prior to the study, no Garry oak trees occurred at PRI in recent history, although large oaks are common 16 km north in the Oak Harbor area.

Methods

A total of 103 naturally occurring seedlings were selected and caged in three of the larger meadows at CNERA, while an additional 26 oak seedlings were left as controls. Due to the shallow soils of the study site, oaks were selected based on ease of access and ability to erect sturdy exclosures. Control oaks were selected based on their proximity to exclosed oaks and similarity in habitat areas. Cages were made using 12.2 cm stucco mesh and anchored to the ground with 30 cm nails, resulting in structures approximately 1 m high and 0.5 m in diameter. Sampling started in 2002 and tree heights and canopy diameter were measured. Ongoing treatment included widening the cages when oak seedling canopy growth had exceeded exclosure dimensions and herbivory was occurring again.

At PRI, a total of 434 nursery-grown oak seedlings were transplanted during the fall to spring period of 2002-03 and 2003-04. The site for transplantation was an old agricultural field located in the northeastern section of the property (Figure 1). The 1.3 ha planting area was divided into four plots, linearly arrayed from north to south, over which two treatment combinations were implemented. All oaks were caged in chicken wire mesh cylinders of similar size to the cages constructed at CNERA, anchored by three or four stakes made of iron reinforcing rod. Cage height varied depending on the initial tree size and shorter cages were closed on top to prevent large herbivores from leaning over and grazing the enclosed plant. Thus, deer and rabbits were

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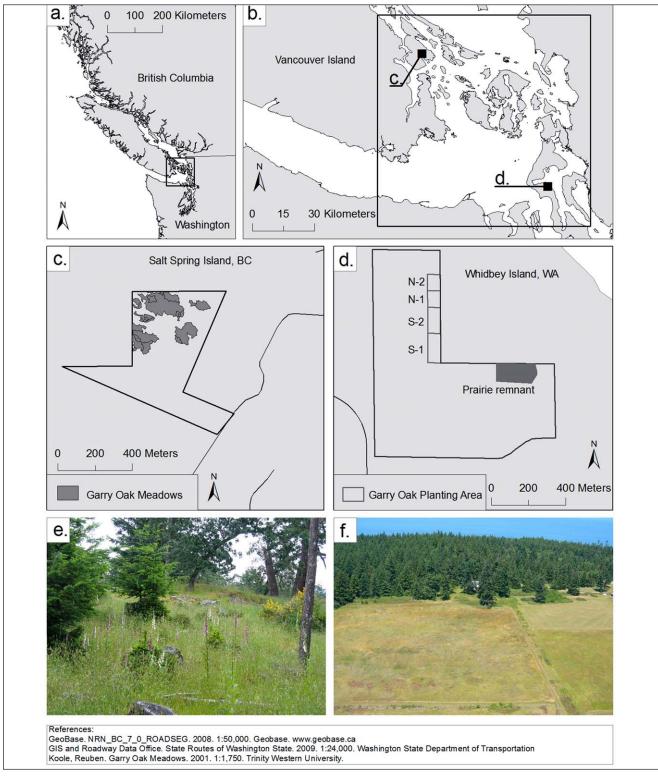


Figure 1. (a) The situation of study sites in the Pacific Northwest. Square indicates enlarged map in (b). (b) The location of Crow's Nest Ecological Research Area (CNERA) on Salt Spring Island, British Columbia, and Pacific Rim Institute for Environmental Stewardship (PRI) on Whidbey Island, Washington. Small black squares indicate areas enlarged in (c) and (d). (c) The distribution of Garry oak (Quercus garryana) meadows on CNERA. Caged and control seedlings are located primarily in the two largest Garry oak meadows. (d) The location of Garry oak seedling plantings on PRI. Seedlings in S-1 and S-2 are protected with cages and vole tubes; seedlings in N-1 and N-2 are protected with cages and weed block. (e) Photograph of CNERA showing a typical Garry oak meadow (photo by Devin Methven). (f) Photograph of PRI showing typical planting area (photo by Ira Buckley).

prevented from browsing the oaks, but the cages did not exclude smaller mammals, such as Townsend's voles.

