SEEDLING ECOLOGY OF GARRY OAKS IN BRITISH COLUMBIA AND DISPERSAL OF GARRY OAK ACORNS BY STELLER'S JAYS

by

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Abstract

Garry oak (*Quercus garryana*) ecosystems are endangered in southern British Columbia and their management requires approaches that ensure adequate oak regeneration. Garry oak acorns are dispersed in B.C. primarily by Steller’s Jays (*Cyanocitta stelleri*) and therefore regeneration must be considered within the context of where and how acorns are dispersed by jays. I planted acorns at different depths and in different habitats to examine factors influencing survival of acorns and seedlings. Depending on habitat type, predators removed 53-100% of acorns that were planted on the surface but 10-92% of acorns buried in ground cover or soil. Predation on buried acorns was extremely high in all habitats with sparse herb, dense shrub, and moderate to high tree cover. Of the acorns that were not predated, >83% of buried acorns produced seedlings, but, perhaps because of desiccation, only <60% of acorns on the surface produced seedlings in most habitats. In most habitats, >65% of first-year seedlings survived to their second year. Some habitats that had high seedling emergence had relatively low seedling survival and *vice versa*. Many seedlings died from desiccation in habitats with thin soil on a south-facing slope.

I observed caching of acorns by Steller’s Jays to investigate the role of the jays in dispersal of Garry oaks. Steller’s Jays cached acorns between a few centimetres to at least 600 m from harvesting locations, and probably transported some acorns more than 1 km. Almost all cached acorns were hidden within ground cover or soil. Steller’s Jays preferred to cache acorns in habitats with extensive tree and shrub cover but sparse herb cover. Jays cached approximately one half of their acorns in these habitats, where seedling establishment is low because of high rates of acorn predation and sapling recruitment is likely poor because of shade from dense trees and shrubs. However, half of their acorns were cached in other habitats, some of which provide
conditions favourable for oak regeneration. Conservation of Garry oak ecosystems in B.C. must include retention of ecological processes and management at both the stand and landscape levels.
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Chapter 1: General Introduction

Garry oak is a dominant tree in 5 imperiled or critically imperiled plant communities of British Columbia (B.C. Conservation Data Centre Tracking List, unpublished). These plant communities host approximately 75 species of endangered, threatened, or vulnerable plants (12.5% of all such plants in British Columbia) and thus are important to the biodiversity of the province (Erickson 1996). Garry oak ecosystems in British Columbia have been reduced in area and fragmented by agricultural and urban development. Urbanization and invasions of exotic plant species continue to place these ecosystems at increasing risk (Roemer 1972, Meidinger and Pojar 1991, Erickson 1996, Ussery 1997).

Conservation of Garry oak ecosystems requires an understanding of ecological processes so that effective approaches to management can be developed. The ecology of Garry oak, although poorly understood, is critical to address concerns about inadequate regeneration of Garry oak on southeastern Vancouver Island (Erickson 1996). Lack of information about the reproductive ecology of Garry oaks has resulted in various “best guess” prescriptions to promote regeneration, and occasional disagreement among managers (pers. obs.).

The objective of my study is to investigate seedling ecology and dispersal of Garry oaks in British Columbia. Acorns of Garry oaks are dispersed in B.C. primarily by Steller’s Jays, and therefore regeneration of Garry oaks must be considered within the context of where and how acorns are dispersed by jays. In Chapter 2, I examine factors that influence survival of acorns and seedlings. I planted acorns in an experiment designed to assess mortality of oaks in relation to planting depth, habitat type, and vegetation cover. In Chapter 3, I integrate these results with the behaviour of Steller’s Jays to investigate the role of jays in dispersal of Garry oaks. I observed Steller’s Jays collecting, transporting, and caching acorns. To determine the consequences of this behaviour on Garry oak ecosystems, I compared the suitability for oak
regeneration of burial depths and habitats used by jays for caching acorns with the suitability of other burial depths and habitats. In Chapter 4, I provide recommendations for management of Garry oaks on southeastern Vancouver Island.

My study is limited to an investigation of reproduction of Garry oaks by seed. Garry oaks can also reproduce vegetatively by sprouting from rhizomes or from dormant buds along the trunk or root collar, especially following damage or death of the shoot from fire or other disturbances (Sugihara and Reed 1987, Agee 1993). Garry oaks in the Bald Hills of Redwood National Park originated primarily from vegetative reproduction (Sugihara and Reed 1987), but the relative importance of reproduction from seeds and sprouts throughout a range of environmental conditions is unknown (Agee 1993). Acorn dispersal plays a critical role in the reproduction of many species of oaks at the landscape level. Resprouting can account only for within-stand regeneration, but seeds are required for movement of offspring away from parents. My study contributes to our understanding of the reproduction of Garry oaks by seed.
Chapter 2: Seedling Ecology of Garry Oaks in British Columbia

Abstract

Regeneration of Garry oaks (*Quercus garryana*) may be inadequate to sustain oak populations. Processes that mediate oak regeneration can be influenced by where acorn-hoarding animals take acorns and how deep the acorns are buried at these hoarding sites. I planted acorns to determine the role of habitat type and burial depth on emergence and first-year survival of Garry oak seedlings. In all habitats that I examined, vertebrates removed > 53 % of acorns placed on the ground surface. However, in approximately one half of the habitats, vertebrates removed < 49 % of acorns buried in the ground cover or soil. Predation on buried acorns was high in habitats with sparse herb, dense shrub, and moderate to high tree cover. Predation on buried acorns was low in habitats with various structural characteristics, including those with dense herb cover and sparse shrub or tree cover. The mortality rate of buried acorns that were not removed by predators was low (< 17 %) in all but one habitat. Perhaps because of desiccation, the mortality rate of surface acorns was > 40 % in all but one habitat. Regardless of burial depth, once seedlings emerged, seedling survival was > 65 % in most habitats. Some habitats with high seedling emergence had relatively low seedling survival, and *vice versa*. In habitats on a south-facing slope, characterized by rocky outcrops and absence of conifers, many seedlings died from desiccation. Other seedling mortality may have been caused by shoot browsing, root browsing, or insect herbivory. Seedling survival was not related to percent cover of overstorey vegetation, indicating that first-year Garry oak seedlings were not protected by shade and can survive in habitats with limited light.
Introduction

Regeneration of oaks (Quercus spp.) is a common problem at a wide range of locations throughout the world (Muick and Bartolome 1987, Lorimer et al. 1994, Herrera 1995, Ziegenhagen and Kausch 1995). Studies have examined the effects of predation, herbivory, competition, water and heat stress, and shading on survival and germination of acorns as well as survival and growth of seedlings (e.g. Plumb and Pillsbury 1987, Standiford 1991). Results of these studies vary depending upon oak species, acorn burial depth, site (geographical location, slope, aspect), and year (weather, populations of acorn predators and herbivores).

Most studies have approached the issue of oak regeneration from the perspective of within-stand replacement, yet this is only part of the process. Oaks rely upon food-hoarding animals, particularly squirrels and jays (Vander Wall 1990), for acorn dispersal. These animals bury acorns as a future food reserve, but may not recover all of the acorns that they bury, thereby effectively “planting” the acorns at hoarding locations. This type of dispersal has the potential to concentrate seeds in particular habitats, which may be within, adjacent to, or far from oak stands. Studies have examined factors related to oak regeneration in different microhabitats within stands (Griffin 1971, Coblentz 1980, Muick and Bartolome 1987, Kikuzawa 1988, Borchert et al. 1989, Barnhardt et al. 1991, Davis et al. 1991, Crow 1992, Lorimer et al. 1994, Hubbard 1995, Ashton and Larson 1996, Erickson 1996) and in a few selected habitats adjacent to stands (Kikuzawa 1988, Williams et al. 1991, Crawley and Long 1995, Herrera 1995, Hubbard 1995). However, none have examined a wide variety of habitat types representing the potential range of acorn dispersal sites.

I investigated regeneration of Garry oaks (Quercus garryana) within a variety of habitats on southern Vancouver Island, British Columbia. The Garry oak is the only native oak in B.C. Urban development and invasions of exotic plant species pose serious threats to Garry oak ecosystems (Roemer 1972, Meidinger and Pojar 1991, Erickson 1996, Ussery 1997). Dramatic
changes to Garry oak ecosystems have also occurred as a result of fire exclusion in British Columbia and throughout most of the range of Garry oaks (Thilenius 1968, Norton 1979, Barnhardt et al. 1987, Reed and Sugihara 1987, Sugihara and Reed 1987, Turner 1991, Riegel et al. 1992, Agee 1993, Erickson 1996, Ussery 1997, Hastings et al. in press). These changes in the extent, species composition, vegetation structure, and disturbance regimes of Garry oak ecosystems can alter recruitment patterns, and there is growing concern about the adequacy of regeneration of Garry oaks in British Columbia (Erickson 1996). On southeastern Vancouver Island, Steller’s Jays (Cyanocitta stelleri) have historically been the primary agents that disperse acorns. Eastern gray squirrels (Sciurus carolinensis), which were introduced to the region in the 1960’s and have since increased in number (Bennett 1993), now also disperse acorns.

My objectives are to determine the effects of acorn burial depth and habitat on Garry oak regeneration. Both factors are influenced by food-hoarding animals, and have the potential to play important roles in Garry oak reproduction. My study investigates the role of acorn burial depth and habitat on acorn and seedling mortality, and examines the cumulative effects of mortality processes on reproductive success of Garry oaks.

**Study Species**

Garry oaks range from southern British Columbia to southern California, reaching their greatest height (about 30 m) in Oregon and southwestern Washington (Silen 1958). Within B.C., Garry oaks are found from Courtenay south along the eastern edge of Vancouver Island, on the Gulf Islands, and at 2 disjunct stands in the Fraser Valley (Stein 1990). Garry oaks grow on various sites and soil types, and can tolerate both flooding and drought (Stein 1990).

Garry oaks are monoecious and produce separate male and female flowers in spring. The acorns mature over summer (Stein 1990) and in B.C. drop primarily in September and early October (pers. obs.). Garry oak, like all other species of its genus, is a mast seeder, and produces
highly variable acorn yields among years and among trees (unpubl. data). Garry oak is a member of the subgenus *Lepidobalanus*; hence, its acorns are not dormant and usually germinate within weeks of falling if they retain sufficient moisture (Stein 1990). The seedlings rapidly develop deep taproots (Stein 1990), but shoots do not emerge until spring or early summer of the following year (Stein 1990, pers. obs.). Young oak seedlings depend upon reserves stored in the cotyledons for early growth (Crow 1988). Dormant buds on the root collar of Garry oak seedlings can sprout in response to browsing, stem die-back, or other causes (Hibbs and Yoder 1993).

**Study Area**

My research was conducted in Metchosin (48°23'N, 123°32'W) on the southern tip of Vancouver Island, British Columbia. Metchosin is in the Coastal Douglas-fir biogeoclimatic zone, with mild wet winters and warm dry summers (Meidinger and Pojar 1991). Although frost occurs in 9 months of the year, no month has an average daily minimum temperature below freezing (Environment Canada climate summary, William Head station). Mean monthly precipitation ranges from a high of more than 140 mm in December and January, primarily in the form of rain, to a low of 16 mm in July. Drought conditions prevail from June through August but may also extend into May and September.

Two sites were used, Mary Hill and Rocky Point, about 2 km apart. The study was conducted within approximately 10 ha at each site. Each site is a mosaic of patches of different habitat types. Most of Mary Hill is a south-facing slope. Much of the site has thin soil and prominent rocky outcrops. Introduced Scotch broom (*Cytisus scoparius*) shrubs are common. Dominant tree species include Garry oak, Douglas-fir (*Pseudotsuga menziesii*), and arbutus (*Arbutus menziesii*). The oak cover is primarily in savanna form, with individual trees having large rounded crowns and growing within a rocky, grass- and shrub-covered matrix.
The site at Rocky Point is relatively flat, and has rocky outcrops as well as areas with deeper soil. The most common tree species are Garry oak, Douglas-fir, grand fir (*Abies grandis*), and shore pine (*Pinus contorta*). Most of the oaks comprise a woodland (approx. 300-450 stems/ha; Chatwin 1997, unpubl. data), with narrow crowns concentrated in the upper stratum. Patches of Scotch broom are present in a large meadow. Red alder (*Alnus rubra*), willow (*Salix spp.*), Pacific ninebark (*Physocarpus capitatus*) and ocean spray (*Holodiscus discolor*) dominate wet areas.

**Methods**

**Experimental Design**

Acorns were planted in a split-plot, completely randomized design to test the effects of habitat and burial depth on acorn and seedling mortality (Fig. 2.1). Planting plots consisting of 30 acorns each were established in 7 habitat types at Mary Hill and 8 habitat types at Rocky Point. I used 6 replicates of each habitat type at each site, for a total of 42 plots at Mary Hill and 48 at Rocky Point. Three different planting depths were nested within the plots: on the surface, under the ground cover (leaf litter, matted grass roots, moss, or lichens), and buried in soil just below the surface of the soil. These depths include those that acorns attain when they fall from the trees, and those attained by acorns buried by Steller's Jays (Chapter 3). Ten acorns were planted on their sides at each planting depth within each plot. Planting depth was randomly assigned to each of the 30 positions within each plot. Planting positions were 0.5 m apart in 2 parallel rows which were 0.5 m apart. A total of 2700 acorns was planted.

Habitat types tested in the experiment were among the most common habitats at the sites, as well as those most frequently used by Steller's Jays for hoarding acorns (Chapter 3). At Mary Hill, these were: conifer canopy (CC), conifer edge (CE), herb (under grass cover; HB), oak canopy (OC), oak edge (OE), shrub (under broom cover; SB), and small dense clumps of
Figure 2.1. Locations of acorn planting plots in different habitat types at a) Mary Hill and b) Rocky Point in Metchosin, B.C. (•, conifer canopy; ©, conifer edge; V, conifer sapling patch; °, herb; *, oak canopy; +, oak edge; 0, riparian; x, shrub; -, small clump). At each plot (c), acorns were planted on the surface, below the ground cover, and in the soil.
mixed cover (usually oak and arbutus trees, Douglas-fir saplings or trees, and often with a shrub component; SC). Habitat types at Rocky Point were: CC, CE, HB, OC, OE, SB, conifer sapling patches under oak canopy (CS), and riparian (seasonally wet; RP). Canopy and edge plots (CC, CE, OC, OE) were established on sites that had a minimum of shrub growth, although low-hanging foliage of the trees often contributed to shrub-layer cover, particularly in the edge plots. I selected patches of representative habitat, incorporating a representative range of variation within each habitat type. Plot choice and orientation were limited by the size, shape, and number of such patches. Plots in different habitat types were interspersed as much as possible within the distribution of habitat patches at the study sites.

Habitat Description

I visually estimated vegetation cover within a 5-m radius from the center of each planting plot to quantify the vegetation structure of the habitat types. Although the planting plots were rectangular, a circular area was used for visual estimation to ensure consistency with another aspect of a larger study (Chapter 3). Total percent cover was estimated for 3 vegetation layers: herb (0 to 1 m high), shrub (> 1 to 5 m high) and tree (> 5 m high). I used the protocol developed by the B.C. Ministries of Environment and Forests (Luttmerding et al. 1990), which estimates the area of the ground encircled by a vertical projection of the crown edge.

Acorn Planting

Acorns were collected for the planting experiment during two weeks beginning 19 September 1994. They were gathered from the ground beneath approximately two dozen highly productive oak trees scattered throughout the sites. Acorns with insect emergence holes or that were small, spotted, desiccated, cracked, or otherwise blemished were discarded (McCreary no date). The remaining acorns were placed in a tub of water and “floaters” were discarded because
“floaters” have a high probability of being desiccated or insect infested (McCreary *no date*).

