

Consumer-based limitations drive oak recruitment failure

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Abstract. A number of North American oaks are experiencing recruitment failure, with explanatory hypotheses including a range of consumer- or resource-based limitations. Using a factorial experiment with transplanted seedlings, we demonstrate how direct and indirect consumer effects prevent recruitment by *Quercus garryana*, a keystone savanna species of northwestern North America. Foremost, intense herbivory by mostly exotic small mammals severely damaged or killed 100% of unprotected seedlings during winter. Many damaged seedlings survived but were 64% smaller in size and produced 75% fewer leaves. Herbivory by deer had no detectable impact despite being long hypothesized as a major contributor to oak decline. Indirectly, herbivory altered the outcome of moisture limitation and competition. Without small mammals, summer drought and a dense exotic grass cover associated with fire suppression significantly reduced growth but caused little mortality. With small mammals, both significantly increased mortality of herbivore-damaged seedlings. Herbivore damage also increased the likelihood of severe insect attack, possibly due to reduced investment in foliar defense by recovering seedlings. These results show that no single factor necessarily prevents seedling establishment by oaks, but that the combination of herbivory, undisturbed exotic grass swards, and summer drought creates an almost insurmountable barrier for recruitment.

Key words: climate change; consumers; Garry oak ecosystem; herbivory; insect defoliation; mycorrhizal fungi; oak recruitment failure; *Quercus garryana*; resources.

INTRODUCTION

Oak species are failing to regenerate in many regions of North America but the causes remain unclear (Abrams 2003). Being a keystone savanna species, the effects of oak decline are predicted to cascade across all trophic levels, especially for obligate taxa (Rice et al. 1993, Manning et al. 2006). Hypotheses for oak recruitment decline tend to focus on shifts in the intensity of one or the combination of consumer-based or resource-based limitations, including increased herbivory (Gonzales and Arcese 2008), intensified competition often associated with grass invasion and fire suppression (Gordon and Rice 2000, Abrams 2003, Bond and Keeley 2005), weakened or eliminated ectomycorrhizal associations that may reduce resource uptake (Dickie et al. 2007a, b), and intensified climatic variability (Kueppers et al. 2005). All are likely to interact, but their relative importance is unclear.

Uncertainty over the relative importance of consumer- or resource-based limitations extends far beyond oak recruitment limitation, especially in the context of global environmental change (Chase et al. 2000, Paine 2000, Shurin et al. 2006, Hillebrand et al. 2007). In isolation, both consumers and resources have been shown to strongly influence a range of population- and community-level parameters of producers in terrestrial and

aquatic systems (Worm et al. 2002, Gruner et al. 2008). Environmental change can simultaneously affect both consumers and resources (e.g., by influencing resource supply rates, disturbance frequency, or food web structure), creating strong interdependent effects between them but also obscuring their relative importance (Hillebrand et al. 2007). For consumer pressure in particular, there can be variable and interacting effects of environmental change on how large herbivores, small herbivores, and insects impact plant populations, although these have been rarely examined in concert (Pringle et al. 2007, Gruner et al. 2008). All of these issues apply to oak-dominated systems. Resource supply rates for oaks, for example, have been transformed by climate change, grass invasion, and broken ectomycorrhizal pathways (D'Antonio and Vitousek 1992, Kueppers et al. 2005, Dickie et al. 2007b). Alternatively, consumer pressure on oaks has potentially intensified in association with the simultaneous occurrence of expanding ungulate populations, intense small-mammal browsing, and insect invasion (Fuchs 2001, MacDougall 2008).

Here, we experimentally test limiting factors for recruitment by *Quercus garryana*, a widespread oak species of lowland and coastal savannas extending from British Columbia to California. Like many oaks suffering recruitment failure, remnant stands are composed almost entirely of older trees (Devine et al. 2007, Pellatt et al. 2007). This species shows no evidence of reproductive difficulties, as it produces large numbers of viable acorns in most years (Devine et al. 2007). Seedling

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densities can be high but rarely grow tall enough to penetrate the understory grass canopy (Pellatt et al. 2007). This lack of recruitment by *Q. garryana* beyond the seedling stage has been attributed to a range of factors, including the interaction between long-term fire suppression and competition from exotic grasses (MacDougall 2005, Gedalof et al. 2006), intense herbivory associated with large populations of black-tailed deer (Gonzales and Arcese 2008, MacDougall 2008), reduced ectomycorrhizal diversity associated with habitat loss and the isolation of remnant trees (Valentine et al. 2004), or possibly infestation by exotic insects. Alternatively, recruitment by *Q. garryana* may simply be highly episodic, where interannual variability in precipitation associated with the regional sub-mediterranean climate results in recruitment windows rarely opening (Koenig and Knops 2005, Pellatt et al. 2007). We examine the individual and interacting effects of these factors on seedling growth and survival using a factorial experiment combining herbivory, competition from exotic grasses, watering to offset summer drought, and soil transfer treatments that serve as a mycorrhizal inoculant (Dickie et al. 2007b).

