Dispersal of Garry Oak Acorns by Steller's Jays

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ABSTRACT

Acorns of Garry oaks (*Quercus garryana*) in British Columbia are dispersed primarily by Steller's jays (*Cyanocitta stelleri*). We conducted a planting experiment and observed caching by Steller's jays to examine factors influencing acorn and seedling survival and to assess the role of the jays in oak regeneration. Almost all acorns cached by jays were hidden beneath ground cover or soil and thus protected from predation and desiccation. Steller's jays preferred to cache acorns in habitats with abundant tree and shrub cover but sparse herb cover. Approximately 50% of the acorns were cached in these habitats, but seedling establishment was low because of acorn predation. The rest of the acorns were cached in other habitats. Some of these habitats provided conditions favourable for oak regeneration. Conservation of Garry oak ecosystems must incorporate strategies that will retain dispersal and regeneration processes.

Key words: acorn, *Cyanocitta stelleri*, food hoarding, Garry oak, *Quercus garryana*, seed dispersal, seedling, Steller's jay.

Garry oak ecosystems are among the most endangered in Canada. Agricultural and urban development coupled with introductions of exotic plant species such as Scotch broom (*Cytisus scoparius*) and orchard grass (*Dactylis glomerata*) have contributed to the destruction, degradation, and fragmentation of these ecosystems in British Columbia (Ussery 1997). Furthermore, fire exclusion threatens Garry oak ecosystems in British Columbia as it does throughout most of the range of Garry oaks (Agee 1993). Prior to European settlement, Coast Salish peoples of southern Vancouver Island burned Garry oak ecosystems regularly to enhance productivity of camas (*Camassia quamash* and *C. leichtlinii*), a nutritious bulb that comprised one of their staple foods (Turner 1991). These fires maintained the open vegetation structure of Garry oak savannahs. Without fire, conifers and other woody species encroach into oak savannahs.

Changes to the extent, species composition, vegetation structure, and disturbance regime of Garry oak ecosystems can affect oak regeneration. As a result, there is growing concern about the adequacy of regeneration of Garry oaks in British Columbia (Erickson 1996). Garry oaks in British Columbia rely upon Steller's jays for acorn dispersal. The jays bury acorns singly in the ground to use as overwinter food, but may not recover all of the acorns they bury, thereby dispersing seeds to caching locations. Regeneration must therefore rely on where and how acorns are dispersed by the jays.

Our objectives were to examine factors influencing acorn and seedling survival and to assess the role of Steller's jays in regeneration of Garry oaks. We examined the effects of acorn burial depth and habitat type on Garry oak regeneration. Both factors are influenced by food-hoarding animals and may be important in Garry oak reproduction. In addition, we determined burial depths and habitats used by Steller's jays to cache acorns and assessed the implications of jay behaviour to reproduction of Garry oaks.

STUDY AREA

Our research was conducted in Metchosin on the southern tip of Vancouver Island, British Columbia. Two sites were used, Mary Hill and Rocky Point, about 2 km apart. 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. The oak cover is primarily in savannah form. Rocky Point is relatively flat, and has rocky

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outcrops as well as areas with deeper soil. Most of the oaks at Rocky Point comprise a woodland.

METHODS

Planting Experiment

We collected acorns from productive oak trees scattered throughout the study sites in September 1994. We selected undamaged acorns and planted them between 10 and 17 October 1994. We planted 2,700 acorns in a split-plot, completely randomized design to test the effects of burial depth and habitat on acorn and seedling mortality. We used 6 replicates of each habitat type at each site. Although most habitat types occurred at both sites, there were a few differences. "Small clump" habitat was present only at Mary Hill. Two habitats, "conifer sapling" and "riparian," were present only at Rocky Point. Ten acorns were planted at each of 3 planting depths within each planting plot: on the surface, under ground cover (leaf litter, matted grass roots, moss, or lichens), and buried in soil just below the soil surface. We visually estimated vegetation cover within a 5-m radius from the centre of each planting plot. Total percent cover was estimated for 3 vegetation layers: herb (0–1 m high), shrub (>1–5 m high) and tree (>5 m high). Plots were revisited in June 1995 and 1996 to determine presence of acorns and seedlings, and condition of acorns and seedlings if they were present.

Data were analyzed using analysis of variance (ANOVA), with habitat and depth as the 2 treatment factors. Values were calculated as proportions and arcsine squareroot transformed to improve normality. For depth comparisons, significant *F*-tests were followed by multiple comparisons of means with sequential Bonferroni adjustments (Rice 1989). For habitat comparisons, significant *F*-tests were followed by Tukey's honestly significant difference tests, which are more powerful than the Bonferroni method when comparing numerous means (SPSS 1997).