Acorns from all collections were combined and initially stored damp in plastic bags at room temperature (McCreary *no date*). I noticed fungus growing on the acorns in late September and on 30 September transferred them to cold storage at the Pacific Forestry Centre.

I planted acorns between 10 and 17 October 1994. Removable strings marked at 0.5 m intervals were stretched between stakes designating the ends of the rows. I hung a plumb bob at each mark and planted an acorn below the tip. A few of the acorns had germinated and had radicles up to a few mm long when they were planted. To control for effects of weather variation, each site was visited on alternate days. In addition, I planted one replicate of each habitat type before starting the next set of replicates.

**Data Collection**

Plots were revisited in June 1995 and 1996. Strings were again stretched between the stakes and the position below each 0.5 m mark was searched. In 1995, I determined if a seedling (defined as an acorn that had developed at least 1 shoot) was present or absent. If a seedling was absent, I determined if the acorn was present or absent. I assumed that absence indicated predation. If the acorn was present, I noted whether it had germinated, and if it exhibited presence or absence of damage. If a seedling was present, I noted the presence or absence of damage. Shoots of many desiccated seedlings were dead, but because oaks have the capacity to resprout, I did not disturb the roots of these seedlings. In 1996, I omitted acorn information and checked the roots of those seedlings with dead or absent shoots to determine if the seedling was alive. Twelve percent of all planted acorns produced multiple seedlings, each having separate cotyledons, roots, and shoots. I considered seedlings originating from the same acorn a single seedling for the purposes of my study. A multiple seedling was considered alive if at least one of the individuals survived and damaged if damage was evident on at least one of the individuals.
Data Analysis

Because of differences in habitat types between sites, all data were analyzed separately for each site. Statistical significance is reported at the 95 percent confidence level.

Data regarding acorn predation were analyzed in an ANOVA, with habitat and depth as the two treatment factors. Values were calculated as proportions and arcsine square root transformed to improve normality (Zar 1984). Variation among replicate plots was used as the error term for habitat. The interaction between replicate plots and depths within habitats was used for testing the interaction between habitats and depths and for testing the effect of depth. The interaction between habitats and depths was significant at Rocky Point, so depth analyses were subsequently conducted separately for each habitat type, and habitat analyses were performed within each depth. Separate analyses within depths and within habitats were also conducted at Mary Hill to facilitate comparison between the two sites.

Because all 3 planting depths were used within each planting plot, I used a randomized complete block model to test depth within habitats. Significant F-tests were followed by multiple comparisons of means with sequential Bonferroni adjustments based on the number of comparisons within each habitat at each site (Rice 1989). I used one-way ANOVA to test habitat effects, and multiple comparisons of habitat types were performed with Tukey’s honestly significant difference tests, which are more powerful than the Bonferroni method when comparing a large number of means (SPSS 1997a). Spearman rank correlations were used to investigate relationships between acorn predation and vegetation cover. This non-parametric method was used because it relies on few assumptions regarding data distributions (Zar 1984). The mean values for each habitat type comprised the data for these correlations. I used sequential Bonferroni adjustments based on the number of comparisons within each site.

To assess the implications of habitat and depth on acorn mortality due to factors other than predation, I calculated percent mortality of planted acorns that were still present in June
1995. Percentages were calculated for each replicate habitat-depth combination, and averaged among replicate plots. In some cases, too few acorns escaped predation to properly assess subsequent acorn mortality. Hence, I analyzed only habitat-depth combinations that had a minimum of 9 acorns remaining in a minimum of 3 different plots. Because the number of acorns and plots varied widely among depths and habitats, statistical comparisons were not conducted.

Wide variation in the number of replicates with emerged seedlings at Rocky Point (from 2 to 6) precluded statistical comparison of the effect of habitat type on seedling mortality. Inspection of the data indicated that first-year seedling mortality was similar across habitats at this site. Statistical analysis was possible for Mary Hill because there were at least 5 replicates with emerged seedlings per habitat. I used one-way ANOVA to analyze the effect of habitat on mortality of seedlings at Mary Hill. Because many of the plots had few or no emerged seedlings at one or more depths, all depths were combined for this analysis; the impact of initial planting depth is probably minimal due to the rapid taproot growth during the seedlings' first winter.

Data were calculated as proportions and arcsine squareroot transformed. To balance the design, I randomly selected 5 replicates from those habitats that had 6 plots with emerged seedlings. I used Tukey's honestly significant difference to compare overall mortality among habitats. Spearman rank correlations with sequential Bonferroni adjustments were used to investigate the relationships between seedling desiccation and vegetation cover and between seedling mortality from undetermined causes and vegetation cover.

Finally, I assessed the cumulative effects of all mortality factors on both acorns and seedlings for different depths and habitats. I used bar graphs of seedling abundance, calculated as the mean percent of planted acorns, to assess seedling production after one year and after two years for each treatment combination.
Results

Acorn Predation

Planting Depth

Planting depth affected the number of acorns removed from the plots by predators, but results varied between sites and among habitats (Fig. 2.2, Tables 2.1-2.3). Variability among plots was high in most habitats, especially for acorns planted in the ground cover and the soil. Effects of planting depth were most pronounced at Mary Hill, where deeper planting resulted in significantly lower predation across habitat types (Fig. 2.2, Tables 2.1 and 2.3). At Mary Hill, more differences among depths were evident than at Rocky Point when habitats were analyzed separately (Table 2.3). Predation was extremely high for acorns planted on the surface at Mary Hill, exceeding 74% in all habitats, and reaching 100% in conifer canopy plots (Fig. 2.2). Predation of buried acorns at Mary Hill ranged between 27 (oak edge, soil) and 88% (conifer canopy, ground cover; Fig. 2.2).

Surface acorns also suffered high predation in all habitats at Rocky Point (53 to 97%; Fig. 2.2). No significant differences were found among planting depths in 3 of the habitats (Table 2.2). These were the 3 habitats with the highest overall predation (shrub, conifer sapling, and riparian). Surface acorns had significantly higher predation than those planted in the ground cover in all of the remaining habitats except conifer canopy and oak edge (Table 2.3), where relatively high variability (Fig. 2.2) may have obscured differences between means. In 6 out of the 8 habitat types, predation of ground cover acorns was higher than that of soil acorns, but none of the differences were significant. Between 10 (herb, soil) and 92% (conifer sapling and riparian, ground cover; Fig. 2.2) of buried acorns were lost to predators.
Figure 2.2. Effects of habitat type and planting depth on predation of Garry oak acorns at two sites in Metchosin, B.C. N = 6 replicates for each habitat type. Ten acorns were planted in each replicate habitat-depth combination. Habitat types are: HB = herb; OC = oak canopy; SB = shrub; CE = conifer edge; OE = oak edge; CC = conifer canopy; SC = small dense clumps, usually of oak, conifer saplings, and arbutus; CS = conifer sapling patch within the oak stand; RP = riparian. Planting depths are: surface (on top of ground cover), ground cover (under leaf litter, grass roots, moss, lichens), and soil (just below soil surface). Habitat types at Mary Hill are displayed in order of decreasing area of ground surface covered with vegetation in the herb layer. Habitat types at Rocky Point are displayed in order of decreasing area of ground surface covered with vegetation in the herb layer with minor exceptions (differences of 2.5% or less). ND designates no data because the habitat type was not present at the site.
Table 2.1. Split-plot ANOVA table of the effects of habitat and planting depth on predation of Garry oak acorns at two sites in Metchosin, B.C. N = 6 replicates for each habitat type. Ten acorns were planted in each replicate habitat-depth combination. Values were calculated as proportions and arcsine squareroot transformed before analysis.

<table>
<thead>
<tr>
<th>Site</th>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mary Hill</td>
<td>Habitat</td>
<td>5.55</td>
<td>6</td>
<td>0.93</td>
<td>5.47</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td>Between plot error</td>
<td>5.91</td>
<td>35</td>
<td>0.17</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Depth</td>
<td>8.69</td>
<td>2</td>
<td>4.34</td>
<td>90.72</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td>Habitat x Depth</td>
<td>0.40</td>
<td>12</td>
<td>0.03</td>
<td>0.69</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>Within plot error</td>
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<td>70</td>
<td>0.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>23.90</td>
<td>125</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rocky Point</td>
<td>Habitat</td>
<td>17.67</td>
<td>7</td>
<td>2.52</td>
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<tr>
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<td>Depth</td>
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<td>2.62</td>
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<td>Habitat x Depth</td>
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<td>0.02</td>
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<tr>
<td></td>
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<td>80</td>
<td>0.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>37.07</td>
<td>143</td>
<td></td>
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<td></td>
</tr>
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</table>
Table 2.2. Randomized complete block ANOVA results for the effect of planting depth on predation of Garry oak acorns in different habitats at Rocky Point in Metchosin, B.C. N = 6 replicates for each habitat type. Ten acorns were planted in each replicate habitat-depth combination. Values were calculated as proportions and arcsine square root transformed before analysis.

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
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<td>Herb</td>
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<td>2</td>
<td>1.16</td>
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<tr>
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</tr>
<tr>
<td></td>
<td>Error</td>
<td>0.49</td>
<td>10</td>
<td>0.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oak canopy</td>
<td>Depth</td>
<td>1.50</td>
<td>2</td>
<td>0.75</td>
<td>13.15</td>
<td>&lt;0.01</td>
</tr>
<tr>
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<td>Block</td>
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<td>0.16</td>
</tr>
<tr>
<td></td>
<td>Error</td>
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<td>10</td>
<td>0.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrub</td>
<td>Depth</td>
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<td>2</td>
<td>0.04</td>
<td>0.76</td>
<td>0.50</td>
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<td>4.21</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>0.51</td>
<td>10</td>
<td>0.05</td>
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<td></td>
</tr>
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</tr>
<tr>
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<td>0.11</td>
<td></td>
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<tr>
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<td>Error</td>
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<td>10</td>
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<tr>
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<td>Error</td>
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<td>10</td>
<td>0.06</td>
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<td></td>
</tr>
<tr>
<td>Conifer sapling</td>
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<td>0.21</td>
<td>2</td>
<td>0.11</td>
<td>1.51</td>
<td>0.27</td>
</tr>
<tr>
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<td>0.15</td>
<td>2.06</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>0.70</td>
<td>10</td>
<td>0.07</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Riparian</td>
<td>Depth</td>
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<td>0.06</td>
<td>2.11</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>Block</td>
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<td>5</td>
<td>0.12</td>
<td>4.20</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>0.29</td>
<td>10</td>
<td>0.03</td>
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</tr>
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</table>
Table 2.3. Multiple comparisons of the effect of planting depth on predation of Garry oak acorns at two sites in Metchosin, B.C. N = 6 replicates for each habitat type. Ten acorns were planted in each replicate habitat-depth combination. Values were calculated as proportions and arcsine square root transformed before analysis. Comparisons were not conducted for conifer sapling, riparian, or shrub habitats at Rocky Point because of insignificant F-tests. Asterisks denote statistical significance (P < 0.05 with sequential Bonferroni adjustments based on the number of comparisons within each habitat at each site). ND designates no data because the habitat type was not present at the site.

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Comparison</th>
<th>Surface - Soil</th>
<th>Surface - Ground cover</th>
<th>Ground cover - Soil</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mary Hill</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All combined</td>
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<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Herb</td>
<td>*</td>
<td>*</td>
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<td></td>
</tr>
<tr>
<td>Oak canopy</td>
<td>*</td>
<td>*</td>
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</tr>
<tr>
<td>Shrub</td>
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<tr>
<td>Conifer edge</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Oak edge</td>
<td>*</td>
<td>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conifer canopy</td>
<td>*</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Small clump</td>
<td>*</td>
<td>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conifer sapling</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Riparian</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Rocky Point</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herb</td>
<td>*</td>
<td>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oak canopy</td>
<td>*</td>
<td>*</td>
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<td></td>
</tr>
<tr>
<td>Shrub</td>
<td>*</td>
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<td>Conifer edge</td>
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<td>Oak edge</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Small clump</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Conifer sapling</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Riparian</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
</tbody>
</table>
Habitat

Predation varied among habitat types, with trends differing between sites and among depths (Fig. 2.2, Tables 2.1, 2.4, and 2.5). Differences among habitats were more pronounced at Rocky Point than at Mary Hill, and were greatest for acorns planted in the ground cover (Fig. 2.2, Table 2.5). Differences among habitats for acorns planted on the surface were small in magnitude. The three habitat types present in only one of the two sites (small clumps, conifer sapling, and riparian) had consistently high predation. These habitats are highly preferred by Steller’s Jays (Chapter 3). Predation was also high in conifer canopy habitat at Mary Hill and in shrub habitat at Rocky Point. At both sites, herb habitat was among those with the lowest predation. Oak edge and oak canopy habitats at Mary Hill and conifer edge habitat at Rocky Point also had relatively low predation.

I found no significant correlations at Mary Hill between predation and vegetation cover (Table 2.6). Predation of Rocky Point acorns planted in the ground cover layer was negatively correlated with herb cover. There were no significant correlations with cover in the shrub or tree layers. At both sites, habitats preferred by jays had low herb, high shrub, and moderate to high tree cover (small clump, conifer sapling, and riparian; Fig. 2.3), and these had among the highest predation levels. Structural characteristics of other habitats with high predation (conifer canopy at Mary Hill; shrub at Rocky Point) varied. Habitats with the lowest predation (herb, oak edge, and oak canopy at Mary Hill; herb and conifer edge at Rocky Point) tended to have high herb and low to moderate shrub cover, but structure varied considerably.

Other Acorn Mortality

Planting depth had a considerable effect upon mortality of acorns that were not removed by predators (Figs. 2.4 and 2.5). At Mary Hill, mortality of acorns planted on the surface was between 64 and 75% across habitats (Fig. 2.4). Mortality of surface acorns at Rocky Point was
Table 2.4. One-way ANOVA table of the effect of habitat type on predation of Garry oak acorns planted at different depths at Rocky Point in Metchosin, B.C. N = 6 replicates for each habitat type. Ten acorns were planted in each replicate habitat-depth combination. Values were calculated as proportions and arcsine square root transformed before analysis.

<table>
<thead>
<tr>
<th>Depth</th>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface</td>
<td>Habitat</td>
<td>2.64</td>
<td>7</td>
<td>0.38</td>
<td>4.61</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>3.26</td>
<td>40</td>
<td>0.08</td>
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<td></td>
</tr>
<tr>
<td>Ground cover</td>
<td>Habitat</td>
<td>9.32</td>
<td>7</td>
<td>1.33</td>
<td>15.45</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>3.45</td>
<td>40</td>
<td>0.09</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil</td>
<td>Habitat</td>
<td>7.43</td>
<td>7</td>
<td>1.06</td>
<td>7.41</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>5.73</td>
<td>40</td>
<td>0.14</td>
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</tr>
</tbody>
</table>
Table 2.5. Tukey's honestly significant differences tests for the effect of habitat type on predation of Garry oak acorns planted at different depths at two sites in Metchosin, B.C. N = 6 replicates for each habitat type. Ten acorns were planted in each replicate habitat-depth combination. Values were calculated as proportions and arcsine square root transformed before analysis. Habitat types are as in Fig. 2.2.