METHODS

Study area

Our study area was the Quamichan Garry Oak preserve in the Cowichan Valley of southeastern Vancouver Island, British Columbia, Canada (48°48' N, 123°38' W). It is a 35-ha old-field site that was plowed, planted with exotic grasses, and grazed from the 1860s to 2001. Prior to the 1860s, the site was likely a heterogeneous fire-influenced mixture of savanna forbs, grasses, bracken fern, shrubs, and sporadic oak trees (MacDougall et al. 2004). Today, fire is suppressed and oak density remains low, while the understory is dominated by perennial agronomic grasses with low densities of exotic pasture legumes (e.g., *Vicia sativa*, *Trifolium dubium*).

This oak-dominated system is part of a complex of prairie, savanna, and oak woodland that extends south to California (MacDougall et al. 2004). In British Columbia, it is associated with a highly variable sub-mediterranean climate, with local rainfall averaging 1100 mm per annum that mostly falls from October to May. The summer drought period can be pronounced, with monthly rainfall averaging <10 mm in some years, which can result in high oak seedling mortality (Gonzales and Arcese 2008). The oak (*Quercus garryana*) is required by a number of obligate plants and animals, including epiphytic bryophytes, butterflies, and birds that feed heavily on its acorns in fall and are important for dispersal (Fuchs et al. 2000, McIntosh and Miles 2005, Hellmann et al. 2008, Pelini et al. 2009).

On Vancouver Island, habitat loss has reduced this ecosystem to <10% of its former range (Lea 2006, Vellend et al. 2008) although oak trees remain relatively abundant in fields, yards, and roadsides. In many

remnant sites, a pronounced burst of oak recruitment occurred between the mid 1800s–early 1900s (Pellatt et al. 2007), coinciding with the extirpation of Roosevelt elk and the temporary reduction of deer by intense subsistence hunting. Since then, however, there has been little recruitment of oak juveniles (Pellatt et al. 2007) possibly due to large increases in the size of deer herds (MacDougall 2008). Deer herds currently range from 10 to 40 individuals/km² on Vancouver Island, with herd sizes >4–15 individuals/km² associated with negative effects on tree recruitment (McTaggart-Cowan 1945, Martin and Baltzinger 2002, Gonzales and Arcese 2008). Remnant sites on Vancouver Island can have high densities of small oak seedlings in the understory, suggesting that acorn production and viability are high although these seedlings almost always remain below the grass canopy (Pellatt et al. 2007, Gonzales and Arcese 2008). Small mammals that potentially prey on oak seedlings are Townsend's vole (*Microtus townsendii*), deer mouse (*Peromyscus maniculatus*), and the European rabbit (*Oryctolagus cuniculus*) introduced in the late 1800s. Insects that cause high levels of oak defoliation, all of which are exotic, include jumping gall wasps (*Neuroterus saltatorius*), oak leaf phylloxera (*Phylloxera glabra*), winter moth (*Operophtera brumata*), and gypsy moth (*Lymantria dispar*) (Roland and Myers 1987). Population levels of small mammals and insects, and their relative impacts on growth and mortality of *Q. garryana* seedlings, are largely unknown (Roland and Myers 1987, Wilson and Carey 2001).

Experimental design

We established a 24-block split-plot factorial design (Table 1) using planted oak seedlings with treatments of disturbance, watering, the addition of ectomycorrhizal fungi using soil transfers (Dickie et al. 2007a, b), deer exclosures (hereafter referred to as “fences”), and small-mammal exclosures (hereafter “exclosures”). Each block was 5 × 5 m, containing 20 planted oak seedlings ($N = 480$ seedlings). Seedlings were derived from local sources (Cowichan Valley), grown outdoors in 5-L pots for 3–4 years, and then planted in the experimental blocks in September 2007, near the start of the annual rainy season.