Observations of Steller's Jays

We observed Steller's jays from August to October 1994. Each field day, 2 observers walked through different areas of Mary Hill or Rocky Point in search of hoarding activity by Steller's jays. We noted the transport distance of all observations of acorn transport by jays. For each observation of acorn caching, the observer waited until the jay departed and attempted to locate the cached acorn. If the acorn was located, burial depth of the acorn was recorded and the acorn was subsequently replaced. We classified the habitat in which each acorn was cached and estimated total percent cover of vegetation in the herb, shrub, and tree layers for circular plots (5-m radius) centred at the cache location.

We used chi-square tests of homogeneity to compare use and availability of habitat types. If chi-square tests were significant, we calculated confidence intervals around the differences between use and availability (Marcum and Loftsgaarden 1980), with sequential Bonferroni adjustments to control experimentwise Type I error (Rice 1989).

Table 1. Effects of planting depth and habitat type on percentages of Garry oak acorns removed by predators at Mary Hill in Metchosin, British Columbia, 1995.

Planting depth[a]	Mean percent removal
Surface	89.5A[b]
Ground cover	60.7B
Soil	44.6C
Habitat type[c]	
Small clump	83.9A[b]
Conifer canopy	83.9A
Shrub	77.8AB
Conifer edge	59.4AB
Oak canopy	50.5B
Oak edge	49.4B
Herb	49.4B

[a] $F_{2,70} = 90.72, P < 0.01$.
[b] Within planting depth or habitat types, means with the same letters are not different ($P < 0.05$).
[c] $F_{6,35} = 5.47, P < 0.01$.

RESULTS

Planting Experiment

Predation on planted acorns was the primary cause of reproductive failure in our experiment. Predation was extremely high for acorns planted on the surface at Mary Hill (Table 1). Deeper planting significantly lowered predation across habitat types. Predation also varied among habitats at Mary Hill. Our experimental design did not permit us to identify which vertebrate species were removing the acorns.

At Rocky Point, an interaction between habitat and depth precluded analysis of depth effect across habitats and habitat effect across depths. Depth effects within each habitat were less consistent than those at Mary Hill, but trends were similar. Predation varied among habitats within each depth (ANOVA and Tukey tests, $P < 0.05$).

Vegetation structure of habitats with low predation at both sites varied, as did vegetation structure of habitats with high predation. All 3 habitats characterized by sparse herb cover, dense shrub cover, and moderate to high tree cover ("small clump" at Mary Hill; "conifer sapling" and "riparian" at Rocky Point) were among those with high predation.

Of the acorns that were not predated, many of those on the surface died (70% and 68% at Mary Hill and Rocky Point respectively), but buried acorns had less than 15% mortality at both sites. Causes of acorn mortality could not be identified in most cases.

Mortality of seedlings at Mary Hill between 1995 and 1996

Table 2. Habitat selection by Steller's jays for caching of Garry oak acorns at 2 sites in Metchosin, British Columbia, 1994.[a]

Habitat type	Mary Hill[b]	Rocky Point[c]
Small clump[d]	+	
Riparian[d]		+
Conifer sapling[d]		+
Conifer edge	0	0
Oak edge	0	0
Mixed canopy	0	0
Mixed edge	0	0
Oak canopy	0	-
Conifer canopy	-	0
Rocky outcrop	-	0
Shrub	-	-
Herb	-	-

[a] preferred = "+" (use > availability, $P < 0.05$); avoided = "-" (use < availability, $P < 0.05$); "0" = no selectivity (use = availability, $P < 0.05$).

[b] n = 179 (use) and 356 (availability).

[c] n = 132 (use) and 409 (availability).

[d] Habitat type present at only 1 site.

varied among habitats (ANOVA and Tukey tests, $P < 0.05$). Seedling desiccation, the only identified cause of seedling mortality, was an important factor in "shrub," "oak canopy," "oak edge," and "herb" habitats at Mary Hill (11–59%). Many of the planting plots in these habitats had thin soil and rocky outcrops, characteristics less prominent in the other habitat types. These habitats are the only ones at Mary Hill lacking a conifer component. Seedling mortality due to undetermined causes was relatively constant among habitats at Mary Hill (<25%). Virtually no desiccation of seedlings occurred at Rocky Point. Seedling mortality was low (<18%) in all habitats at Rocky Point.