<table>
<thead>
<tr>
<th>Depth</th>
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<th></th>
<th>Rocky Point</th>
<th></th>
<th></th>
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</tr>
</thead>
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<td>Subset 1</td>
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<td>Subset 3</td>
<td>Subset 1</td>
<td>Subset 2</td>
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<td>OC</td>
<td>OE</td>
<td>HB</td>
<td>CE</td>
<td>SC</td>
<td>SB</td>
</tr>
<tr>
<td>Surface</td>
<td>HB</td>
<td>OC</td>
<td>OE</td>
<td>CE</td>
<td>SC</td>
<td>SB</td>
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<td>Ground Cover</td>
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<td>HB</td>
<td>CE</td>
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<td>OC</td>
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<td>HB</td>
<td>CE</td>
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<td>OE</td>
<td>OC</td>
<td>CC</td>
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<td>OC</td>
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<td>CC</td>
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Table 2.6. Spearman’s rank correlations between percent predation of acorns planted at different depths and percent vegetation cover at two sites in Metchosin, B.C. Percent cover in the herb (0 to 1 m high), shrub (> 1 to 5 m high) and tree (> 5 m high) layers was estimated for a 5-m radius circle centred on the midpoint of each planting plot. N = 7 at Mary Hill and n = 8 at Rocky Point. Asterisk denotes statistical significance (P < 0.05 with sequential Bonferroni adjustments based on the number of comparisons within each site).

<table>
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<th>Ground cover</th>
<th>Soil</th>
</tr>
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<td>-0.54</td>
<td>-0.57</td>
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<tr>
<td></td>
<td>Shrub</td>
<td>0.22</td>
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<td>0.38</td>
<td>0.32</td>
<td>0.25</td>
</tr>
<tr>
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<td>Herb</td>
<td>-0.82</td>
<td>-0.93*</td>
<td>-0.85</td>
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<td>Shrub</td>
<td>0.61</td>
<td>0.76</td>
<td>0.76</td>
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<tr>
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<td>Tree</td>
<td>0.47</td>
<td>0.47</td>
<td>0.29</td>
</tr>
</tbody>
</table>
Figure 2.3. Percent cover of vegetation for planting plots in different habitat types at two sites in Metchosin, B.C. Percent cover in the herb (0 to 1 m high), shrub (> 1 to 5 m high) and tree (> 5 m high) layers was estimated for a 5-m radius circle centred on the midpoint of each planting plot. N = 6 replicates for each habitat type. Habitat types are as in Fig. 2.2. ND designates no data because the habitat type was not present at the site.
Figure 2.4. Effects of habitat type and planting depth on mortality of Garry oak acorns planted at different depths at Mary Hill in Metchosin, B.C. Percentages are based on the total number of planted acorns that were not removed by predators. Habitat-depth combinations are displayed only if there was a minimum of 9 acorns in at least 3 plots. Numbers of acorns and plots are: surface: 15,4 (HB), 10,5 (OC), 10,4 (OE); ground cover: 34,6 (HB), 36,6 (OC), 11,4 (SB), 31,5 (CE), 37,6 (OE), 9,5 (SC); soil: 42,6 (HB), 43,6 (OC), 28,6 (SB), 35,6 (CE), 44,6 (OE), 22,4 (CC), 19,5 (SC). Mortality categories indicate whether or not acorns had germinated before they died. Habitat types are as in Fig. 2.2. ND designates no data because sample size was insufficient or because the habitat type was not present at the site.
Figure 2.5. Effects of habitat type and planting depth on mortality of Garry oak acorns planted at different depths at Rocky Point in Metchosin, B.C. Percentages are based on the total number of planted acorns that were not removed by predators. Habitat-depth combinations are displayed only if there was a minimum of 9 acorns in at least 3 plots. Numbers of acorns and plots are: surface: 21.6 (HB), 28.5 (CE), 15.5 (OE), 9.4 (CC); ground cover: 56.6 (HB), 23.6 (OC), 53.6 (CE), 31.6 (OE), 22.4 (CC); soil: 54.6 (HB), 31.6 (OC), 11.3 (SB), 49.6 (CE), 38.6 (OE), 31.6 (CC), 12.3 (CS). Mortality categories indicate whether or not acorns had germinated before they died. Habitat types are as in Fig. 2.2. ND designates no data because sample size was insufficient or because the habitat type was not present at the site.
more variable, ranging from 25 % in conifer canopy habitat to 93 % in herb habitat (Fig. 2.5). In
contrast, mortality of buried acorns (beneath ground cover and in soil) was < 17 % in all habitats
at both sites, except in oak edge habitat at Rocky Point, where acorn mortality was 36 and 52 %
for acorns planted in the ground cover and soil respectively (Figs. 2.4 and 2.5). Causes of acorn
mortality were difficult to determine. A few acorns had emergence holes from larvae of
Curculio occidentalis or Melissopus latiferreanus, which feed on acorns and often cause seed
mortality (Stein 1990). Many of the acorns germinated before they died, although the small
proportion of acorns that germinated before planting must be considered when interpreting the
data (Figs. 2.4 and 2.5). Radicles of most of the germinated acorns did not exceed 1 or 2
centimetres in length.

Seedling Mortality

Seedling mortality between emergence in 1995 and June 1996 was consistently low at
Rocky Point, ranging from 0 % in riparian to 17 % in conifer canopy habitat (Fig. 2.6).
Mortality was more variable across habitats at Mary Hill (Fig. 2.6, Tables 2.7 and 2.8), and
contrasted markedly with levels of acorn predation. Conifer canopy habitat had the lowest
seedling mortality (4 %; Fig. 2.6, Table 2.7) but the highest predation on acorns (Fig. 2.2, Table
2.5). Oak edge and oak canopy habitats had the highest seedling mortality (70 % and 44 %
respectively; Fig. 2.6, Table 2.7) but the lowest predation on acorns (Fig. 2.2, Table 2.5).

Seedling desiccation was an important mortality factor in some habitats at Mary Hill
(Fig. 2.6). It had the most severe effect in oak edge plots, killing 58 % of the seedlings and
accounting for 83 % of all seedling mortality. Seedling desiccation was also evident in shrub,
oak canopy, and herb plots. Percent desiccation neither increased nor decreased with increasing
vegetation cover (Table 2.9), but the 4 habitats with substantial levels of seedling desiccation are
Figure 2.6. Mortality of seedlings from Garry oak acorns planted in 1994 at two sites in Metchosin, B.C. Percentages are out of total number of seedlings emerged in June 1995. Numbers of seedlings and plots are: Mary Hill: 72,6 (HB), 76,6 (OC), 38,6 (SB), 63,6 (CE), 77,6 (OE), 46,6 (CC), 27,5 (SC); Rocky Point: 48,6 (HB), 50,6 (OC), 17,4 (SB), 92,6 (CE), 41,6 (OE), 46,6 (CC), 15,3 (CS), 9,4 (RP). Mortality categories are: desiccate 1995 (desiccation evident in 1995, mortality confirmed in 1996); desiccate 1996 (no sign of desiccation 1995, mortality from desiccation in 1996); and other (unidentified cause). Habitat types are as in Fig. 2.2. ND designates no data because the habitat type was not present at the site.
Table 2.7. One-way ANOVA table of the effect of habitat type on mortality of first-year Garry oak seedlings at Mary Hill in Metchosin, B.C. N = 5 replicates for each habitat type. Values were calculated as proportions and arcsine square root transformed before analysis.

<table>
<thead>
<tr>
<th>Site</th>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mary Hill</td>
<td>Habitat</td>
<td>2.31</td>
<td>6</td>
<td>0.39</td>
<td>3.46</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>3.12</td>
<td>28</td>
<td>0.11</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>5.44</td>
<td>34</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.8. Tukey’s honestly significant difference tests for the effect of habitat type on mortality of first-year Garry oak seedlings at Mary Hill in Metchosin, B.C. N = 5 replicates for each habitat type. Values were calculated as proportions and arcsine square root transformed before analysis.

<table>
<thead>
<tr>
<th>Subset 1</th>
<th>Subset 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conifer canopy</td>
<td>Small clump</td>
</tr>
<tr>
<td>Small clump</td>
<td>Conifer edge</td>
</tr>
<tr>
<td>Conifer edge</td>
<td>Shrub</td>
</tr>
<tr>
<td>Shrub</td>
<td>Herb</td>
</tr>
<tr>
<td>Herb</td>
<td>Oak canopy</td>
</tr>
<tr>
<td></td>
<td>Oak edge</td>
</tr>
</tbody>
</table>
Table 2.9. Spearman’s rank correlations between percent desiccation of first-year Garry oak seedlings and percent vegetation cover at Mary Hill in Metchosin, B.C. Cover was estimated for a 5-m radius circle centred on the midpoint of each planting plot. N = 7. No correlations are significant (P > 0.05 with sequential Bonferroni adjustments).

<table>
<thead>
<tr>
<th>Vegetation layer</th>
<th>$r_s$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herb</td>
<td>0.52</td>
</tr>
<tr>
<td>Shrub</td>
<td>-0.04</td>
</tr>
<tr>
<td>Tree</td>
<td>-0.43</td>
</tr>
</tbody>
</table>
the only habitats lacking a conifer component. Many of the plots, particularly oak edge plots, have thin soil and rocky outcrops, characteristics less prominent in the other habitat types. On average, 94% of all Mary Hill seedlings killed by desiccation were severely stressed and perhaps dead by late June 1995. Few seedlings suffering drought stress survived; 78% of all seedlings with signs of desiccation in June 1995 died by June 1996.

Losses of seedlings through desiccation were minimal at Rocky Point in both 1995 and 1996 (Fig. 2.6). At both sites, I was unable to determine the causes of mortality for seedlings classified as “other.” The vast majority of these seedlings were no longer present. Seedling mortality due to undetermined causes was not correlated with vegetation cover (Table 2.10).

Seedling Abundance

Because of the cumulative losses of acorns and seedlings caused by various mortality factors, few seedlings resulted from acorns planted on the surface at either study site (Figs. 2.7 and 2.8). Few seedlings (18% or less) emerged in shrub, conifer sapling, or riparian habitats at Rocky Point, but many seedlings emerged in herb and conifer edge habitats (> 73%) from acorns planted in the ground cover and soil (Fig 2.8). These differences in emergence reflect primarily variation in acorn predation among depths and habitats (Fig. 2.2), with some contribution from other undetermined causes of acorn failure (Figs. 2.4 and 2.5). Ranks of seedling numbers across habitats within burial depths remained constant between years with few exceptions (Fig. 2.8), a consequence of relatively consistent seedling mortality rates (Fig. 2.6).

Seedling production was more dynamic at Mary Hill (Fig. 2.7). Relative ranks among habitats changed considerably between 1995 and 1996. Oak edge habitat showed the greatest change in rank between years, particularly for acorns planted in the soil. For acorns buried in the soil, this habitat contained the highest number of seedlings (70%) in 1995 but the lowest (17%) in 1996. Similar to Rocky Point, acorns buried in herb and conifer edge habitats had among the
Table 2.10. Spearman’s rank correlations between percent mortality of first-year Garry oak seedlings from undetermined causes and percent vegetation cover at Mary Hill in Metchosin, B.C. Cover was estimated for a 5-m radius circle centred on the midpoint of each planting plot. N = 7. No correlations are significant (P > 0.05 with sequential Bonferroni adjustments).

<table>
<thead>
<tr>
<th>Vegetation layer</th>
<th>$r_s$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herb</td>
<td>0.29</td>
</tr>
<tr>
<td>Shrub</td>
<td>0.39</td>
</tr>
<tr>
<td>Tree</td>
<td>0.04</td>
</tr>
</tbody>
</table>
Figure 2.7. Effects of habitat type on numbers of Garry oak seedlings produced from acorns planted at different depths at Mary Hill in Metchosin, B.C. Acorns were planted in 1994. N = 6 replicates for each habitat type. Ten acorns were planted in each of 6 replicates of each habitat-depth combination. Habitat types are as in Fig. 2.2. ND designates no data because the habitat type was not present at the site.
Figure 2.8. Effects of habitat type on numbers of Garry oak seedlings produced from acorns planted at different depths at Rocky Point in Metchosin, B.C. Acorns were planted in 1994. N = 6 replicates for each habitat type. Ten acorns were planted in each of 6 replicates of each habitat-depth combination. Habitat types are as in Fig. 2.2. ND designates no data because the habitat type was not present at the site.
highest seedling emergence (> 51 %) in 1995, and produced the greatest number of 2-year-old seedlings (> 41 %) in 1996. In both years, shrub, conifer canopy and small clump habitats had low abundance of seedlings (< 17 %) originating from acorns planted in the ground cover. Differences among depths and habitats resulted mainly from acorn predation, seedling desiccation, and unknown causes of seedling mortality (Figs. 2.2 and 2.6).

Discussion

Two different age-specific mortality factors dominated the results of my study. These accounted for most of the effects of habitat and planting depth on Garry oak regeneration. Variation in seedling emergence was determined largely by acorn predation. Desiccation was the only identified cause of seedling mortality and was responsible for a large proportion of seedling deaths in some habitats.

Acorn Mortality

Extremely high predation of acorns on the ground surface has been documented in a number of studies, with burial consistently improving acorn survival (Shaw 1968, Griffin 1971, Barnett 1977, Borchert et al. 1989, Crawley and Long 1995, Herrera 1995). In studies that compared predation at different burial depths, deeper burial resulted in reduced acorn losses in most cases (Shaw 1968, Griffin 1971, Tietje et al. 1991, Auchmoody et al. 1994). I expect simple burial of acorns to have a marked constraint on acorn consumption by predators that orient by sight (mammals and birds) as well as those that orient by smell (mammals). In contrast, a depth gradient would affect species that forage by smell in a somewhat continuous, but species-specific, manner, but would have little effect on visual predators (Vander Wall 1990). Relative effects of different depths on acorn predation should thus be a function of relative densities of different acorn predators. This relationship would interact with the effect of
habitat, because different animals are present in different densities, and have different foraging
success, in different habitats.

Mary Hill and Rocky Point support a diversity of acorn predators. I observed all of the
local acorn-consuming species (Table 2.11) except mice and voles during my study. Of the local
species, eastern gray squirrels (Barnett 1977, Pigott et al. 1991, Crawley and Long 1995), deer
mice (Borchert et al. 1989, Adams et al. 1991, Tietje et al. 1991), mule deer (Griffin 1976,
Bowyer and Bleich 1980, Borchert et al. 1989), and Steller’s Jays (Griffin 1976, Chapter 3) can
have significant impacts on acorn survival. Although populations of acorn predators were not
measured, deer and squirrels were common, and numbers of Steller’s Jays on southern
Vancouver Island were high in 1994-1995 (Pearce 1995, Campbell et al. 1997).

High predation on surface acorns is a predictable consequence of these high populations
of acorn consumers. Because of the number of mammalian predators, I also expected higher
predation for ground cover than for soil acorns. In addition, Steller’s Jays actively forage within
the ground cover in some habitats, turning over leaves and other surface debris, but do not appear
to randomly probe into soil (but see below). However, differences in acorn survivorship between
these two depths were significant only at Mary Hill. Patterns at Rocky Point were less
consistent, but analysis for Rocky Point was limited to within-habitat comparisons only, with
resultant loss of statistical power. Low power, combined with high variability in predation levels
within habitats, may have obscured differences that may exist in at least some of the habitats.

Populations of acorn predators, acorn mast production, and availability of alternative
foods fluctuate among years; hence, predation pressure will vary accordingly (Janzen 1971).
Acorn production (unpubl. data) and numbers of Steller’s Jays were relatively high in 1994, but
an overall assessment of predation is not possible without further information. Nonetheless, the
results of my study and other studies indicate that acorn burial is essential for acorn survival in
most if not all years. Acorns and leaves of Garry oaks drop during overlapping periods in the
Table 2.11. Vertebrate species associated with Garry oak habitats in British Columbia that consume acorns. Derived from Van Dersal (1940), Silen (1958), and Chatwin (1993).