The disturbance treatment was continuous plowing, which removed 100% of the perennial grass cover in one-half of the 24 blocks. Initially, the area was deep-plowed (~50 cm) in June 2004. Exposure to sun and moisture limitation during the summer of 2004 killed most of the turned-over sod. Subsequent shallow-plowing starting in fall 2004 eliminated all surviving perennial grass and reduced the soil seed bank. A cover of annual winter wheat was planted in 2005 and 2006 to reduce soil erosion and weed recruitment. After the seedlings were planted, continuous weeding and mowing removed any encroaching vegetation.

The watering treatment, covering one-half of the plowed and unplowed blocks, began in June 2008.

TABLE 1. ANOVA results for 12 plots within the unplowed grass sward, showing factors influencing Garry oak (*Quercus garryana*) seedling height and leaf production on Vancouver Island, British Columbia, Canada.

Source	F	P
Seedling height		
Light	5.94	0.016
Water × light × moisture	5.92	0.016
Water × light	3.94	0.049
Moisture × light	3.44	0.07
Moisture	1.62	0.21
Water	0.74	0.39
Water × moisture	0.15	0.70
Leaf production		
Light	10.2946	0.002
Water	5.3412	0.02
Moisture	0.5817	0.45
Water × moisture	0.4265	0.52
Water × light × moisture	0.1096	0.74
Moisture × light	0.0104	0.91
Water × light	0.0079	0.93

Note: For all *F* values, *df* = 1, 129.

Summer soil moisture deficits typically intensify in this sub-mediterranean system by this time (MacDougall 2005), and can cause oak seedling mortality (Gonzales and Arcese 2008). Water was heavily applied to all areas by a hose until the ground appeared saturated. The ectomycorrhizal treatment used the soil transfer method described by Dickie et al. (2007a, b), which can have significant positive effects on oak seedling growth and survival in old fields. The soil came from an adjacent savanna property that has never been plowed and has a continuous oak cover (MacDougall 2005). Soil was collected to the mineral layer (≤ 20 cm), within the drip-line of the oak canopy. Approximately 0.25 L of savanna soil was added prior to planting of the seedlings in the old field, representing 5% of the volume of the 5-L root ball. The fenced treatment for deer was an 8-foot (2.4 m) high wire fence surrounding 12 of the 5×5 m blocks. The fencing had 25×25 cm openings, sufficient for small mammals to pass through. One-half of the area in the deer fences was then further enclosed with fine-gauge plastic chicken wire to exclude small mammals. This enclosure was 1 m high, with an additional 50 cm folded along ground to inhibit tunneling by voles. Six-inch (15.2 cm) metal staples were driven into the ground to secure the fold and to further restrict tunneling.

Immediately following planting, all seedlings were measured for total leaf production and height (centimeters from ground level). These variables were then remeasured in May 2008 and August 2008. We recorded all evidence for damage by herbivores, including invertebrates (clipping, defoliation), and the timing of mortality. Insect defoliation was categorized as severe ($>50\%$ leaf removal), moderate (1–50% removal), or none. Because high concentrations of rabbit pellets in the fenced areas were observed in early spring 2008, we counted densities of rabbit and deer pellets at that time

using a single 5×1 m transect across the middle of each block (Wood 1988). Separate transects were used within each fenced and exclosure plot. Soil moisture was measured at the base of each seedling in May and August 2008 using a Hydrosense TDR meter (Campbell Scientific, Edmonton, Alberta, Canada). Percentage full light was measured at the same time in the undisturbed grass plots by contrasting light levels at the seedling crown vs. above the grass canopy (100 cm light sensor bar; Apogee Scientific, Englewood, Colorado, USA). Light was not measured in the disturbance plots because all values were $\sim 100\%$ full light. Leaf production and seedling height were converted to the percentage difference (positive or negative) observed from September 2007 to August 2008, to account for small but significant size differences among seedlings at the time of planting.