For plots South 1 and South 2 (S-1 and S-2), seedlings were planted in late 2002 (N = 106) and early 2003 (N = 64), respectively. These seedlings were caged and plastic "vole tubes" were placed around each trunk. The vole tubes consisted of corrugated plastic tubing 3.8 to 5.1 cm in diameter and 15 cm long. A slit was made down one side of the tubing in order to install the tube and to allow for expansion of the oak trunk's girth in subsequent years. Tubing was buried ca. 5 cm below the soil surface to deny small mammals access to the upper root and root crown. Seedlings in plots North 1 and North 2 (N-1 and N-2) were planted in the fall of 2003 (N = 133) and early spring of 2004 (N= 131), respectively. They were caged using the same materials as S-1 and S-2, but instead of vole tubes, we surrounded each transplant with 91 cm \times 91 cm \times 0.02 mm plastic weed block (Arbortec Industries Ltd., Penticton, BC) to inhibit plant competition.

Oaks were propagated from a local source of native Garry oaks on Whidbey Island, and grown in 4 L pots in a greenhouse for one year. There is a possibility that the seedling oaks acquired mycorrhizae or inoculum while growing in these containers. No spatial pattern was incorporated when the oaks were outplanted. An auger was used to drill holes and oaks were manually planted; they were not root pruned prior to planting. Seedlings were initially watered once every 6 weeks, 20 L per oak, from June through August during the 2003 and 2004 seasons. Beginning in 2006, we measured oak height and noted mortality each June. Browsing damage from small mammals, determined to be largely caused by Townsend's voles, was observed throughout the study but became particularly severe in 2008. In 2008 we assessed oak damage in plots S-1, S-2 and N-2 using a rating of heavily gnawed (> 40% of surface damaged), slightly gnawed (< 40% damaged), or no gnawing observed. To determine the extent to which Townsend's voles utilized the oak seedlings and if vole feeding was localized to specific parts of the seedlings, we recorded damage on stems and branches separately. Vole activity in and around cages was assessed by monitoring the number of vole tunnels observed entering/ exiting the caged areas, and the number of vole nests found within each caged area. Cages were widened for seedlings that had expanded beyond the boundaries of the enclosures, as was done at CNERA.

Data were analyzed using SPSS version 16.0 (SPSS 2008). We used t tests to evaluate significant differences (P < 0.05) between treatments.

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Results

In general, by 2009, the exclosed oak seedlings at CNERA were taller than those at PRI, although the two sites cannot be directly compared because the CNERA trees were selected from seedlings already growing in 2001, whereas the trees at PRI were planted between 2002 and 2004 (Table 1). A more striking difference is seen in terms of mortality, with the 90% survival of caged seedlings at CNERA greatly exceeding the 30-50% survival rate seen at PRI, even though the latter were watered for the first two growing seasons. Abundant deer populations were observed at both locations, and additionally sheep were frequently seen at CNERA. Deer were observed browsing at the top of some of the PRI cages.

TABLE 1. Comparison of current growth (height values) for Garry oak seedlings (*Quercus garryana*) from Salt Spring Island, BC (Crow's Nest Ecological Research Area: CNERA) and PRI in 2009 (Pacific Rim Institute for Environmental Stewardship: Pac Rim). The initial mean height of CNERA seedlings in 2001 was 26.2 cm and 25.3 cm for caged and control seedlings, respectively; initial height was not measured for PRI seedlings.

Treatment	Mean height (±SD) (cm)	Maximum height (cm)	% survival	Initial year	N
CNERA caged	63 (46)	203	90	2001	103
CNERA control	28 (16)	70	73	2001	26
Pac Rim N-1	32 (21)	85	42	2003	133
Pac Rim N-2	53 (20)	115	50	2004	131
Pac Rim S-1	29 (21)	69	15	2002	64
Pac Rim S-2	35 (20)	96	46	2003	69