*Introduced species. *Congenerics identified as acorn consumers, but no specific reference found regarding the species.

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Latin Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Birds</strong></td>
<td></td>
</tr>
<tr>
<td>California Quail°</td>
<td>Callipepla californica</td>
</tr>
<tr>
<td>Band-tailed Pigeon</td>
<td>Columba fasciata</td>
</tr>
<tr>
<td>Pileated Woodpecker</td>
<td>Dryocopus pileatus</td>
</tr>
<tr>
<td>Downy Woodpecker</td>
<td>Picoides pubescens</td>
</tr>
<tr>
<td>Hairy Woodpecker</td>
<td>Picoides villosus</td>
</tr>
<tr>
<td>Northern Flicker</td>
<td>Colaptes auratus</td>
</tr>
<tr>
<td>Steller's Jay</td>
<td>Cyanocitta stelleri</td>
</tr>
<tr>
<td>Northwestern Crow</td>
<td>Corvus caurinus</td>
</tr>
<tr>
<td>Chestnut-backed Chickadee*</td>
<td>Poecile rufescens</td>
</tr>
<tr>
<td>Red-breasted Nuthatch*</td>
<td>Sitta canadensis</td>
</tr>
<tr>
<td>European Starling°</td>
<td>Sturnus vulgaris</td>
</tr>
<tr>
<td><strong>Mammals</strong></td>
<td></td>
</tr>
<tr>
<td>Eastern cottontail°</td>
<td>Sylvilagus floridanus</td>
</tr>
<tr>
<td>Eastern gray squirrel°</td>
<td>Scuirus carolinensis</td>
</tr>
<tr>
<td>Red squirrel</td>
<td>Tamiasciurus hudsonicus</td>
</tr>
<tr>
<td>Deer mouse</td>
<td>Peromyscus maniculatus</td>
</tr>
<tr>
<td>Townsend’s vole*</td>
<td>Microtus townsendii</td>
</tr>
<tr>
<td>Raccoon</td>
<td>Procyon lotor</td>
</tr>
<tr>
<td>Mule deer</td>
<td>Odocoileus hemionus</td>
</tr>
</tbody>
</table>

36
autumn, although the majority of acorns fall one or more weeks before most of the leaves (pers. obs.). This coincidence is crucial for reproduction within oak stands or under oaks growing in other habitats, because some fallen acorns become covered by leaves. Acorns dispersed by squirrels (Barnett 1977) and Steller’s Jays (Chapter 3) are also buried, and thus have increased probability of successful seedling establishment if they escape recovery by their dispersers.

Effects of habitat were reflected in differences between sites and among habitat types within each site and they interacted with depth of acorn burial. Detailed investigation of contributing variables was not conducted, and interpretation of the results is therefore limited. For example, the role of planting depth on acorn mortality was more pronounced at Mary Hill, while habitat had a greater effect at Rocky Point. However, my data do not offer an explanation for this difference. In addition, factors contributing to relative results among specific habitats are not clearly elucidated. The relationships between vegetation cover and predation are inconsistent. Variability within habitat types was high. Despite these limitations, some trends did emerge.

Three habitat types with similar structure (small clump at Mary Hill; conifer sapling and riparian at Rocky Point) had among the highest predation levels. These habitats have moderate to high tree cover, and the lowest herb cover of all habitat types. Cover in the shrub layer is extensive and dense. Steller’s Jays preferentially use these habitats for hoarding acorns, and were frequently observed foraging for acorns on the surface and in the ground cover. However, acorns planted in the soil in these habitats also suffered extremely high predation. I do not know if acorns became dislodged from the soil and were eaten by jays, if jays foraged in the soil but were not observed, or if other predators were important in these habitats.

Low predation, especially at Rocky Point, was associated with high herb and low shrub cover. Other studies note various relationships between predation and vegetation cover and report lower predation with less cover in the shrub (Callaway 1992, Herrera 1995), tree
layers. My results are consistent with behaviour of Steller's Jays; jays were rarely observed foraging in open habitats. In contrast, squirrels were often seen foraging under open oak canopies, and deer forage predominately under highly productive oaks while the acorns are falling (Griffin 1976, Borchert et al. 1989). Because of these observations, I expected high acorn losses in oak habitats, but this was not the case.

Although I could not identify mortality factors for most of the acorns that failed for reasons other than predation, desiccation may have been important (Shaw 1968, Borchert et al. 1989, Tietje et al. 1991, Hubbard 1995). Failure was common for acorns planted on the surface, but not for buried acorns. Buried acorns are protected from the effects of occasional dry periods, but acorns on the surface do not share this advantage.

Mortality of acorns planted on the surface can also occur if the radicles cannot penetrate hard soils (Griffin 1971). There is no evidence that this was an important factor in my study. More than half of the acorns planted on the surface that were not removed by predators lost viability before they germinated. It is more likely that stress began shortly after I planted the acorns, killing some acorns before and some acorns shortly after they germinated. Desiccation of acorns could account for the observed pattern of mortality in my experiment.

Acorn germination occurs shortly after the acorns drop in the autumn, but this is contingent upon sufficient moisture to maintain viability (Stein 1990). Survival of germinated acorns also requires adequate moisture. Because of inter-annual fluctuations in the timing of acorn release and the extent of the drought period, survival may vary across years. If the timing of acorn fall and precipitation do not coincide, high rates of desiccation may occur. I planted the acorns in mid-October, later than acorns usually fall, and after the autumn rains had begun. As a result, desiccation effects were probably minimized by my study design, and differences among depths are probably more pronounced in many if not most years. Acorns that are buried by
Steller's Jays or squirrels are afforded protection, but those that are dispersed by gravity are more vulnerable, unless they become covered by fallen leaves.

Differences among habitats in mortality of acorns that were not removed by predators were more pronounced at Rocky Point than at Mary Hill. I do not know why this was the case, nor do I know why mortality was particularly pronounced in oak edge habitat.

**Seedling Mortality**

Desiccation was the only identified source of seedling mortality, but death from undetermined causes occurred in all habitats except riparian at Rocky Point. Because many desiccated shoots that were observed in 1995 persisted until 1996, it is unlikely that many of the seedlings that were not desiccated in 1995 but disappeared between 1995 and 1996 had died from desiccation.

Shoot browsing can cause mortality (Griffin 1971, Griffin 1976, Bowyer and Bleich 1980, Callaway and D'Antonio 1991, Callaway 1992, McPherson 1993). Many Garry oak seedlings in my study were browsed, in contrast to Garry oak seedlings in other regions (Stein 1990, Hibbs and Yoder 1993). However, because oaks with dead or damaged shoots readily resprout, browsed seedlings may survive if they have sufficient reserves (Shaw 1974, Crow 1988). For example, the stem age of Garry oak seedlings in Oregon averaged 4.6 years, while the roots averaged 13.8 years (Hibbs and Yoder 1993). Mortality may result primarily from severe or ongoing stresses. While other studies that describe seedling mortality generally do not appear to distinguish between shoot disappearance and seedling death, I was able to precisely locate planted seedlings and determine if a live root persisted. Seedlings that had been browsed close to ground level commonly resprouted. Although I do not know how many of the seedlings that disappeared between June 1995 and June 1996 were browsed during that time period, I saw no evidence that browsing caused seedling mortality.
Insect herbivory can also kill oak seedlings if reserves are depleted (Shaw 1974, McPherson 1993). Most seedlings in my study had some insect damage in June, but I do not know the extent of damage over summer and cannot assess whether seedling survival was affected. Mortality may also have resulted if the seedling roots were consumed by rodents (Stein 1990, Davis et al. 1991).

Rainfall in May 1995 was unusually low (13.4 mm; Environment Canada climate summary, William Head station) and was likely responsible for the seedling desiccation observed in June of that year. Although rainfall was higher than average from June through August, drought occurred in September (total precipitation 22.3 mm), and probably killed stressed seedlings that may have otherwise resprouted. Unlike the possibly more incremental effects of browsing and insect herbivory, desiccation appeared to readily kill first-year seedlings. This is supported by the low survival of seedlings that suffered moisture stress in 1995.

Some studies have attributed the majority of oak seedling mortality to moisture stress (Griffin 1971, Callaway and D’Antonio 1991, Davis et al. 1991). Physiographic and edaphic features appear to play a role in seedling desiccation in my study. Desiccation mortality was confined to Mary Hill, a south-facing slope, in habitats that had thinner soil and more rocky outcrops than other habitats at the site.

Habitats exhibiting seedling desiccation lacked coniferous trees. This may reflect the fact that Douglas-fir seedlings are drought-intolerant and cannot establish on xeric sites, or where severe competition or other features contribute to high levels of moisture stress (Roemer 1972, Barnhardt et al. 1987). Garry oak seedlings, on the other hand, rapidly develop deep taproots (Stein 1990), which confers a high degree of drought tolerance. Despite the mortality that occurred in these habitats, many oak seedlings survived. Recruitment might be virtually nonexistent in very dry years, but numerous seedlings would be expected to persist under conditions with average or higher levels of precipitation.
Shade intolerance is a common characteristic of oaks. Survival and growth of seedlings of many oak species decline under limited light site conditions, although threshold light levels for optimum performance varies among species (Shaw 1974, Crow 1992, Lorimer et al. 1994, Ziegenhagen and Kausch 1995, Ashton and Larson 1996). Effects of browsing and insect damage can be heightened if seedlings are unable to replenish lost tissues because of insufficient light (Shaw 1974, Crow 1992). Shade can also improve survival of oak seedlings by reducing heat or water stress or providing protection from herbivores (Bowyer and Bleich 1980, Crow 1988, Callaway and D’Antonio 1991, Muick 1991, Williams et al. 1991, Callaway 1992). The inability of Garry oaks to persist after conifers encroach into former oak ecosystems has been well documented (Norton 1979, Barnhardt et al. 1987, Reed and Sugihara 1987, Sugihara and Reed 1987, Agee 1993) and declines of mature Garry oaks that have been overtopped by conifers indicate shade intolerance (Stein 1990). However, specific responses of immature Garry oaks to different light levels are not clear. Neither desiccation mortality nor mortality from unknown causes was correlated with overstorey vegetation in my study. Shade did not benefit Garry oak seedlings nor was there evidence of shade intolerance. Garry oaks evidently become shade intolerant at a later stage of development. Reserves remaining in the cotyledons or translocated from the cotyledons to the taproot may be sufficient to sustain first-year Garry oak seedlings in light-limited environments (Crow 1992), including those with dense overstorey vegetation.

Conclusions and Recommendations

My study reveals that: 1) burial of acorns in the ground cover or soil is essential for Garry oak reproduction; 2) some relationships between mortality processes and vegetation structure can be discerned, but these relationships are complex; and 3) Garry oak survival rates can be similar in habitats with very different structural characteristics. However, habitat quality for young Garry oaks is dynamic. Habitat quality can vary with fluctuations in acorn mast
production, changing densities of acorn predators and seedling herbivores, and variation in precipitation levels. Further research should be conducted to investigate these variables. Habitat quality can also change as the oaks reach different developmental stages. In my study, some good habitats for the acorn stage became relatively poor habitats for the newly emerged seedlings, and vice versa. Habitat quality may be similarly dynamic as the oaks continue to develop. Although my study indicates that early survival may be sufficient in some habitats to produce 2-year-old seedlings, differential survival at later stages can result in markedly different seedling and sapling distributions (Muick and Bartolome 1987). For example, casual observations indicate that, although seedlings occur in different habitats at both Mary Hill and Rocky Point, saplings approaching 2 m in height are present only in open, rocky locations at Mary Hill. It appears that, in some habitats, factors that limit recruitment exert their influence during later stages of oak development. Further investigation is required to determine mortality processes at later developmental stages.
Chapter 3: Dispersal of Garry Oak Acorns by Steller's Jays

Abstract

I observed harvesting, transporting, and caching of Garry oak \textit{(Quercus garryana)} acorns by Steller's Jays \textit{(Cyanocitta stelleri)} to assess the role of the jays in acorn dispersal. I watched Steller's Jays that I encountered as I traversed 2 study sites in British Columbia during August, September, and October 1994. I also classified substrates and habitats and described vegetation structure at cache sites and at locations along transects in the study sites. The jays used visual, tactile, and perhaps aural cues to select mature, relatively undamaged acorns for caching. Jays cached acorns between a few centimetres and at least 600 m from harvest locations and probably transported some acorns more than 1 km. Scattered trees in a meadow were used by jays as stopover points during transport journeys and appeared to facilitate acorn dispersal. More than 77% of acorns were cached on their sides, which permits unimpeded extension of the epicotyl. Virtually all cached acorns were buried in the substrate and 88-92% were fully hidden from view. Seventy five-76% of acorns were cached in the ground cover and only one acorn was cached more than 1 cm below the soil surface. Hidden, buried acorns are less likely to be taken by acorn predators or desiccate than those on the surface. Steller's Jays did not prefer or avoid substrates (rock, wood) unsuitable for seedling establishment. Steller's Jays preferred locations with extensive tree and shrub cover and sparse herb cover for caching acorns. All habitat types in the study sites characterized by this vegetation structure were used in greater proportion than they were available. Steller's Jays avoided locations with sparse tree cover, sparse shrub cover, or dense herb cover. Habitats preferred by Steller's Jays are unfavourable for seedling emergence because a high proportion of acorns buried in these habitats are subsequently removed by acorn predators. Low light levels in preferred habitats may also be unfavourable for survival and growth of older Garry oak seedlings and saplings. Although jays preferred some
habitat types, approximately half of the cached acorns were distributed among non-preferred habitats. Survival of acorns and first-year seedlings is relatively high in some of these non-preferred habitats, and many have more available light than habitats preferred by Steller’s Jays. Use of non-preferred habitats may be essential for effective acorn dispersal by Steller’s Jays and may be facilitated by juxtaposition of patches of preferred and non-preferred habitats. Although less than 2% of cached acorns produced seedlings, individual Steller’s Jays probably cache thousands of acorns per season and are probably responsible for the presence of Garry oak seedlings far from mature oaks. Steller’s Jays are probably the primary dispersal agent for Garry oaks in British Columbia, but this dispersal system may be less effective than those of oaks dispersed by other species of jays. Irregular occupation of Garry oak habitats in B.C. by Steller’s Jays and habitat preferences of the jays place substantial constraints on the numbers of acorns buried in suitable habitats.

**Introduction**

A growing body of literature describes mutualistic interactions between seed-hoarding animal species and plants (see Vander Wall 1990 for review). Animals take seeds and hide them in the ground for future use, thereby accumulating food reserves for use during periods of shortages and, in some cases, to feed offspring (Chettleburgh 1952, Turcek and Kelso 1968, Bossema 1979, Roberts 1979, Vander Wall and Balda 1981, Smith and Reichman 1984, Sherry 1985, DeGange et al. 1989, Johnson and Webb 1989). Seed burial can benefit plants by reducing predation and providing favourable conditions for germination and seedling establishment (Chapter 2). Transport of seeds away from the parent may help plants minimize density-dependent predation, disease, herbivory, or competition. Dispersal of seeds by animals may also enhance genetic exchange among plants, assist plants in colonizing rare, disturbed, or isolated habitats, and provide plants with a mechanism to shift range in response to climate change.
Effective seed dispersal requires that the animals harvest viable seeds, place the seeds in suitable habitats, and cache the seeds in a manner and in substrates suitable for germination, seedling establishment, and development to maturity (Bossema 1979, Darley-Hill and Johnson 1981, Vander Wall and Balda 1981, Johnson and Webb 1989). In addition, seeds must be stored in sufficient numbers or recovery rates of seeds by the caching animals must be low enough to allow establishment of plant offspring (Bossema 1979, Darley-Hill and Johnson 1981, Vander Wall and Balda 1981, Johnson and Adkisson 1985, Jensen and Nielsen 1986, Johnson and Webb 1989). Dispersal of acorns of oaks (Quercus spp.) is attributed to seed-caching animals.