Statistical analysis

We used a two-step regression analysis that first determined the factors associated with seedling browsing (seedlings alive but clipped) and seedling mortality, and then examined the factors influencing seedling height, leaf production, and insect herbivory among surviving seedlings. For browsing and mortality, we used a generalized linear mixed model to account for the binary data (e.g., mortality = yes or no). The analysis followed a split-plot design with plowing, watering, and fencing as the main effects, and exclosures and soil inoculum as the split effects. Blocks were treated as random factors, and the remaining variables as fixed. Post hoc contrasts were conducted using *t* tests ($\alpha = 0.05$) on the odds ratio estimates. For seedling height and leaf production we used a linear mixed model based on the differences between those measures at the time of original planting (September 2007) vs. May 2008 and August 2008. The random and fixed factors were the same as those used in the generalized linear mixed model. The height and leaf data were $\log + 1$ transformed prior to taking these differences to normalize their distribution. Post hoc comparisons followed Fisher's protected LSD procedure (i.e., restricting post hoc *t* test comparisons to significant higher order interactions). Light and soil moisture levels, and differences in insect herbivory were also analyzed using a linear mixed model, with post hoc contrasts using *t* tests. All analyses were conducted on JMP 8.0 (SAS Institute 2008).

RESULTS

Seven months after planting, most of the seedlings outside of the exclosures were heavily browsed, clipped to ground level, dug up with evidence of root browsing, or killed (Fig. 1). Browsing was explained solely by the interaction of two factors: ploughing and herbivory ($\chi^2 = 38.3$, *df* = 2, $P < 0.0001$). Seedlings were more likely to be browsed in plowed areas vs. areas with grass ($t = -2.3$, $P = 0.024$), with seedlings in the small-mammal exclosure showing no signs of browsing regardless of

grass cover. In the plowed areas, there was no difference in the numbers of seedlings browsed or killed in the fenced vs. open areas ($\chi^2 = 0.38$, $df = 2$, $P < 0.53$), suggesting the browsing by black-tailed deer was minimal.

Almost all of the browsing damage (>98%) occurred over the winter period (September–May). Of the 310 herbivore-damaged seedlings during this time, many (74%) were able to recover enough to produce at least one leaf during summer, but seedling size and leaf production were reduced compared to the enclosure plots (height, 64% less, $F_{2,387} = 7.3$, $P = 0.001$; leaf production, 75% less, $F_{2,387} = 9.1$, $P = 0.0002$; Fig. 1).

For those seedlings that died, two mechanisms were responsible: the direct effect of intense winter browsing, or the indirect effect of browsing where seedlings recovered enough to produce leaves in May but perished over the summer. Winter mortality was explained by the interaction between plowing and herbivory ($\chi^2 = 17.2$, $df = 2$, $P = 0.0002$), with higher numbers of killed seedlings in the plowed fenced areas (28% of all seedlings) and plowed open areas (18% of all seedlings) (t tests). The high mortality in the fenced areas was associated with dense concentrations of rabbit pellets compared to all other areas ($F_{1,20} = 4.95$, $P = 0.03$, t test), suggesting that rabbits congregated there for some reason. Pellet counts in the plowed enclosures were 8.4 pellets/m², compared to 0.8 pellets/m² in the plowed open areas. No pellets were detected in the grass plots. Deer pellets were sporadic (0.2 pellets/m²) and showed no relationship with grass cover ($F_{1,20} = 0.62$, $P = 0.44$). There was no evidence for herbivore impacts on the grasses, based on the lack of significant differences in canopy height among the fenced, enclosed, and unfenced areas ($F_{2,239} = 0.14$, $P = 0.70$).

Mortality in summer was associated with significant pairwise interactions among plowing, watering, and herbivory (plowing \times watering $\chi^2 = 10.3$, $df = 1$, $P = 0.0013$; plowing \times herbivores $\chi^2 = 17.4$, $df = 2$, $P = 0.0002$; watering \times herbivores $\chi^2 = 6.9$, $df = 2$, $P = 0.032$). These interactions were explained by higher levels of mortality by herbivore-damaged seedlings in the unwatered grass plots (t tests). Of the 80 browsed seedlings that died over the summer, 93% occurred in the grass-covered plots, of which 78% were in unwatered areas.

This suppressive grass effect was associated with a negative relationship between canopy height and ground-level light availability (Fig. 2A), which in turn reduced leaf production, and to a lesser degree, seedling height for surviving seedlings (Table 1; Fig. 2B, C). The positive effects of watering on leaf production ($F_{1,239} = 5.14$, $P = 0.024$), seedling height ($F_{1,239} = 4.3$, $P = 0.038$), and the survival of clipped seedlings all suggest that soil moisture is also highly limiting in these grass swards.