Growth in the height of caged seedlings at CNERA from 2001 to 2009 outpaced growth in control seedlings (Figure 2b). By 2009, the average height of exclosed oaks (63 cm) was 225% of the controls (28 cm) (Table 1). Mean seedling height of caged seedlings increased in every observation interval. Furthermore, variability was low when compared to the control group, suggesting that most of the caged individuals increased in height. The slight increase in coefficient of variation (CV) in 2009 for the caged group was the result of a few seedlings growing much taller than the others (Table 2). In contrast, mean seedling height in the control group showed both increases and decreases, representing the variable effects of herbivory. The CV grew continuously as the variability in the control group increased. Survival was similar to the caged trees until 2007, after which the two groups diverged. By 2009, survival of caged trees

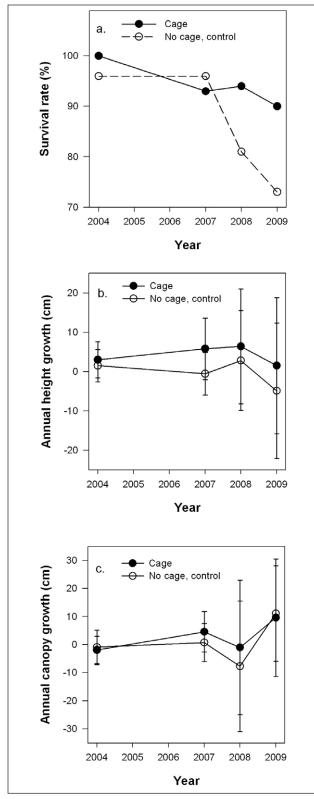


Figure 2. (a) Survival rate, (b) mean ± one standard deviation annual height growth increments, and (c) mean ± one standard deviation annual canopy growth increments for cage and control trials at the Crow's Nest Ecological Research Area (CNERA), Salt Spring Island, BC. Negative values are due to mortality or browse damage.

TABLE 2. Mean Garry oak (*Quercus garryana*) seedling height (cm) in observed years and coefficient of variation (CV) at on Salt Spring Island, BC (Crow's Nest Ecological Research Area: CNERA).

	Con	Control		Caged	
Year	Mean	CV	Mean	CV	
2001	25.3	0.46	26.2	0.33	
2004	30.0	0.48	35.1	0.49	
2007	28.4	0.60	53.6	0.45	
2008	33.6	0.66	58.2	0.40	
2009	28.1	0.73	62.9	0.58	

had fallen to 73%, while exclosed oaks only declined to 90% (Table 1, Figure 2).

Crown width growth of control seedlings at CNERA was similar to caged seedlings; by 2009 exclosed seedling crowns were only 11% broader (Figure 2). Crown width growth was visibly restricted by cages in some cases.

At PRI, surviving Garry oak seedlings increased in mean height from 2006-2009 within all treatments (data not shown). However, the annual rate of growth tended to decrease for both treatments, with the weed block seedlings showing a decline in annual growth between 2008 and 2009 (Figure 3). Annual height growth was significantly greater for weed block trees than vole tube trees in 2008 (P = 0.03; t = -2.2; df = 80) but not in 2009 (P = 0.49; t = -0.7; df = 132). Both treatments experienced relatively high levels of mortality. By 2009, survival fell to < 50% of the original seedlings planted in the weed block treatments and < 30% in the vole tube treatments (Figure 3).

Until 2006, weed block treatments at PRI resulted in 30% higher survival of Garry oak seedlings than in treatments without weed block. However, as the vole population increased towards the peak in 2008, extensive vole damage became noticeable, and much of the oak mortality could be attributed to vole activity. This was particularly evident in 2008 when the field was heavily tunneled by voles. In exclosures where the weed block had been retained, vole tunneling and digging by larger mammals around many cages clearly indicated that the voles were using the combination of weed block and wire cage as shelter and refuge from predators, such as dogs and coyotes.