Dispersal of Garry oak acorns in British Columbia probably depends primarily upon acorn caching by Steller’s Jays. Northwestern Crows (Corvus caurinus) and Common Ravens (C. corax), the only other corvid species in B.C. regularly present in Garry oak habitats (Campbell et al. 1997), hoard acorns infrequently if at all (pers. obs.). Eastern gray squirrels were introduced into the region in the 1960’s (Bennett 1993). As the population and range of eastern gray squirrels increases on southeastern Vancouver Island, their role in acorn dispersal may also be increasing. However, this role is probably limited because adult squirrels excise the embryo of acorns of white oaks (subgenus Lepidobalanus; Barnett 1977, Fox 1982, Pigott et al. 1991), including Garry oaks (pers. obs.), prior to caching.

Despite anecdotal references to acorn caching by Steller’s Jays (Grinnell 1936, Brown 1963, Goodwin 1986, Bent 1988, Stewart and Shepard 1994), studies detailing the role of these jays in acorn dispersal are lacking. Bossema (1979) found that acorn selection, transport, and caching by European Jays resulted in dispersal of pedunculate oaks (Quercus robur) to favourable habitats. Nilsson (1985) concluded that European jays cache acorns of Q. robur and Q. petraea in a spruce forest, where seedling and sapling survival exceeds that within an oak stand. Similarly, Blue Jays facilitate oak (Quercus spp.) dispersal to favourable habitats (Darley-Hill and Johnson 1981, Johnson and Webb 1989). Vander Wall and Balda (1981) compared harvest, transport, and storage of piñon pine (Pinus edulis) seeds among Clark’s Nutcrackers, Piñon Jays, Steller’s Jays, and Western Scrub-Jays. They described Steller’s Jays as moderately specialized for these activities, and determined that Steller’s Jays disperse piñon pine seeds to higher elevation ponderosa pine (P. ponderosa) forests and thereby afford the piñon pines the ability to shift range in response to climate change.

My study examines harvesting and caching of Garry oak acorns by Steller’s Jays on southern Vancouver Island, British Columbia. More specifically, I investigate acorn selection, transport distance, cache placement (in terms of acorn orientation, burial depth, substrate, and
habitat), and fate of hoarded acorns. I assess the implications of these factors for Garry oak dispersal and regeneration.

Study Species

Garry Oak

The range of Garry oak extends from southern British Columbia to southern California (Stein 1990). Within B.C., Garry oaks are found from Courtenay south along the eastern edge of Vancouver Island, on the Gulf Islands, and at 2 disjunct stands in the Fraser Valley (Stein 1990). Agricultural and urban development have fragmented the landscape on southeastern Vancouver Island, isolating Garry oak trees and stands and altering the character of remnant ecosystems (Erickson 1996, Ussery 1997).

Garry oak, like all others of its genus, is a mast seeder, and produces highly variable acorn yields among years and among trees (Stein 1990, unpubl. data). The acorns mature over summer (Stein 1990) and in B.C. drop primarily in September and early October (pers. obs.). Acorn sizes range from about 1.5 to 3.5 cm long and 1.0 to 3.0 cm in diameter (unpubl. data). Garry oak is a member of the subgenus Lepidobalanus; hence, its acorns are not dormant and usually germinate within weeks of falling if they retain sufficient moisture (Stein 1990). The seedlings rapidly develop deep taproots (Stein 1990), but shoots do not emerge until spring or early summer of the following year (Stein 1990, pers. obs.).

Steller’s Jay

The Steller’s Jay occurs from southeastern Alaska, through western Canada and the United States, and south to Nicaragua (Campbell et al. 1997). Habitats occupied by Steller’s Jays are varied, and include well-treed urbanized areas and coniferous and mixed coniferous-deciduous forests, especially edges, clearings, and riparian areas (Guiguet 1954, Goodwin 1986,
Steller’s Jays are generally resident or limited latitudinal or altitudinal migrants, but irruptive populations also occur in some regions (Guiguet 1954, Brown 1963, Westcott 1969, Vander Wall and Balda 1981, Morrison and Yoder-Williams 1984, Goodwin 1986, Bent 1988, Stewart and Shepard 1994, Campbell et al. 1997). Occupancy by jays of Garry oak habitat on southern Vancouver Island is seasonal and irruptive, varying among years from apparently none to vast numbers of individuals (Guiguet 1954, Stewart and Shepard 1994, Campbell et al. 1997). Populations of Steller’s Jays on southern Vancouver Island were high in 1994-95 (Pearce 1995, Campbell et al. 1997). The jays usually begin to arrive in mid-August, probably from more northerly locations (Stewart and Shepard 1994, Campbell et al. 1997). They leave the Garry oak habitats in the spring and remain away for the duration of the breeding season (Stewart and Shepard 1994, Campbell et al. 1997).

Steller’s Jays eat a wide variety of seeds, fruits, invertebrates, small vertebrates, eggs, and carrion (Guiguet 1954, Westcott 1969, Goodwin 1986). Acorns comprise a substantial, if not the major, portion of the diet when they are available (Van Dersal 1940, Brown 1963, Westcott 1969, Goodwin 1986, Bent 1988, Stewart and Shepard 1994). The esophagus of the jay is distensible for approximately 1/3 of its length, and is used as a storage structure for transporting acorns and other seeds (Vander Wall and Balda 1981, pers. obs.). Specialized adaptations of the bill, jaw, and cranium of Steller’s and other New World jays comprise a “buttress complex,” allowing efficient piercing and peeling of acorns (Zusi 1987).

**Study Area**

My research was conducted in Metchosin (48°23’N, 123°32’W) on the southern tip of Vancouver Island, British Columbia. Two sites were used, Mary Hill and Rocky Point, about 2 km apart. The study was conducted within approximately 20 ha at each site. Each site consists of a mosaic of patches of different habitat types, including coniferous and deciduous forest,
rocky outcrops, meadows, and shrubs. The oak cover at Mary Hill is primarily in savanna form, with individual trees having large rounded crowns and growing within a rocky, grass- and shrub-covered matrix. Most of the oaks at Rocky Point comprise a woodland (approx. 300-450 stems/ha; Chatwin 1997, unpubl. data), with narrow crowns concentrated in the upper stratum.

Methods

Field Methods

Observations of Acorn Harvest, Transport, and Caching by Steller’s Jays

Observations of Steller’s Jays were conducted from August to October 1994. Each field day, two observers walked through different areas of a study site in search of acorn hoarding activity by Steller’s Jays. These activities were often conspicuous because groups of approximately 5-10 (or more) jays tended to converge upon harvesting and hoarding areas (see below). These groups were relatively noisy and easy to find. Upon finding one or more jays, an observer recorded observations in a particular area until the jay(s) shifted location. If the jay(s) continued to cache in a single area for an extended period (more than an hour or two at a time), the observer left the area and searched for hoarding activity in another part of the study site. All parts of each study site were traversed on a regular basis. Each study site was visited on alternate days with few exceptions.

Two observers recorded all observations of transport of one or more acorns by Steller’s Jays. We noted when we observed the full transport distance (i.e. if we witnessed both the beginning and end of the journey). Jays frequently landed in trees for brief periods along transport routes. Distances between stopovers and total journey distances were visually estimated and periodically verified with optical rangefinders.

We recorded general harvesting and caching behaviour of Steller’s Jays. For each observation of acorn caching, the observer waited until the jay departed and subsequently
attempted to locate the cached acorn. If the acorn was located, the following information was recorded: acorn length, acorn condition, burial depth, orientation of the acorn, and how much of the acorn was covered from view. Burial depth information included substrate layer (on the surface; in the ground cover, including leaf litter, matted grass roots, moss, lichens, and coarse woody debris; or in the soil) and depth below the soil surface for those acorns that were buried in soil. The acorn was then replaced and the ground restored as close as possible to its original condition. Field notes described the precise location of the acorn, and flagging tape was attached within a few metres of the cache location so that I would be able to find the acorn the following year. Distance and direction from the flagging tape to the different caches varied to avoid leading acorn predators to the acorns. I returned to marked cache locations in June 1995 and noted presence or absence of a seedling. If no seedling was present, I subsequently searched for the hoarded acorn and noted if it was present or absent.

**Description of Hoarding Habitat and Available Habitat**

I classified the habitat in which each acorn was cached. At Mary Hill, the habitat types were: conifer canopy (CC), conifer edge (CE), herb (HB), mixed canopy (MC), mixed edge (ME), oak canopy (OC), oak edge (OE), rocky outcrop (RO), shrub (SB), and small dense clumps of mixed cover (usually oak and arbutus trees, Douglas-fir saplings or trees, and often a shrub component; SC). Habitat types at Rocky Point were CC, CE, HB, MC, ME, OC, OE, RO, SB, conifer sapling patches under oak canopy (CS), and riparian (seasonally wet; RP).

I visually estimated vegetation cover by strata to quantify vegetation structure at cache locations. I estimated cover for 3 vegetation layers: herb (0 to 1 m high), shrub (> 1 to 5 m high) and tree (> 5 m high), each within circles of 1-m and 5-m radius. I used the protocol developed by the B.C. Ministries of Environment and Forests (Luttmerding et al. 1990), which estimates the area of the ground encircled by a vertical projection of the crown edge. I also recorded
composition of the substrate (e.g. soil, rock, moss, matted grass roots, leaf litter, or coarse woody debris) at each hoarding location. In some cases, I could not determine the precise location of the cached acorn. If this caused uncertainty regarding any of the habitat measurements, the relevant data were omitted.

I classified habitat types and measured habitat characteristics along transects in both study sites to estimate habitat availability. I established parallel transects 25 m apart in each site. Every 25 m along each transect, I classified habitat type, visually estimated percent cover of vegetation by strata, and recorded substrate composition. Methods were the same as those used at hoarding locations.

Data Analysis

Because types and attributes of habitats differed between Mary Hill and Rocky Point, I analyzed data separately for each site except data pertaining to acorn size and condition. I used descriptive methods to analyze data pertaining to transport distances and acorn size, condition and burial depth. Statistical significance is reported at the 95 % confidence level for analyses involving statistical tests.

I used chi-square tests of homogeneity to compare use and availability of hoarding substrates and of habitat types (Marcum and Loftsgaarden 1980). Differences between use and availability of habitat types were significant, so I conducted comparisons of use and availability within each habitat type to determine which habitats were preferred or avoided by Steller's Jays. I constructed confidence intervals around the differences between use and availability with the formula (Marcum and Loftsgaarden 1980):

$$(p_i - p_0) \pm Z_{a/2} \sqrt{\frac{(p_0)(q_0)}{n_c} + \frac{(p_0)(q_0)}{n_t}}^{0.5}$$
where:

\[ p_{ci} = \text{the proportion of caches in habitat } i \]
\[ p_{ti} = \text{the proportion of transect locations in habitat } i \]
\[ q_{ci} = 1 - p_{ci} \]
\[ q_{ti} = 1 - p_{ti} \]
\[ n_c = \text{the total number of caches} \]
\[ n_t = \text{the total number of transect locations} \]

Confidence intervals that include 0 are not significantly different. I used a sequential Bonferroni adjustment of the alpha values based on the number of comparisons within each site to control experimentwise Type I error (Rice 1989).

I further described differences between use and availability of habitat types with Ivlev’s electivity indices (Lechowicz 1982). Indices were calculated as:

\[ \frac{(p_{ci} - p_{ti})}{(p_{ci} + p_{ti})} \]

Positive indices indicate usage greater than availability, and can hold a maximum value of 1. Negative indices indicate usage less than availability, and can hold a minimum value of -1.

Distributions of data for percent cover of vegetation at cache and transect locations were not normal and varied in shape. I therefore used Kolmogorov-Smirnov tests to compare use and availability (SPSS 1997b). I conducted separate tests for each vegetation layer and for measurements made within 1-m and 5-m radius circles. I applied sequential Bonferroni corrections based on the number of comparisons within each site. Data were subsequently divided into 5 cover classes (0-20 %, 21-40 %, etc.) to facilitate detailed examination of differences between use and availability.

Because Steller’s Jays harvest and cache acorns in social groupings, it was not possible to obtain independent observations. I controlled for this lack of independence by remaining with groups of jays for a maximum of an hour or two, and subsequently leaving to search the site for harvesting and hoarding activity of other jays. In addition, the number of site visits and the fact that two observers were simultaneously in different areas of the study sites provided a degree of
independence to the observations. However, conclusions drawn from results of statistical tests
should be treated with some caution.

Results

General Harvesting and Hoarding Behaviour

In 1994, Steller's Jays first appeared in the study area in mid-August. Early sightings
were primarily of individual jays but by late August, jays were often in groups of up to 10 or
more birds. Group size appeared to decrease to approximately 5 jays in September. Besides
groups of jays, sightings of individuals and pairs occurred throughout the observation period.
Although I was unable to determine the numbers of jays harvesting and/or caching acorns at the
study sites, there appeared to be 25 to 50 individuals at Mary Hill, and probably fewer at Rocky
Point.

Subsequent to appearing in the study area, jays spent considerable time roaming through
the oak trees. I first witnessed acorn harvest, transport, and consumption by jays on 29 August.
The jays continued to frequent the oaks and sporadically harvest acorns for the next 10 days.
Harvesting activity abruptly increased on 9 September, and jays continually transported acorns
from morning until evening for a period of 3 - 4 weeks. Individual birds harvested 1, 2, or 3
acorns for simultaneous transport, usually from the same tree or from closely adjacent trees.
After mature acorns began to fall, jays also harvested acorns from the ground.

Jays carried single acorns in their esophagus or tip of their bill. When transporting 2
acorns, jays either carried both in the esophagus, or 1 in the bill and the other in the esophagus.
One acorn was always held in the bill and 2 in the esophagus when jays transported 3 acorns.
Acorns were always transported without their caps.
The vast majority of transported acorns were probably cached by the jays. I rarely saw jays eat acorns that they had transported more than a short distance from the parent tree. Instead, jays usually carried a single acorn closer to the trunk of the parent tree or an adjacent tree to consume it. Piercing and consuming an acorn required extended and vigourous activity, and the interior canopy may have provided greater stability as well as cover from predatory hawks.

After harvesting 1-3 acorns for hoarding, Steller’s Jays transported them to a hoarding area. When they arrived at the hoarding area, the birds often flew first into a tree at approximately mid-height, then hopped from branch to branch towards the ground. After reaching the ground, jays hopped around seeking the caching location. If more than one acorn was transported, all acorns were usually first disgorged at one spot on the ground. One acorn was then picked up and carried up to a few metres in the bill or the esophagus to the cache site, where the jay probed its bill into the substrate and poked (if carried in the bill) or dropped (if carried in the esophagus) the acorn into the depression. Frequently jays tested a number of locations by probing with their bill before caching the acorn. Jays often hammered upon acorns after burial, and usually covered them with leaf litter, moss, or other loose materials in the vicinity. After burying the first acorn, jays returned to the disgorging location and proceeded in a similar fashion with the remaining acorns. Distances between caching sites of acorns that were transported together ranged from a few centimetres to approximately 10 m, with the majority (81%) between 0.25 and 3 m. Jays that transported a single acorn in the esophagus did not always disgorge it before selecting the cache site.