There was no individual or interacting effect of the soil transfer treatment on seedling height ($F_{1,387} = 1.06$, $P = 0.30$), leaf production ($F_{1,387} = 1.41$, $P = 0.23$), or survival

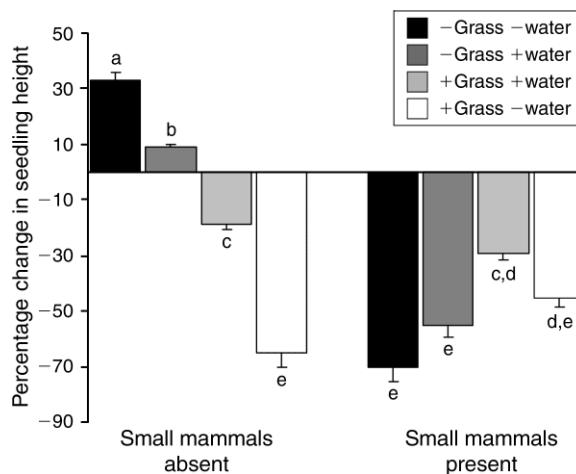


FIG. 1. Percentage change in seedling height from the time of initial planting in September 2007 to the following August 2008, with and without the presence of small-mammal herbivores. Error bars represent \pm SE. Lowercase letters indicate statistical relatedness among the treatments derived from t tests.

by the August sampling period ($\chi^2 = 3.67$, $df = 1$, $P = 0.07$).

Severe insect defoliation (>50% removal of leaves) was higher on herbivore-damaged seedlings in the unplowed areas compared to any other treatment combination ($F_{2,387} = 9.55$, $P < 0.0001$; t tests), suggesting that browsing subsequently influenced leaf palatability for insects. In contrast, among undamaged seedlings, those receiving water were more likely to suffer moderate levels of insect damage (1–50% removal, $F_{1,387} = 18.44$, $P < 0.0001$; t test). There was no relationship between the intensity of insect browsing (severe, moderate, none) and the likelihood of seedling mortality in the summer (i.e., severely defoliated seedlings were not more likely to die; $F_{2,79} = 1.25$, $P = 0.16$; t test).

DISCUSSION

A range of factors have been implicated in oak recruitment failure, ranging from consumer-based limitations associated with browsing to resource-based limitations involving climate change. Here, a combination of limiting factors was detected, driven primarily by consumer-based impacts associated with small-mammal herbivory. Directly, browsing damaged or killed most unenclosed seedlings over the winter. Indirectly, browsing increased their susceptibility to mortality from grass competition and moisture limitation, and made them more prone to severe insect defoliation. On its own, grass cover significantly suppressed seedling performance but rarely caused mortality. It also reduced predation by small mammals and insects, possibly because the seedlings were harder to detect. Although watering reduced grass suppression, the supplementation of resource flows to seedlings in general had relatively