Though exclosure cages of both types showed significant vole activity in 2008, evidence of activity was higher in cages with weed block (Table 3). In the weed block plots, cages exhibiting vole activity increased from 28 to 101 in the N-1 plot between 2007 and 2008,

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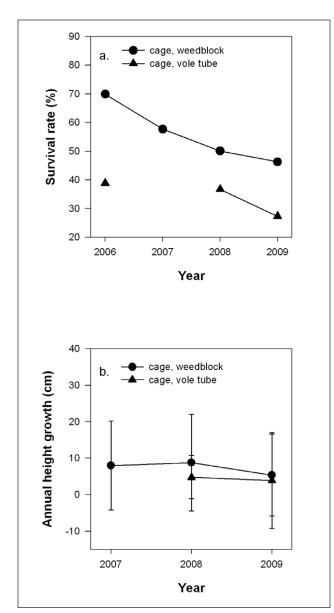


Figure 3. (a) Survival rate, and (b) mean ± one standard deviation annual height growth increments for various treatments at Pacific Institute for Environmental Stewardship (PRI), Whidbey Island, WA. Negative values are due to mortality or browse damage.

with 91% of the exclosures that retained weed block exhibiting vole activity. On the N-2 plot in the same time period, the number of exclosures with vole activity increased from 17 to 46, with 62% of the exclosures with weed block showing vole activity. For cages with vole activity, intensity of use was also higher in cages with weed block. The N-2 plot cages averaged 1.8 tunnels per tree, while the South plots averaged 1.4 tunnels per tree (Table 3). Also in 2008, 48% of all exclosures with weed block across the North plots harbored a vole nest, whereas only 11% of exclosures

TABLE 3. Vole damage frequency in combined South plots (with vole tubes) and N-2 (with weed block) at PRI on Whidbey Island at the Pacific Institute for Environmental Stewardship observed in 2008 (values in percent); Heavily gnawed stem (>40% damage); heavily gnawed branches (>40% damage); slightly gnawed stem (<40% damage). Vole damage was not recorded in N-1 in 2008.

	Study plots	
Damage type	South	N-2
Heavily gnawed stem	54.1	32.9
Heavily gnawed branches	4.1	7.6
Heavily gnawed stem and branches	16.2	25.3
Slightly gnawed stem	5.4	8.9
Other vole damage	2.7	n.a.
Total vole damage	82.5	74.7
Number of tunnels per tree	1.4	1.8
N	74	79

without weed block had a vole nest. The impact of this activity was also heavier in the weed block cages. Across the North plantings in 2008, oak saplings in 49% of the exclosures with vole activity suffered mortality while only 37% of saplings in exclosures without vole activity died (Figure 3).

During the peak of the vole population in 2008, the overall incidence of damage to various parts of the plant was higher in exclosures with vole tubes than with weed block (Table 3). More than half of the damage in the vole tube cages (54.1%) was heavy gnawing on the main stem above the vole tube. In many plants with vole tubes (16.2%), the damage extended onto the lower branches. In 2008 it was observed that the vole tubes had subsided over the preceding years so that less of the stem was protected than when the tubes were originally installed. With weed block the incidence of plants suffering heavy gnawing damage to both stem and trunk was higher (25.3%), but taken together a smaller proportion of plants suffered heavy damage to the stem alone or the stem and lower branches (58.2%, in contrast to 70.3% for plants with vole tubes). The "other damage" on the seedlings indicated in Table 3 appeared to be primarily due to browsing by deer that were able to access the oaks from the tops of the protective cages despite efforts to fashion the wire mesh as a cover for many of the cages.

Discussion

Mortality levels in this study were higher than the 10% mortality observed by Devine et al. (2007a, b), particularly at PRI where more than 50% mortality was observed. Two major sources of mortality at PRI were

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likely voles and lack of moisture; low summer rainfall may have contributed to the mortality at CNERA as well. The results indicated that CNERA on Salt Spring Island was more suitable for growing Garry oak seedlings than the PRI on Whidbey Island, perhaps because the CNERA had slightly more precipitation from May to October and was more shaded. Although CNERA is relatively open, partial shade is provided by interspersed mature Garry oak trees, small conifers and shrubs. With additional watering, PRI would likely support more rapid growth because of the deeper soils, but these soils being well drained are prone to experience drought periods during the summer months. Watering of seedlings at PRI did take place June through August of 2003 and 2004, but the two years of watering may have been insufficient to prevent mortality in subsequent years.