When jays finished caching the transported acorns, they usually flew into the lower branches of a nearby tree, then hopped from branch to branch up the tree. They often paused at the top of the tree and looked around before flying away. Steller’s Jays often departed the hoarding area in the direction from which they had come. Although I was usually able to see only a portion of each of these flights, the jays appeared to fly back to the same harvesting area.
Each group of jays tended to concentrate upon the same harvesting and hoarding areas for periods of time, flying back and forth between the two. These periods seemed to last for up to a few hours or more within a given day. Many harvesting and hoarding areas within the study sites were also visited repeatedly by jays throughout the season. On a few occasions, I witnessed large numbers of jays (10 or more) harvesting acorns from the same tree or group of trees. These jays appeared to cache acorns in at least two different areas and thus may have represented 2 or more smaller groups converging on the same harvesting area.

Harvesting and caching activity decreased substantially by early October. I last observed Steller’s Jays transporting acorns on 14 October. Limited acorn hoarding activity may have continued beyond that date.

**Acorn Selection**

Steller’s Jays hoarded only mature acorns, rejecting the large proportion of available acorns that ceased development while they were a small size. Hoarded acorns averaged 23 mm ± 4 mm SD in length and ranged from 14 to 33 mm (n = 151). Less than half of the acorns collected in acorn traps under a sample of trees at the study sites were 14 mm or longer, and a large proportion of the acorns were only a few mm in length (unpubl. data). Because only one of the oak trees with acorn traps was a favoured harvesting tree, detailed comparisons between acorns from traps and hoarded acorns are not appropriate, but selection by jays for mature acorns is evident.

Steller’s Jays cached relatively undamaged acorns. Fifty-four percent of hoarded acorns had no fungus, spots, cracks, misshapen morphology, vertebrate damage, weevil emergence holes, rot, or any other detectable defects. In comparison, less than one third of acorns ≥ 14 mm in length collected in the acorn traps were undamaged (unpubl. data). Although acorns cached by Steller’s Jays are not directly comparable to acorns collected in traps, the large difference in
quality between cached acorns and those in traps suggests that Steller’s Jays selected undamaged acorns for caching. In addition, jays harvested acorns from the ground as well as from trees; hence quality of available acorns was probably less than that represented by collections from acorn traps. Acorns are more susceptible to fungus, rot, and vertebrate damage on the ground than they are in trees or traps.

Steller’s Jays appeared to use a variety of methods to assess acorn suitability for caching. Visual, tactile, and perhaps aural cues were likely used to select which acorns to harvest from trees, because jays closely peered at acorns, and tapped and tugged on them. When harvesting from the ground, jays frequently picked up acorns, manipulated them in the bill, and subsequently either dropped or transported them.

Transport Distances

Observed distances of acorn transport journeys by individual jays ranged from less than 1 to 600 m (Fig. 3.1). The distribution of observations may not reflect the distribution of actual journeys, because I did not witness the entire distance for most of the transport journeys, and shorter distances are more easily observed when visibility is limited. Nonetheless, data indicate that jays transport acorns very short distances, at times remaining beneath the canopy of the parent tree, as well as distances > 0.5 km. On one occasion, I observed a group of jays that appeared to be traveling back and forth between harvesting and hoarding areas. I followed the group for approximately 1 km, and had not yet reached the full distance traveled by the jays. Other groups of jays also appeared to be transporting acorns for similar distances.

The number of transport journeys and the range of transport distances observed at Mary Hill were much greater than those at Rocky Point (Fig. 3.1). Bias may have contributed to these differences, because most of Mary Hill is open habitat and is a slope, and consequently visibility is better at Mary Hill than at Rocky Point. It is also likely that actual numbers and distances of
Figure 3.1. Transport distances of Garry oak acorns by Steller’s Jays at two sites in Metchosin, B.C. Observation categories are: full distance (the entire transport journey was observed, including both acorn harvest and caching) and partial distance (a portion of the transport journey was observed, lacking observation of acorn harvest, caching, or both). N = 605 at Mary Hill and n = 141 at Rocky Point.
journeys were greater at Mary Hill. For example, Steller's Jays rarely crossed and were never observed transporting acorns across a large meadow at Rocky Point (approximately 150 by 300 m), despite the unobstructed visibility at this location. Jays at Mary Hill frequently carried acorns farther than 150 m, and at times farther than 300 m (Fig. 3.1).

Habitat structure may have played a role in the differences in transport distances between the two sites. The meadow at Rocky Point contained no trees, but open expanses at Mary Hill contained numerous scattered oak, Douglas-fir, and other trees. These trees were frequently used by jays as stopover points. The jays usually landed mid-canopy, spiraled around the tree trunk as they made their way to the top of the canopy, then paused and surveyed the area for a brief period before continuing their journey. Distances between stopovers tended to be considerably shorter than total transport distances at Mary Hill but not at Rocky Point (Figs. 3.1 and 3.2), because small journey segments between stopovers summed to longer total transport distances. In addition, journey segments at Mary Hill ranged beyond 0.5 km, but at Rocky Point did not exceed 150 m (Fig. 3.2).

**Acorn Orientation, Burial Depth, and Substrate**

Most acorns (95 % at Mary Hill, n = 80; 78% at Rocky Point, n = 55) were cached on their sides. The rest were buried with the basal end oriented up (5 % at Mary Hill; 16 % at Rocky Point) or down (0 % at Mary Hill; 6 % at Rocky Point). Depth of cached acorns was remarkably similar between sites (Fig. 3.3). Virtually all acorns were buried. Most buried acorns were in the ground cover layer (75-76 %), with the remainder in the soil (22-25%). Only 2 acorns (2%) were placed on the ground surface, both at Mary Hill. Acorns were not buried deeply in the soil. Sixty nine percent of the acorns buried in soil were only partly within the soil layer, and only one acorn was deeper than 1 cm below the soil surface.
Figure 3.2. Distances traveled between stops by Steller’s Jays when transporting Garry oak acorns at two sites in Metchosin, B.C. Observation categories are: full distance (the entire segment was observed, including both the beginning and end of the segment) and partial distance (a portion of the segment was observed, lacking observation of the beginning of the segment, the end of the segment, or both). N = 918 at Mary Hill and n = 150 at Rocky Point.
Figure 3.3. Burial depth of Garry oak acorns cached by Steller’s Jays at two sites in Metchosin, B.C. Burial depths are: surface (on top of ground cover), ground cover (within leaf litter, matted grass roots, moss, lichens, or coarse woody debris), and soil. N = 91 at Mary Hill and n = 63 at Rocky Point.
Most caches were well hidden within the substrate. Eighty-eight percent at Mary Hill (n = 91) and 92 % at Rocky Point (n = 63) were fully covered, and only the 2 acorns cached on the surface had more than 50% of their top surface exposed to view.

Steller’s Jays showed no selectivity for substrate type (Mary Hill, $X^2_{0.05, 2} = 5.25, P > 0.05$; Rocky Point, $X^2_{0.05, 2} = 2.02, P > 0.05$; Fig. 3.4). Jays did not prefer or avoid substrates unsuitable for root establishment (rock or wood). Jays used rock or wood only if it had a crevice or was covered with a thin layer of soil, moss, lichens, or leaf litter in which to lodge and cover the acorn.

**Hoarding Habitat**

**Habitat Type**

Steller’s Jays used some habitats to hoard acorns in greater proportion than they were available in the study sites, and used other habitats less than they were available (Mary Hill, $X^2_{0.05, 9} = 1547.28, P < 0.01$; Rocky Point, $X^2_{0.05, 10} = 2725.77, P < 0.01$; Fig. 3.5). Small clump habitat at Mary Hill and riparian habitat at Rocky Point were highly preferred by Steller’s Jays. More than 40 % of all caches were located in these habitats in spite of the fact that they comprised only 10 % (small clump) or 5 % (riparian) of the study site. At Rocky Point, conifer sapling habitat comprised only 5 % of the site, but was used for 17 % of all hoards. Electivity indices for these preferred habitats are all 0.58 or greater (Table 3.1). At both sites, shrub and herb habitats comprised between 8 and 27 % of the area, but less than 2 % of the caches were located in each (Fig. 3.5). Electivity indices for shrub habitat are -0.55 and -0.68 at Mary Hill and Rocky Point respectively, and approach -1 for herb habitat, especially at Rocky Point (Table 3.1). Conifer canopy and rocky outcrop habitats at Mary Hill and oak canopy habitat at Rocky Point were also avoided (Fig. 3.5, Table 3.1). Although electivity indices for oak edge and
Figure 3.4. Use and availability of substrates for caching of Garry oak acorns by Steller’s Jays at two sites in Metchosin, B.C. Use is based upon substrates where acorns were cached by jays (n = 170 at Mary Hill and n = 125 at Rocky Point) and availability is based upon substrates at positions every 25 m along transects located 25 m apart (n = 356 at Mary Hill and n = 409 at Rocky Point). Rock includes bare rock and rock covered with leaf litter, moss, lichens, and/or up to a few cm of soil. Wood consists of exposed roots and coarse woody debris, including bare wood and wood covered with leaf litter, moss, lichens, and/or up to a few cm of soil. Two acorns cached on tree branches at Mary Hill are also included in “wood.”
Figure 3.5. Use and availability of habitat types for caching of Garry oak acorns by Steller’s Jays at two sites in Metchosin, B.C. Use based upon habitat types where acorns were cached by jays (n = 179 at Mary Hill and n = 132 at Rocky Point) and availability is based upon habitat types recorded at positions every 25 m along transects located 25 m apart (n = 356 at Mary Hill and n = 409 at Rocky Point). Habitat types are: HB = herb; SB = shrub; RO = rocky outcrop; CC = conifer canopy; ME = mixed edge; MC = mixed canopy; OE = oak edge; OC = oak canopy; CE = conifer edge; SC = small dense clump, usually of oak, conifer saplings, and arbutus; CS = conifer sapling patch within the oak stand; RP = riparian. Habitat types are displayed in order of increasing electivity indices (Table 3.1) at Mary Hill. Asterisks denote statistically significant differences between use and availability (Chi-square tests of homogeneity followed by construction of confidence intervals around the difference between use and availability within habitats, P < 0.05 with sequential Bonferroni adjustments based upon the number of comparisons within each site). ND designates no data because the habitat type was not present at the site.
Table 3.1. Ivlev’s electivity indices (Lechowicz 1982) for caching of Garry oak acorns by Steller’s Jays at two sites in Metchosin, B.C. Indices calculated as \((p_{ci} - p_{ti}) / (p_{ci} + p_{ti})\) where \(p_{ci} =\) proportion of cached acorns in habitat \(i\) and \(p_{ti} =\) proportion of transect locations in habitat \(i\). Positive values indicate usage greater than availability. Negative values indicate usage less than availability. ND designates no data because the habitat type was not present at the site.

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<th>Habitat type</th>
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<td>Mary Hill</td>
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<td>Shrub</td>
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<tr>
<td>Rocky outcrop</td>
<td>-0.50</td>
</tr>
<tr>
<td>Conifer canopy</td>
<td>-0.42</td>
</tr>
<tr>
<td>Mixed edge</td>
<td>-0.09</td>
</tr>
<tr>
<td>Mixed canopy</td>
<td>0.07</td>
</tr>
<tr>
<td>Oak edge</td>
<td>0.12</td>
</tr>
<tr>
<td>Oak canopy</td>
<td>0.14</td>
</tr>
<tr>
<td>Conifer edge</td>
<td>0.15</td>
</tr>
<tr>
<td>Small clump</td>
<td>0.65</td>
</tr>
<tr>
<td>Conifer sapling</td>
<td>ND</td>
</tr>
<tr>
<td>Riparian</td>
<td>ND</td>
</tr>
</tbody>
</table>
mixed edge habitats at Rocky Point suggest selection (Table 3.1), differences between use and availability are not significant.

Despite the high degree of selectivity for the preferred habitat types, only about half of the acorns were cached in these habitats (Fig. 3.5). The remainder were scattered to greater or lesser degrees among the other habitats.

Vegetation Cover

At both sites, Steller's Jays preferred locations with sparse herb cover and avoided locations with dense herb cover (Fig. 3.6, Table 3.2). This selectivity was more strongly expressed for herb cover within 1 m of the locations than for herb cover within 5 m of the locations. Differences between use and availability were more pronounced at Rocky Point than at Mary Hill. At Rocky Point, 70% of the cache locations but only 16% of transect locations had ≤ 20% herb cover within a 1-m radius, and 65% of transect locations but only 9% of caches had > 80% herb cover within the same radius. At Mary Hill, 65% of the cache locations but only 27% of transect locations had ≤ 20% herb cover within a 1-m radius, and 44% of transect locations but only 9% of caches had > 80% cover within a 1-m radius. The numbers of caches and transect locations were both distributed relatively evenly among the intermediate classes of herb cover for both radii at both sites.

Steller’s Jays preferred to cache acorns at locations with substantial shrub cover (Fig. 3.7, Table 3.2). Similar to the herb layer, selectivity for shrub cover was more pronounced within a 1-m radius and at Rocky Point. Forty-nine percent (Mary Hill) and 56% (Rocky Point) of acorns were cached at locations with > 80% shrub cover within a 1-m radius, despite the fact that only 31% (Mary Hill) and 21% (Rocky Point) of transect locations were in this cover class. In contrast, jays avoided locations with little or no shrub cover. At Mary Hill, 35% of transect locations had ≤ 20% shrub cover within 1 m, but jays buried only 18% of caches in locations
Figure 3.6. Percent cover of the herb layer (0 to 1 m high) for locations of acorns cached by Steller's Jays and locations along transects at two sites in Metchosin, B.C. Cover was estimated for 1-m and 5-m radius circles centred on the caches and on points every 25 m along transects located 25 m apart. Mary Hill caches n = 172 (1-m radius) or 173 (5-m radius) and transects n = 356. Rocky Point caches n = 131 and transects n = 409.
Figure 3.7. Percent cover of the shrub layer (> 1 to 5 m high) for locations of acorns cached by Steller’s Jays and locations along transects at two sites in Metchosin, B.C. Cover was estimated for 1-m and 5-m radius circles centred on the caches and on points every 25 m along transects located 25 m apart. Mary Hill caches n = 174 (1-m radius) or 177 (5-m radius) and transects n = 356. Rocky Point caches n = 132 and transects n = 409.
Figure 3.8. Percent cover of the tree layer (> 5 m high) for locations of acorns cached by Steller’s Jays and locations along transects at two sites in Metchosin, B.C. Cover was estimated for 1-m and 5-m radius circles centred on the caches and on points every 25 m along transects located 25 m apart. Mary Hill caches n = 177 and transects n = 356. Rocky Point caches n = 131 and transects n = 409.
Table 3.2. Kolmogorov-Smirnov D statistics for comparisons of percent cover of vegetation at locations where Garry oak acorns were cached by Steller’s Jays with percent cover of vegetation at locations along transects at two sites in Metchosin, B.C. Percent cover in the herb (0 to 1 m high), shrub (>1 to 5 m high) and tree (> 5 m high) was estimated for 1- and 5-m radius circles centred on the caches and on points every 25 m along transects located 25 m apart. Mary Hill caches n = 172-177 and transects n = 356. Rocky Point caches n = 131-132 and transects n = 409. All comparisons significant for 2-tailed tests with sequential Bonferroni adjustments based on the number of comparisons within each site, P < 0.05.

<table>
<thead>
<tr>
<th>Site</th>
<th>Herb layer</th>
<th>Shrub layer</th>
<th>Tree layer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1-m radius</td>
<td>5-m radius</td>
<td>1-m radius</td>
</tr>
<tr>
<td>Mary Hill</td>
<td>0.38</td>
<td>0.34</td>
<td>0.21</td>
</tr>
<tr>
<td>Rocky Point</td>
<td>0.61</td>
<td>0.60</td>
<td>0.43</td>
</tr>
</tbody>
</table>
lacking shrubs. At Rocky Point, 58% of transect locations had ≤ 20% shrub cover within 1 m, but jays buried only 17% of caches in locations lacking shrubs. At Rocky Point, the 2 highest classes of shrub cover within a 5-m radius (61-80% and 81-100%) were most preferred for caching acorns. At Mary Hill, the 61-80% cover class was preferred.