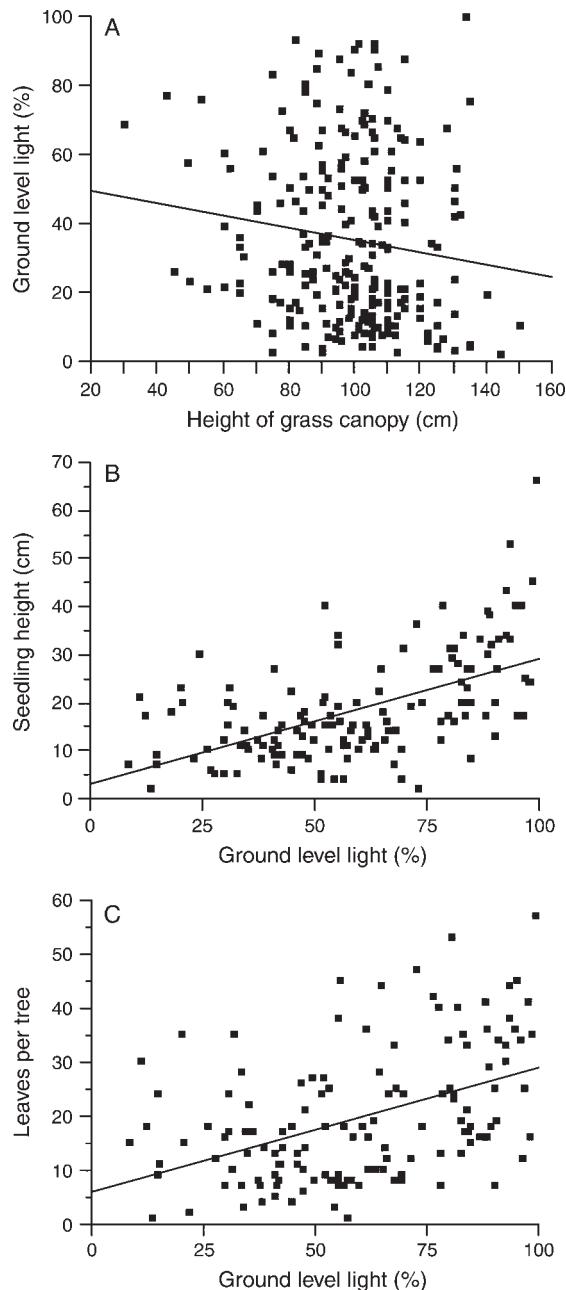


FIG. 2. (A) Ground level light (% full light) in the grass understory by height of the grass canopy ($F_{1,11} = 6.09$, $P = 0.0143$), (B) oak seedling height by ground level light (% full light) within the unplowed grass sward ($F_{1,11} = 69.1$, $P < 0.0001$), and (C) number of leaves per oak seedling by ground level light ($F_{1,11} = 41.7$, $P < 0.0001$).

minor (watering) or no impact (soil transfers) on seedling growth and survival. In combination, the prevalent natural conditions in this system at present (intense herbivory from small mammals, high grass cover associated with long-term fire suppression, and moisture-limited summers) appear to represent an almost insurmountable barrier for successful recruitment.

Intense browsing by small mammals has been observed in many plant communities, impacting species composition and abundance sometimes based on the relative palatability of the vegetation (Summerhayes 1941, Batzli and Pitelka 1970, Freedland 1974, Ostfield et al. 1997, Howe et al. 2006, Orrock et al. 2006, 2009, MacDougall and Wilson 2007). These effects are sometimes associated with natural fluctuations in small-mammal populations, with the largest impacts on vegetation occurring at the abundance peaks (Krebs et al. 1973). We have no data at present describing small-mammal dynamics in our system on Vancouver Island, although several factors associated with the transformation of this savanna ecosystem suggest that small-mammal populations and impacts could be large, based on observations elsewhere (e.g., Boonstra and Krebs 1977, Taitt et al. 1981, Diffendorfer et al. 1995, Edwards and Crawley 1999, Borer et al. 2006, Pringle et al. 2007). These include predator reductions (e.g., barn owls; Fuchs 2001), widespread habitat loss (Vellend et al. 2008) that may restrict juvenile immigration and elevate local population densities, increased plant cover associated with grass invasion and loss of grazers (the regional extirpation of Roosevelt elk, the local removal of sheep and cattle; MacDougall 2008), and the possibility of agricultural subsidization associated with nearby pasture (see Polis et al. 1997).

Whatever the small-mammal population densities might be, browsing appears to represent a substantial recruitment bottleneck through which few oak seedlings escape unscathed. The identity of these mammals is not entirely clear but our evidence strongly suggests European rabbits. The most significant damage occurred in areas lacking grass cover. Rabbits often prefer open areas because predators are more visible (Iason et al. 2002, Bakker et al. 2009), whereas voles mostly restrict their foraging to areas with dense cover (Taitt et al. 1981, Taitt and Krebs 1983, Bakker et al. 2009). The strong fencing effect that we observed, with the highest pellet concentrations and greatest damage within the 8-foot (2.4 m) tall fenced blocks, may also be an effect of predation if the rabbits perceived less risk in these areas. The concentration of herbivory in the winter further indicates rabbits, given that vole population sizes are generally smallest at this time (Chitty and Phipps 1966, Gipps et al. 1981). The targeting of seedlings by rabbits in the winter may occur because alternative food sources are unavailable, potentially resulting in high levels of seedling damage even if rabbit populations are not excessively large.

Whatever the ultimate source of herbivory, many of the seedlings recovered initially from defoliation, as is common with oaks. However, this is unlikely to occur indefinitely because this damage increased susceptibility to mortality by severe insect defoliation, grass competition, and soil-moisture limitation. The strong synergism between small-mammal browsing and severe insect defoliation has not been previously described to our

knowledge. It may derive from the investment by seedlings in resprouting at the expense of defense compounds within leaf tissue (Coley et al. 1985), or increased net photosynthetic assimilation of CO₂ and earlier leaf emergence in response to browsing (Heichel and Turner 1983, Williams and Myers 1984, Roland and Myers 1987). One factor that was unexpectedly irrelevant was herbivory by black-tailed deer, a species known to heavily browse oak saplings and consume large quantities of acorns including *Q. garryana* (Devine et al. 2007) and whose populations on Vancouver Island are large (Gonzales and Arcese 2008). This result could be a function of small-mammal herbivory being so high and immediate that deer impacts never materialize.