Propagation of oak seedlings at CNERA by natural means as compared to the planting of nursery-grown seedlings at PRI was likely another major reason for improved seedling survival on Salt Spring Island. There are many benefits associated with natural propagation, including promotion of mycorrhizal relationships through proximity to adult trees where mycorrhizal networks are already established (Frank et al. 2009). Without extant populations of Garry oak trees at PRI, lack of mycorrhizal inoculum could have limited seedling establishment and warrants further investigation.

On both sites, average growth rates of caged plants were low relative to other sites in Washington; our growth rates were less than 10 cm per year whereas Devine et al. (2007a) recorded rates of 30 cm per year or higher near Olympia, WA. Higher average precipitation in Olympia (129 cm compared to 84 cm and 51 cm at CNERA and PRI, respectively) may have contributed to this difference. However, it should also be noted that the more rapidly growing treatments studied by Devine et al. (2007a) were fertilized or irrigated, and that one of the treatments without fertilizer or irrigation exhibited < 10 cm growth per year in years 3 and 4, even when protected from grazers.

No detailed observations of actual browsing by ungulates on the control Garry oak seedlings were made, but based on observations of browsing on Garry oak in other studies at CNERA, it is reasonable to conclude that the height difference between the control treatments and the caged treatments was due to browsing on control plants. The benefit of caged exclosures was clear at CNERA, where uncaged control trees showed little growth due to ungulate browsing. Also the increased CV for control trees over time inferred that while a few control seedlings were surviving and

exhibiting increased growth, others were being browsed, resulting in little annual growth or even shrinkage. The observations of crown growth also provided evidence for activity of browsers, with the relatively small difference in size of crowns between control and caged seedlings at CNERA likely indicating that the shortstatured control seedlings grew outward in response to browsing whereas caged seedlings were restricted from outward expansion by the cages. Further crown width growth is anticipated in caged seedlings subsequent to cage enlargement in 2007-2009.

Likewise at PRI, caging the seedlings was necessary to protect them from black-tailed deer. Experience at both sites indicated, however, that it is necessary to conduct frequent maintenance on the cages to ensure that growth of the oak seedlings is not restricted by the caging, and that the growing oak trees are still protected from browsing ungulates. The ability to adjust the size of the cage is an advantage over other methods such as using solid exclosures which must be removed to allow oak growth rather than simply enlarging the exclosure as in the case of caging. Additionally, experience at PRI indicated that features designed to enhance tree growth, e.g., weed block (brush blankets) need to be applied judiciously to avoid unintended consequences such as providing vole nesting sites. Although it is clear that other factors (e.g., lack of moisture) may have contributed to high rates of mortality from 2007 to 2008, extensive evidence of foliage clipping, girdling and excavation around the oaks supported the inference that the voles contributed heavily to this mortality.

Although Townsend's voles do not specifically target Garry oak seedlings as a staple food source, the seedlings become vulnerable to girdling by these mammals, particularly in winter months when food is scarce. The vole tubes utilized at PRI enhanced survival of trees, particularly in the first few years after planting when the tubes were newly installed, but the trees still suffered heavy gnawing several years later when the vole tubes were no longer providing effective protection. The survival of young oak seedlings was also enhanced initially by the plastic weed block, possibly by limiting competition from weeds. However, by 2008 when vole populations peaked, the weed block worked against survival of oak seedlings. The thick, waterproof weed block provided excellent cover for vole nests. Thus, use of weed block in these situations ideally should be timed to avoid vole outbreaks and coordinated with the use of vole tubes. The weed block does provide growth and survival benefits in the initial 2-3 years after planting oak seedlings by enhancing soil moisture (Devine et al. 2007a), but in areas with the potential for vole outbreaks, the weed block generally should be removed one or two years after planting (or other weed control measures substituted).