Jays avoided sparsely treed areas at both sites (Fig. 3.8, Table 3.2). Fifty eight percent (Mary Hill) and 49% (Rocky Point) of transect locations had ≤ 20% tree cover within a 1-m radius, but only 40 and 20% of caches respectively were in such locations. Very small proportions of each site had intermediate tree cover values within a 1-m radius, and usage of such locations was similarly negligible. Jays used locations with > 80% tree cover within a 1-m radius in greater proportion than they were available. Locations with intermediate (21-80)% tree cover at a 5-m radius tended to be used more than they were available, but selectivity for sites with > 80% tree cover within a 5-m radius was not evident.

Patterns of habitat use by jays are illustrated in the analysis of vegetation cover by habitat type (Fig. 3.9). Jays preferred habitats that had relatively low to moderate herb cover, high shrub cover, and moderate to high tree cover (Figs. 3.5 and 3.9, Table 3.1). All habitat types with this combination of structural attributes (small clump at Mary Hill; conifer sapling and riparian at Rocky Point) were used in greater proportion than they were available. Habitats avoided by jays (herb, shrub, rocky outcrop, and conifer canopy at Mary Hill; herb, shrub, and oak canopy at Rocky Point) varied in structure. All had dense herb cover, little shrub cover, sparse cover in the tree layer, or a combination of these attributes.

Visibility is better in open habitats. This may have biased my observations by decreasing my ability to detect Steller's Jays in habitats with dense vegetation in the shrub and tree layers. Because habitats with these characteristics are preferred by Steller's Jays, such bias would be conservative, and would not have greatly affected my interpretation of the data.
Figure 3.9. Percent vegetation cover in different habitat types for locations along transects at two sites in Metchosin, B.C. Habitat was classified and cover was estimated in the herb (0 to 1 m high), shrub (>1 to 5 m high) and tree (> 5 m high) layers for 1-m radius circles centred on points every 25 m along transects located 25 m apart. Habitat types are as in Fig. 3.4. Sample sizes at Mary Hill are: 42 (HB), 96 (SB), 36 (RO), 39 (CC), 12 (ME), 24 (MC), 31 (OE), 21 (OC), 19 (CE), 36 (SC). Sample sizes at Rocky Point are: 126 (HB), 32 (SB), 3 (RO), 48 (CC), 8 (ME), 80 (MC), 23 (OE), 37 (OC), 14 (CE), 19 (CS), 19 (RP). ND designates no data because the habitat type was not present at the site.
Fate of Hoarded Acorns

I was unable to find 12 out of 155 marked cache locations because the flagging tape or the branch to which it was attached fell between 1994 and 1995. Two out of the remaining 143 cached acorns (1.4 %) had developed into seedlings. Both were at Rocky Point, one in riparian habitat and the other in oak canopy habitat beneath an elevated section of a downed log. Field notes were precise enough to conduct a thorough search for the hoarded acorns at 111 cache locations. All but three (97.3 %) of these acorns had disappeared, apparently predated either by the jay that cached it, another jay, or another species of vertebrate predator. The three acorns that escaped predation included the two seedlings and an acorn cached in lichens on a rocky outcrop at Rocky Point. This acorn had germinated and subsequently died.

Discussion

Acorn Selection

Steller’s Jays preferentially cache sound, mature acorns. Assessment techniques used by jays in this study include those used by Steller’s Jays for assessing piñon pine seeds (Vander Wall and Balda 1981), plus the additional technique of tapping on the acorns.

Although only 54 % of cached acorns showed no sign of damage, it is likely that the proportion of viable acorns cached by Steller’s Jays was higher. Some of the recorded damage consisted of fungal infection, which can have minimal impact on acorn germination (Andersson 1992). Much of the damage consisted of superficial markings. Most of this was surface spotting, which may indicate the presence of filbert weevil (Curculio occidentalis) or filbertworm (Melissopus latiferreanus) larvae, but can also be present on sound acorns (unpubl. data). Highly effective selection for viable seeds, in some cases approaching 100% accuracy, has been documented for European Jays (Bossema 1979), Piñon Jays (Vander Wall and Balda 1981), Blue Jays (Johnson and Adkisson 1985), and Mexican Jays (Hubbard and McPherson 1972).
1997). Although 24% of piñon seeds transported by Steller’s Jays from a feeding station were inedible, Vander Wall and Balda (1981) suggest that this was due to the similar appearance of the experimental edible and inedible seeds. They believe that Steller’s Jays probably make few errors under natural conditions, because sound and unsound piñon seeds can be distinguished by differences in colour.

My study design did not permit me to assess selection for acorn size beyond determining selection for mature acorns, but size selection can have important implications for effectiveness of acorn dispersal. Larger acorn size has been positively associated with acorn viability (Bossema 1979, Hubbard and MacPherson 1997) and seedling emergence, growth, and survival (Tecklin and McCreary 1991, Rice et al. 1993; but see Auchmoody et al. 1994). In previous studies, Mexican Jays (Hubbard and McPherson 1997) and European Jays (Bossema 1979) selected large acorns, but Blue Jays selected acorns from oak species with small and medium-sized acorns in preference to those of species with large acorns (Darley-Hill and Johnson 1981, Scarlett and Smith 1991). Further research should investigate size selection by Steller’s Jays and the implications for dispersal of Garry oaks.

**Transport Distance**

Steller’s Jays appeared to transport acorns at least 1 km, but it is likely that some transport journeys were considerably longer. Steller’s Jays carry piñon pine seeds up to 3 km (Vander Wall and Balda 1981), and Blue Jays have been observed to transport acorns up to 1.9 km (Darley-Hill and Johnson 1981) and beech nuts (*Fagus grandifolia*) up to 4 km (Johnson and Adkisson 1985).

Seed caching by Blue Jays is credited with the rapid northward migration of eastern oaks and other fagaceous trees during post-glacial warming (Johnson and Webb 1989). Long-distance seed dispersal by jays enabled these heavy-seed tree species to achieve migration rates
equivalent to those of tree species with light, wind-dispersed seeds (Johnson and Webb 1989). Current climate and ecosystem models predict dramatic changes in Pacific Northwest ecosystems as global warming proceeds. Much of what is currently Douglas-fir forest in British Columbia is predicted to be replaced by Garry oak ecosystems (Hebda 1997), and elevational shifts combined with overall range expansion of Garry oak savannas are expected throughout the Pacific Northwest (Franklin et al. 1991). Rapid response by Garry oaks to these changes requires effective long-distance dispersal of acorns. *Sciurus* spp. usually disperse seeds within 10’s of metres of the source, although they occasionally transport them farther than 100 m (Vander Wall 1990). Western Scrub-Jays may not carry seeds farther than 500 m (Vander Wall and Balda 1981), and in the current climatic regime do not range farther north than southern Washington State (Campbell et al. 1997). Seed dispersal by Steller’s Jays will probably be essential for a rapid response of Garry oaks in the Pacific Northwest to climate change, especially in British Columbia and Washington.

Territorial behaviour of jays may play an important role in determining acorn transport distances. Resident Blue Jays and Steller’s Jays, which hold territories year-round, congregate at good foraging patches but cache food within their own territories (Johnson and Webb 1989, Brown 1963). Their territories do not have clearly defined boundaries, but instead consist of zones of relative intraspecific dominance that diminishes with distance from the nest (Brown 1963). Social and territorial organization has not been described for irruptive winter populations of Steller’s Jays, but birds probably establish winter territories (Stewart and Shepard 1994).

Habitat structure is a more important determinant of territory location than food availability for resident populations of Blue Jays (Johnson and Webb 1989). If territorial behaviour for winter populations of Steller’s Jays is similar to that of populations of year-round residents, caching but not foraging locations should reflect territorial occupancy. Steller’s Jays
in my study selected caching locations with distinct vegetation structure, but if and how this relates to selection of territories needs further investigation.

Transport distances traveled by resident Blue and Steller's Jays are determined by the distances between jay territories and foraging areas (Vander Wall and Balda 1981, Johnson and Adkisson 1985, Johnson and Webb 1989). If Steller's Jays established winter territories at or near Mary Hill and Rocky Point, distances between territories and foraging areas would have determined the distribution of transport distances in my study. If the locations of the territories were determined primarily by vegetation structure, distances from acorn sources could vary greatly. Some would be close to acorn sources and others would be farther away. Transport distances would vary accordingly.

Johnson and Webb (1989) suggest that maximum dispersal distances are a consequence of relatively isolated acorn-rich patches of oak trees. Jays will travel as far as necessary to harvest acorns, presumably up to a threshold distance at which the tradeoff between value of the acorns and energetic cost of travel makes such journeys unprofitable. My results indicate that vegetation structure of the intervening habitat is also an important factor. Steller's Jays in my study did not transport acorns across a meadow devoid of trees, but readily crossed larger expanses containing scattered trees. Jays are slow, weak fliers (Vander Wall and Balda 1981), and are probably extremely vulnerable to the many hawks that migrate over the study area in autumn. The scattered trees can provide cover as well as lookout structures for the jays as they transport acorns, and appear to be important landscape components along transport routes. Although Steller's Jays sometimes crossed extensive open areas without making such stopovers in my study, this only occurred at the study site with numerous scattered trees. The trees may have served as potential refugia for the jays if needed, and thus facilitated these longer flights even when they were not used. This interpretation is consistent with other descriptions of flight behaviour of Steller's Jays and Blue Jays. Migrating Steller's Jays were unwilling to cross
expanses of open water (Stewart and Shepard 1994), and Steller’s Jays moved in a secretive
fashion and made frequent stops in the canopy when transporting pine seeds (Vander Wall and
Balda 1981). Blue Jays caching beechnuts in Wisconsin followed fencerows through an open
landscape, and often perched in tall dead snags (Johnson and Adkisson 1985).

Steller’s Jays dispersed acorns over a range of distances in my study. This may be
important for Garry oaks in a landscape that is becoming increasingly developed and fragmented
by urbanization (Erickson 1996, Ussery 1997). If acorns are dispersed widely across the
landscape, specific distances between remnant oak patches is not critical, and there is high
potential for minimizing isolation of a large proportion of the patches. However, my study sites
were relatively undeveloped, and there is little information about transport distances in more
urbanized settings. This information is badly needed to assess the impacts of fragmentation on
Garry oak populations in B.C. Blue Jays transported acorns between 100 m and 1.9 km in
suburban Virginia (Darley-Hill and Johnson 1981), but research is needed to investigate
dispersion of caches of Steller’s Jays in urban and suburban areas of southeastern Vancouver
Island.

**Acorn Orientation, Burial Depth, and Substrate**

Most acorns were cached in substrates suitable for seedling establishment simply
because the majority of the ground surface consisted of suitable substrate. Steller’s Jays were
not deterred by a hard surface such as rock or wood underlying a thin layer of soft or loose
materials, and they buried acorns to shallow depths whether the underlying substrate was hard or
soft. However, the jays spent considerable effort covering the acorns from view.

Burial and hiding of Garry oak acorns is critical for acorn survival. Predation is the
primary cause of mortality for dispersed, viable acorns, and predation is significantly greater for
acorns on the ground surface than for acorns that are hidden and buried (Chapter 2). Predation
might be minimized with deeper burial, but bill length may prevent the jays from burying or retrieving acorns that exceed shallow depths (Vander Wall 1990). In addition, the time and energy invested in burying and retrieving acorns at deeper depths may not pay off for Steller’s Jays. Differences in predation levels between acorns cached in the ground cover layer and acorns cached in the soil are not as great as differences between surface acorns and those cached in the ground cover layer (Chapter 2).

Acorn burial by Steller’s Jays provides a second advantage to dispersed acorns of Garry oaks. Acorns lying exposed on the surface are subject to desiccation, but buried acorns are protected (Chapter 2). Shallow burial appears to provide as much advantage as deeper burial. Acorns buried at both experimental depths showed minimal evidence of desiccation (Chapter 2).

The acorns cached by Steller’s Jays were primarily in a horizontal orientation. This is in contrast with the vertical orientation of caches of Western Scrub-Jays (McBride et al. 1991). Epicotyls of vertically oriented acorns can become trapped within the acorn shell, significantly reducing seedling emergence rates (McBride et al. 1991). Garry oak acorns cached by Steller’s Jays are able to extend epicotyls free of this impediment.

**Hoarding Habitat**

Steller’s Jays selected locations with sparse herb cover, dense shrub cover, and dense tree cover to cache acorns. Cached acorns were concentrated in all of the habitat types that shared this complex structure. Habitat selection was more pronounced at a fine scale (1-m radius) than at a coarser scale (5-m radius).

Steller’s Jays used trees to survey the landscape before leaving caching areas, and may have chosen hoarding locations with tree cover because of the proximity of these lookouts. Dense vegetation in the shrub layer may have been important for shielding caching jays from hawks. Sparse herb-layer vegetation would allow jays to see and memorize visual cues at
hoarding locations; vertical beacons are used as cues by European Jays for cache recovery (Bossema 1979) and may also be important for Steller's Jays. These hypotheses for the functional significance of the vegetation characteristics are untested, but provide direction for further research.

When jays fly in to a caching site, vegetation in the tree layer would be visible first and from a relatively broad perspective. As the jays hop from branch to branch towards the ground, vegetation in the shrub layer and then in the herb layer would become visible to them, and their perspective would be progressively narrower as the jays approach the ground. I therefore expected selection to operate at a coarser scale for higher vegetation than for vegetation closer to the ground, but this was not the case. Particularly surprising is the preference for dense tree cover within a 1-m radius, which implies that the jays maintain an awareness of tree cover directly above them, even under dense shrub cover.

Garry oak acorns planted in the 3 habitats (small clump, riparian, and conifer sapling) highly preferred by Steller’s Jays suffered extremely high predation levels (Chapter 2). Because predation was the primary cause of acorn mortality, seedling emergence was consequently among the lowest in these habitats in comparison to other common habitat types at Mary Hill and Rocky Point. I frequently observed Steller’s Jays foraging in these preferred caching habitats, indicating that jays may have been responsible for much of this predation. However, I do not know what the relative impacts were of different acorn predators in different habitats at the sites.

Survival of first-year seedlings was high in the preferred habitat types, but densities of second-year seedlings from acorns planted in habitats preferred by jays remained low relative to most available habitats (Chapter 2). Because of the dense shrub and tree cover, preferred habitats also have low light levels. Survival of first-year Garry oak seedlings was not affected by
shade, but low light levels will likely contribute to mortality of Garry oaks at later stages of development (Chapter 2).

Other studies report that different species of jays cache near edges and in other structurally complex habitats (Chettleburgh 1952, Bossema 1979, DeGange et al. 1989, Johnson and Webb 1989). My study determined that specific structural components are essential features of habitats preferred by Steller’s Jays. For example, habitat edges with tree cover but minimal shrub cover were not preferred, but “small clumps,” which are structurally similar to edges with dense shrub cover, were preferred.