Competition from exotic grasses has been implicated as a major cause of oak recruitment failure in western North America (D'Antonio and Vitousek 1992, Gordon and Rice 2000). Our results demonstrated a strong suppressive effect of grasses on seedlings, especially light limitation, but no direct and immediate impact on seedling mortality. Instead, the most significant effect was to exacerbate the impacts of herbivore damage. Without grass cover, damaged seedlings mostly recovered; with cover, they mostly perished. As well, seedlings within the grass swards had a higher probability of escaping browsing than seedlings in the open, as would be expected if rabbits are the primary herbivores (Bakker et al. 2009). Their ability to survive within the grasses despite showing sensitivity to light suppression may be explained by the highly heterogeneous light environment we observed in the sward understory (range: <5% to >95% full light). We also speculate, based on observations of insect damage, that invertebrate predator populations could be more active within the intact swards, a hypothesis that we are currently testing.

Overall, these results reveal that dense grass cover is not an absolute barrier for recruitment, consistent with observations of concentrations of small seedlings in many remnant savanna with perennial grass understories (Pellatt et al. 2007). It is also consistent with historical records describing a massive pulse in oak recruitment occurring in the mid- to late-1800s that coincided with the onset of grass invasion on Vancouver Island (Gedalof et al. 2006). Our findings may reflect the absence of annual exotic grasses, which are known to suppress oak recruitment elsewhere by the rapid uptake of soil moisture in early spring (Koukoura and Menke 1995, Gordon and Rice 2000). They may also reflect the functional similarity between the exotic perennial grasses that presently dominate vs. the native perennial grasses that they presumably replaced (MacDougall and Turkington 2004), suggesting that grass suppression of oak seedlings is not strictly a contemporary phenomenon. The suppressive effect of the grasses may have been more pronounced if we planted acorns instead of seedlings, although recent work has shown that seedling establishment from *Q. garryana* acorns is not significantly limited by vegetation cover possibly due to the

large carbohydrate reserves stored in the acorn (Gonzales and Arcese 2008).

Increases in limiting resources have been observed to strongly impact producers in many systems, either directly by stimulating growth (Stevens et al. 2004, Clark and Tilman 2007, Hautier et al. 2009) or indirectly by reducing the impacts of consumers (Chase et al. 2000, Huston 2004, Hillebrand et al. 2007). Here, the net effect of watering on seedling performance was relatively weak compared to herbivory and grass cover. Watering did modify the intensity of small-mammal impacts by reducing mortality, while increasing the likelihood of moderate insect damage on unbrowsed seedlings. In the absence of grass cover, however, watering had no effect on seedling performance regardless of whether small mammals were present. One explanation may derive from the almost complete discordance between the timing of seedling herbivory (mostly winter) and when the effects of moisture increases are most likely to affect leaf production and palatability (summer). As well, many generalizations on consumer–resource linkages in terrestrial systems are based on the impacts of large-mammal effects, which are absent here (Bakker et al. 2006, 2009). Overall, it appears that precipitation increases in the summer could be important for improving seedling performance in the grass swards, but insufficient for successful recruitment given the overriding influence of consumers.

Our results clarify how the stand structure of an increasing number of oak species may develop, with many adults and numerous seedlings but few or no juveniles reaching the sapling stage. The most powerful factor was small nonnative mammals, which killed seedlings directly via browsing, and indirectly by switching grass competition and moisture limitation from suppressive to lethal. None of the factors that we tested were necessarily absolute recruitment barriers; many seedlings recovered from herbivore damage, grass suppression reduced growth but did not directly cause mortality, and watering reduced suppression but also increased the likelihood of moderate levels of insect damage. In combination, however, these factors are preventing seedlings from reaching the sapling stage and beyond. As has been observed in forests of eastern North America (Rooney and Waller 2003), consumer-based limitations in our study system appear likely to shape the future trajectory of stand development, affecting both *Q. garryana* and the obligate species that depend on it.

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