Devine and Harrington (2010) describe three keys to successful establishment of Garry oak seedlings. First, they emphasize the importance of planting quality seedlings. The acorns used at PRI were sorted carefully for quality. The high survival of seedlings (90%) in the CNERA trial highlighted the usefulness of utilizing seedlings that germinated naturally as one method of producing high quality seedlings. Second, they recommend control of vegetation competing for the limited moisture available to oak seedlings. Weed block employed at PRI was helpful to some extent, but only for the first few years of growth. At CNERA, no control was attempted for competing vegetation, and this may have had some impact on the lack of growth in the control seedlings which were heavily browsed by deer and therefore not able to grow above competing vegetation. Third, they recommend protecting seedlings from animal damage. As also noted by Devine et al. (2007a), we saw clear benefits from protecting oak seedlings from deer browsing. Caging compared to the solid tree shelters employed in most of the plantings of Devine et al. (2007a) facilitated more extended protection because the cage size can be enlarged over time.

Literature Cited

- Crow, T. R. 1988. Reproductive mode and mechanisms for self replacement of northern red oak (*Quercus rubra*) a review. Forestry Science 34:19-40.
- Devine, W. D., and C. A. Harrington. 2010. Planting native oak in the Pacific Northwest. Gen. Tech. Rep. PNWGTR-804, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Devine, W. D., C. A. Harrington, and L. P. Leonard. 2007a. Postplanting treatments increase growth of Oregon white oak (*Quercus garryana* Dougl. Ex. Hook.) seedlings. Restoration Ecology 15:212-222.
- Devine, W. D., C. A. Harrington, and D. H. Peter. 2007b. Changes in Oregon white oak (*Quercus garryana* Dougl. ex Hook.) following release from overtopping conifers. Ecological Restoration 25:247-255.
- Dunwiddie, P. W., J. D. Bakker, M. Almaguer-Bay, and C. Sprenger. 2011. Environmental history of a Garry oak / Douglas-fir woodland on Waldron Island, Washington. Northwest Science 85:130-140.
- Frank, J. L., S. Anglin, E. M. Carrington, D. S. Taylor, B. Viratos, and D. Southworth. 2009. Rodent dispersal of fungal spores promotes seedling establishment away from mycorrhizal networks on *Quercus garryana*. Botany 827:821-829.
- Fuchs, M. A., P. G. Krannitz, and A. S. Harestad. 2000. Factors affecting emergence and first-year survival of seedlings of Garry oaks (*Quercus garryana*) in British Columbia, Canada. Forest Ecology and Management 137:209-219.

Longer-term protection strategies for oak seedlings are especially important in areas with high populations of ungulates and relatively slow tree growth, as seen at CNERA and PRI. The challenge of minimizing vole impacts on Garry oak seedlings at PRI further highlights the necessity of protecting seedlings from animal damage. Techniques for protecting and promoting seedling growth may sometimes facilitate vole damage, and thus it is important to use these techniques strategically and monitor vole impacts.

Acknowledgements

The authors are grateful to the summer students who set up the experiment on the CNERA (Andrew Burkinshaw, Reuben Koole and Danica Neufeld), students who measured the oak seedlings in subsequent years as well as students enrolled in the Au Sable Institute of Environmental Studies who helped measure the oaks at PRI. We thank Taylor Strom, Trinity Western University Geography Program, who prepared the maps in Figure 1. We also acknowledge the support of Calvin College to RVD, and financial support from Trinity Western University, Roger and Connie Brummel and the Natural Sciences and Engineering Council of Canada. We thank two anonymous reviewers and special issue editor Peter Dunwiddie for providing excellent suggestions for improving the manuscript.

- Gilligan, L. A., and P. S. Muir. 2011. Stand structures of Oregon white oak woodlands, regeneration, and their relationships to the environment in southwestern Oregon. Northwest Science 85:141-158.
- Gonzales, E. K., and P. Arcese. 2008. Herbivory more limiting than competition on early and established native plants in an invaded meadow. Ecology 89:3282–3289.
- Gonzales, E. K., and D. R. Clements. 2010. Plant community biomass shifts in response to mowing and fencing in invaded oak meadows with non-native grasses and abundant ungulates. Restoration Ecology 18:753-761.
- Hibbs, D. E., and B. J. Yoder. 1993. Development of Oregon white oak seedlings. Northwest Science 67:30-36.
- Jordan, D. A. 2007. Dendrochronological investigation of Garry-oak (*Quercus garryana*) in Crow's Nest Ecological Research Area (CNERA) Saltspring Island, British Columbia. *In* Proceedings of the Annual Garry Oak Ecosystems Recovery Team Research Colloquium, Pacific Forestry Centre, Victoria, BC. P. 13.
- Lea, T. 2006. Historical Garry oak ecosystems of Vancouver Island, British Columbia, pre-European contact to the present. Davidsonia 17:34-50.
- Lilley, P. L., and M. Vellend. 2009. Negative native-exotic diversity relationship in oak savannas explained by human influence and climate. Oikos 118:1373-1382.
- MacDougall, A. S., B. R. Beckwith, and C. Y. Maslovat. 2004. Defining conservation strategies with historical perspectives: a case study from a degraded oak grassland ecosystem. Conservation Biology 18:455–465.