In contrast with my results, other reports describe caching habitats preferred by other species of jays as favourable for oak regeneration (Bossema 1979, Darley-Hill and Johnson 1981, Johnson and Webb 1989). These studies did not compare levels of acorn predation in different habitats, and thereby failed to account for a major factor limiting oak recruitment in some habitats. Site quality in these studies is described largely in terms of light availability. Surprisingly, preferred caching sites for other species of jays are described as relatively open, with high light levels, and thus favourable for shade-intolerant oaks. This is in marked contrast with cache sites preferred by Steller’s Jays in my study. Structural attributes of cache sites preferred by Steller’s Jays include dense mid- and upper-storey vegetation and sparse understorey vegetation. Vegetation structure of habitats used by other species of jays apparently differs considerably.

Despite the pronounced concentration of caches in habitats preferred by Steller’s Jays, half of the acorns were dispersed widely among the remaining habitat types. Some of this dispersion occurred when jays flew into patches of preferred habitat and subsequently crossed boundaries into adjacent patches while searching for hoarding locations. This wide scattering of caches among habitats may be a key component of dispersal of Garry oaks by Steller’s Jays. Seedling emergence and first-year survival vary among these habitats, but some habitats,
especially herb and conifer edge, can produce relatively high densities of second-year seedlings (Chapter 2). In addition, many of these habitats are relatively open and may provide favourable conditions for older Garry oak seedlings and saplings.

**Fate and Numbers of Hoarded Acorns**

With less than 2% of cached acorns producing seedlings, effective dispersal of Garry oaks can only take place if large numbers of acorns are hoarded. I did not estimate numbers of acorns hoarded by Steller’s Jays, but the jays at my study sites appeared to spend most of their time caching acorns for a period of 3-4 weeks. Individual Western Scrub-Jays (McBride *et al.* 1991), Florida Scrub-Jays (DeGange *et al.* 1989), Blue Jays (Darley-Hill and Johnson 1981), and European Jays (Turcek and Kelso 1968) cache several thousand acorns per season, and Steller’s Jays probably cache similar numbers of acorns. Numerous seedlings are growing at Mary Hill and Rocky Point far from mature oaks. These seedlings probably originated from acorns cached by Steller’s Jays. Although I do not know how many seedlings, and ultimately how many mature reproductive trees, develop from acorns dispersed by Steller’s Jays, the evidence indicates that jays successfully disperse Garry oak acorns in British Columbia.

**Conclusions and Recommendations**

Numbers of Steller’s Jays on southern Vancouver Island vary greatly among years and the quantity of acorns produced by Garry oaks is also highly variable among years. Fluctuations in numbers of Steller’s Jays and Garry oak acorns are not synchronous. Variation in numbers of Steller’s Jays shows no discernible pattern (Stewart and Shepard 1994) and cycles of Garry oak acorns are irregular (Stein 1990) or occur over a few years (Silen 1958). This variability can be expected to impact greatly on dispersal of Garry oaks in a given year. Numbers of acorns cached, transport distances, hoarding habitat selection, and acorn fate may vary with absolute
numbers of Steller's Jays and acorns, and with the number of Steller's Jays relative to the
count of acorns available for harvesting and caching. These effects should be investigated.

Garry oaks in British Columbia appear to have a less effective dispersal system than
those of oaks that are dispersed by other species of jays. Irregular occupation of Garry oak
habitats and habitat preferences of Steller's Jays place substantial constraints on the numbers of
acorns buried in suitable habitats. These constraints are not shared by other oak species with jay
dispersal systems that are described in the literature.

Transport and caching of Garry oak acorns by Steller's Jays are both associated with
complex, patchy landscapes. Jays use lookout trees to survey the landscape when transporting
acorns and after leaving caching locations. Patchy, structurally complex landscapes can provide
the best habitat for such surveillance, because isolated trees, woodland trees near edges, and trees
that are taller than the surrounding canopy provide the best views. Preferred caching habitats
(dense shrub and tree cover) are characteristics of some habitat edges, riparian areas within
woodlands, and shrubby patches within forests or woodlands. Patchy landscapes are also
associated with effective acorn dispersal by Steller's Jays. Many acorns were cached in habitats
that were adjacent to preferred habitats. Juxtaposition of patches of preferred habitats with other
habitat types appears to play an essential role in dispersal of Garry oak acorns to favourable sites.
The character of the landscape is thus an integral aspect of the dispersal system of Garry oaks in
British Columbia. As vegetation structure is altered and frequently simplified across the
landscape, acorn dispersal may be negatively affected. More information, especially information
applicable to urbanized areas, will help in predicting the impacts of urban development on
dispersal of Garry oak acorns by Steller's Jays.
Chapter 4: Management of Garry Oak Ecosystems

Garry oak ecosystems comprise far less than 0.5 % of the area of British Columbia but contribute substantially to the floral diversity of the province. They host approximately 12.5 % of province’s red-listed (threatened or endangered) and blue-listed (vulnerable) plants in addition to 20 % of the yellow-listed (potentially vulnerable) plants (Erickson 1996). Approximately 6 % of British Columbia’s vascular plants are limited to Garry oak ecosystems (Erickson 1996). Agricultural and urban development have greatly reduced the area of Garry oak ecosystems and urbanization continues to encroach upon remnant patches (Roemer 1972, Meidinger and Pojar 1991, Erickson 1996, Ussery 1997). Exotic species such as Scotch broom (Cytisus scoparius) and orchard grass (Dactylis glomerata) have invaded these ecosystems and altered vegetation structure and species composition (Meidinger and Pojar 1991, Erickson 1996, Ussery 1997). Furthermore, conifer encroachment as a result of fire exclusion threatens Garry oak ecosystems in B.C. as it does throughout the most of the range of Garry oaks (Thilenius 1968, Norton 1979, Barnhardt et al. 1987, Reed and Sugihara 1987, Sugihara and Reed 1987, Turner 1991, Riegel et al. 1992, Agee 1993, Erickson 1996, Ussery 1997, Hastings et al. in press). Garry oak plant communities within the developed landscape of southeastern Vancouver Island are currently classified as S1 (critically imperiled) and S2 (imperiled) by the B.C. Conservation Data Centre (unpublished). This classification of Garry oak stands underscores the need for conservation strategies that will ensure the survival of Garry oak ecosystems and the species that they sustain.

Conservation of Garry oak ecosystems must include protected areas, and such initiatives are part of the management approach of government agencies, non-governmental organizations, and private citizens through mechanisms such as conservation covenants on private lands. Ecosystem conservation, however, cannot be assured solely by protection of extant stands of Garry oak. Retention and restoration of ecological function must be an integral component of
conservation efforts. Ecological processes such as dispersal and regeneration of Garry oaks must be retained, and management prescriptions must be guided by an understanding of these processes. Most if not all remnant Garry oak stands have been degraded (Erickson 1996, Ussery 1997) and restoration offers opportunities to reinstate vegetation structure, species composition, and ecological function in these stands.

There is concern about inadequate regeneration of Garry oaks in British Columbia, but assessing the current state of oak regeneration in relation to historical regeneration patterns is a complex task. Garry oaks can reproduce by sprouts as well as by seeds, and the relative importance of these reproductive mechanisms under different ecological regimes is not known (Agee 1993). Fire, which stimulates vigorous sprouting, was an important component of Garry oak ecosystem management that was practiced by Indigenous Peoples throughout most or all of the range of Garry oaks (Norton 1979, Boyd 1986, Reed and Sugihara 1987, Sugihara and Reed 1987, Turner 1991, Agee 1993, Erickson 1996, Ussery 1997, Hastings et al. in press). The Straits Salish on southern Vancouver Island burned Garry oak ecosystems in the late summer or fall to promote a bountiful harvest of camas (Camassia quamash and C. leichtlinii), a staple root vegetable which grows in Garry oak savannas and associated meadow habitats (Roemer 1972, Turner 1991, Erickson 1996). These frequent and consequently low-intensity burns maintained the open vegetation structure necessary for camas by eliminating encroaching woody vegetation, including shrubs, Garry oak seedlings and sprouts, and conifer seedlings. Fire-tolerant mature Garry oaks persisted in this fire regime.

Subsequent to European settlement and concomitant policies of fire exclusion, regeneration of Garry oaks has undoubtedly changed in profound but largely unknown ways. What is clear, however, is that in many locations Garry oak seedlings or sprouts proliferated at open sites between the mature trees within former savannas. In the absence of fire, savannas located on relatively deep soils convert to Garry oak woodlands. Conifer seedlings subsequently
flourish under the canopy of the oak woodland and the stand ultimately succeeds to conifer forest
Garry oak regeneration must therefore consider historical and current disturbance regimes,
edaphic characteristics, and current successional state of Garry oak stands. Erickson (1996)
found substantial cover of Garry oaks ≤ 2 m tall in some Garry oak stands and sparse to absent
cover in other Garry oak stands in B.C. Further information is needed to evaluate these data in
relation to historic regeneration patterns. Such an evaluation could help managers formulate
site-specific objectives for within-stand regeneration of Garry oaks.

Regeneration of Garry oaks in B.C., however, is not limited to locations within Garry
oak stands. Acorns are dispersed by Steller’s Jays to a variety of habitats located within stands,
adjacent to stands, and at great distances from stands. Hence, Garry oak regeneration must be
considered at the landscape as well as the stand level. Assessment of regeneration must
incorporate information about where and how jays cache acorns as well as survival and growth
of acorns, seedlings, and saplings at different locations.

I recommend that management for conservation of Garry oaks includes protection of
natural regeneration processes and restoration of these processes where they are disrupted.
Efforts must be applied at both the stand and landscape scales. My results on seedling ecology
and dispersal of Garry oaks in B.C. offer guidance to conservation strategies and prescriptions,
but much potentially useful information is unknown.

To ensure the long term presence of Garry oak ecosystems in British Columbia, I
recommend the following:

1. Efforts to designate remnant patches of Garry oak ecosystems as protected areas should
continue, but adjacent land should also be protected to provide sites for acorn dispersal and
establishment of seedlings. Steller’s Jays prefer habitats with dense shrub cover, dense tree
cover, and sparse herb cover. Habitats with this vegetation structure should be retained to ensure that jays remain as part of the ecosystem. Dispersal of acorns to sites favourable for oak regeneration requires that acorns are also transported by Steller’s Jays to sites with minimal shrub and tree cover. This is facilitated by the juxtaposition of these habitats with habitats preferred by Steller’s Jays. Patchy, complex vegetation structure should therefore be retained if present, and creation or restoration of these conditions should be considered. These prescriptions should be applied to areas surrounding oak stands. This approach should also be considered within Garry oak stands, but must be integrated with management objectives intended to retain or restore historical vegetation structure in the stands. We do not have detailed knowledge of historic stand structure, and therefore do not know to what extent small patches of dense shrub and tree vegetation may have existed within open Garry oak savannas. Furthermore, regeneration of Garry oaks by seed may be relatively less important within oak stands than regeneration by sprout, so dispersal of acorns by Steller’s Jays within oak stands may be less critical than dispersal to surrounding areas. Given our current lack of knowledge, the merit of retaining habitat patchiness within oak stands is unclear. However, attempts should be made and the results monitored.

2. Trees should be retained or planted within large, open expanses to encourage long-distance dispersal by Steller’s Jays. My results indicate that isolated, scattered trees facilitate transport of acorns across large meadows. Such trees may also promote acorn dispersal across urban areas. Steller’s Jays did not transport acorns across a meadow devoid of trees that was 150 m wide, so distances between scattered trees should be considerably less than 150 m. Because Steller’s Jays sometimes transport acorns 600 m and probably more than 1 km from harvest locations, acorn dispersal may be facilitated by scattered trees located at considerable distances from oak stands.
3. Prescribed fire, often in conjunction with other techniques, has been an effective restoration tool in Garry oak ecosystems at a number of locations (Sugihara and Reed 1987, Agee 1993, Hastings et al. in press). Conifer encroachment has been arrested, and Garry oak stands have successfully been restored to open, park-like vegetation structure. However, the response of exotic plants has varied; in some cases, cover of exotics has increased while in others it has decreased (Sugihara and Reed 1987, Agee 1993). Prescribed fire should be considered for management of Garry oak stands on southeastern Vancouver Island. Edaphic and physiographic characteristics, floristic composition, and vegetation structure should be assessed for each Garry oak stand when evaluating the potential efficacy of prescribed fire. If prescribed fires are instituted, responses of the ecosystem must be monitored. In particular, the effects of fire on native and introduced herbs and shrubs as well as upon Garry oak regeneration by seed and sprout are poorly understood and should be examined.

4. Acorn dispersal by Steller’s Jays can be augmented by planting Garry oaks. Because regeneration dynamics within Garry oak stands are complex and poorly understood, oaks should not be planted within Garry oak stands in the absence of clear evidence that regeneration is inadequate. Historic fire regimes apparently hindered the establishment of Garry oak seedlings; hence, bolstering regeneration by planting Garry oaks within stands may be inappropriate. In contrast, because of past and current loss of Garry oak ecosystems on southeastern Vancouver Island, planting Garry oaks throughout the region should be implemented to establish new oak populations. In my planting experiment, acorns buried in some habitats produced relatively high numbers of seedlings. Hence, direct seeding of acorns is probably more cost-effective than transplanting nursery-grown seedlings. Acorns of Garry oaks can be collected during September or October. To maximize viability of planted acorns, large, mature acorns that are devoid of spotting, insect holes, cracks, discoloration, or other
defects should be selected. These acorns should then be placed in water and "floaters" discarded. Acorns should be kept damp until planting, which should occur shortly after acorns are collected. Planting depth should be just below the soil surface beneath ground cover of matted grass roots, leaf litter, or other debris. Acorns should be planted on their sides to minimize the possibility that emerging epicotyls will be trapped within the acorn shell. Acorns should be planted not only in sites where survival of seedlings is high, but also in less suitable sites. Habitats on relatively flat terrain with deep soil, sparse shrub cover, and sparse tree cover are favourable for oak regeneration because of relatively low rates of acorn predation, low rates of seedling desiccation, and little shade to hinder seedling growth. Xeric conditions in habitats with thin soil and sloping terrain may desiccate many oak seedlings, but planting acorns at open, xeric sites may also promote oak regeneration. Conifers and other drought intolerant species cannot invade and outcompete slow-growing oaks, and consequently those oak seedlings that survive drought conditions may develop to maturity. Planting programs should span several years to ensure suitable weather for survival of acorns and establishment of seedlings.

5. Managers must ensure that Steller's Jays continue to frequent Garry oak habitats in British Columbia. Populations of Steller's Jays in British Columbia are increasing (Sauer et al. 1996, Sauer et al. 1997), but our understanding of ecological factors influencing occupancy of Garry oak habitats on southeastern Vancouver Island is limited (Stewart and Shepard 1994). In particular, continued urbanization may result in declines of Steller's Jays in the region. Regular examination of Christmas Bird Count data or other methods should be used to monitor winter populations of Steller's Jays on southeastern Vancouver Island.
Further research is required to extend our understanding of Garry oak dispersal and reproduction. The effects of inter-annual variation on acorn and first-year seedling survival (e.g., acorn production, precipitation, populations of Steller’s Jays, populations of other acorn predators and seedling herbivores) should be investigated. Additional research is needed on acorn consumers and their behaviour which would assist managers in understanding ecological processes in Garry oak ecosystems. Such research should include: effects of introduced eastern gray squirrels on acorn dispersal; selection for acorn size by Steller’s Jays and implications for acorn dispersal; territorial behaviour of winter populations of Steller’s Jays and effect of this behaviour upon distances that acorns are transported and where they are cached; selection by Steller’s Jays for acorn harvesting sites; caching behaviour of Steller’s Jays in developed landscapes; and functional significance of habitat preferences of Steller’s Jays. Most importantly, research on recruitment beyond the seedling stage and the relative contributions of seedlings and saplings to stand regeneration are needed to understand stand dynamics of Garry oak ecosystems and to refine management initiatives.
Literature Cited


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