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- McCreary, D. D., and J. Tecklin. 2001. The effects of different sizes of tree shelters on blue oak (Quercus douglasii) growth. Western Journal of Applied Forestry 16:153-158.
- Michalak, J. 2011. Effects of habitat and landscape structure on Oregon white oak (Quercus garryana) regeneration across an urban gradient. Northwest Science 85:182-193.
- Pellatt, M. G., R. J. Hebda, and R. W. Mathewes. 2001. High resolution Holocene vegetation and climate from Core 1034B, ODP Leg 169S, Saanich Inlet, Canada. Marine Geology 174:211-222.
- Peter, D., and C. Harrington. 2002. Site and tree factors in Oregon white oak acorn production in western Washington and Oregon. Northwest Science 76:189-201.
- Potter, M. J. 1988. Tree shelters improve survival and increase early growth rates. Journal of Forestry 86:39-41.
- Regan, A. C. 2001. The effects of fire on woodland structure and regeneration of Quercus garryana at Fort Lewis, Washington. M.S. Thesis, University of Washington, Seattle.
- Rohlfs, D. A. 1999. A study of acorn feeding insects filbert weevil (Curculio occidentis (Casey)) and Filbertworm (Cydia latiferreana (Walsingham)) on Garry Oak (Quercus garryana) (Dougl.)) in the Southeastern Vancouver Island Area. M.S. Thesis, University of British Columbia, Vancouver.
- Roemer, H. 1993. Vegetation and ecology of Garry oak woodlands. In R. J. Hebda and F. Aitkens (editors), Proceedings of the Garry Oak-Meadow Colloquium, Garry Oak Meadow Preservation Society, Victoria, BC. Pp. 19-24.

Received 2 September 2010 Accepted for publication 17 February 2011

- Schafer, S. L., P. J. Bartlein, and R. S. Thompson. 2001. Potential changes in the distributions of western North America tree and shrub taxa under future climate scenarios. Ecosystems 4:200-215.
- Scott, J. M., M. Murray, R. G. Wright, B. Csuti, P. Morgan, and R. L. Pressey. 2001. Representation of natural vegetation in protected areas: capturing the geographic range. Biodiversity and Conservation 10:1297-1301.
- Shaw, M. W. 1974. The reproductive characteristics of oak. In M. G. Morris, and F. H. Perring (editors), The British Oak: Its History and Natural History. E.W. Classey Ltd., Faringdon, Berkshire, UK. Pp. 162-181.
- SPSS Inc. 2008. SPSS for Windows, standard version 18.0. SPSS Inc. Headquarters, Chicago, Illinois.
- Stein, W. I. 1990. Oregon white oak. In R. M. Burns, and B. H. Honkala (editors), Silvics of North America, Volume 2, Hardwoods. USDA Forest Service, Washington, D.C.
- Thilenius, J. F. 1968. The Quercus garryana forests of the Willamette Valley, Oregon. Ecology 49:1124-1133.
- Turner, N. J. 1999. Time to burn: traditional use of fire to enhance resource production by aboriginal peoples in British Columbia. In: R. Boyd (editor), Indians, Fire and the Land in the Pacific Northwest. Oregon State University Press, Corvallis, OR. Pp. 185-218.
- Williams, K., L. J. Westrick, and B. J. Williams. 2006. Effects of blackberry (Rubus discolor) invasion on oak population dynamics in a California savannah. Forest Ecology and Management 228:187-196.