Two years after planting, acorns planted in "conifer edge" and "herb" habitats had the highest numbers of seedlings at both sites. "'Small clump" habitat at Mary Hill and "conifer sapling" and "riparian" habitats at Rocky Point had among the lowest numbers of oak seedlings.

Observations of Steller's Jays

Steller's jays transported acorns between a few centimetres and 600 m from the parent tree. At least 1 group of jays appeared to transport acorns more than 1 km. Jays did not transport acorns across a meadow (approximately 150 by 300 m) without scattered trees, but readily transported acorns across open habitats wider than 300 m with numerous scattered trees. The jays frequently used the trees as stopover structures, landing in the trees and surveying the area before continuing on transport journeys. Burial depth of cached acorns was remarkably similar between sites. Virtually all cached acorns were buried. Most acorns (75–76%) were buried in the ground cover layer.

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 (chi-square and confidence interval tests, $P < 0.05$; Table 2). Steller's jays preferred to cache acorns in habitats with sparse herb vegetation, dense shrub vegetation, and dense cover in the tree layer. These preferred habitats were "small clump" at Mary Hill, and "conifer sapling" and "riparian" at Rocky Point, habitats with high levels of acorn predation. Steller's jays avoided locations with dense herb cover, sparse shrub cover, or sparse tree cover. Despite the high degree of selectivity for the preferred habitat types, only about 50% of the acorns were cached in these habitats. The remainder were distributed among the other habitats.

DISCUSSION

Burial of Garry oak acorns is critical for acorn survival. By burying acorns in the ground cover and soil, Steller's jays protect cached acorns from removal by predators. Although we could not identify the species that were removing the acorns in our experiment, numerous species of birds and mammals consume acorns, many of which were common at Mary Hill and Rocky Point. Burial probably also protects the acorns from desiccation (Borchert et al. 1989, Tietje et al. 1991) although evidence in our study was suggestive rather than conclusive.

Quality of habitat for regeneration of Garry oak was dynamic in our study. Some habitats were good for acorn survival but were poor for seedling survival, and vice versa. Variation in acorn mortality among habitats resulted primarily from predation. Some of this variation was associated with vegetation structure. In contrast, variation in seedling mortality resulted primarily from edaphic and physiographic factors contributing to seedling desiccation. Habitat quality may be similarly dynamic as the oaks continue to develop. In particular, shade intolerance is commonly associated with Garry oaks (Stein 1990, Agee 1993), and evidently becomes more important at a later stage of development.

Habitat preferences of Steller's jays appear to substantially constrain effective dispersal of Garry oaks to favourable sites. Preferred habitats have high rates of acorn predation. Seedling desiccation did not occur in habitats preferred by Steller's jays. However, numbers of acorns removed by predators exceeded numbers of seedlings killed by desiccation, so that seedling numbers in habitats preferred by Steller's jays were among the lowest of all habitats. Furthermore, because of the dense overstory vegetation in preferred habitats, limited light availability probably also limits survival and growth of older Garry oak seedlings or saplings.

Approximately 50% of the acorns were cached in habitats not preferred by Steller's jays. Much of this dispersion resulted when jays landed in patches of preferred habitat but subsequently moved to adjacent patches of different habitat as they searched for caching sites. Some of these habitats were favourable for oak regeneration. This wide scattering of caches among habitats may be a key component of effective dispersal of Garry oaks by Steller's jays.

MANAGEMENT RECOMMENDATIONS

Conservation of Garry oak ecosystems requires protection not only of extant stands of Garry oak but also management of sites capable of supporting Garry oaks. Ecological processes including dispersal and regeneration of Garry oaks must be retained, and management prescriptions must be guided by an understanding of these processes. Steller's jays transport and cache acorns within, adjacent to, and at long distances from oak stands. Hence, oak regeneration must be considered at both the stand and landscape levels.

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

1. Efforts to protect remnant patches of Garry oak ecosystems should continue, but adjacent land should also be protected to provide sites for acorn dispersal and seedling establishment.
2. Steller's jays prefer habitats with sparse herb cover, dense shrub cover, and dense tree cover. Habitats with this vegetation structure should be retained to ensure that jays remain 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 sparse shrub and tree cover. This process 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.
3. Scattered trees should be planted in open areas to facilitate transport of acorns by Steller's jays.
4. Because Garry oak ecosystems have been severely fragmented and reduced in area, acorns should be planted to establish new oak populations. Planting of acorns just below the soil surface, in habitats on flat terrain with deep soil and sparse overstory vegetation, will ensure greatest survival of acorns and seedlings. Acorns should also be planted in sloping, thin-soiled habitats, where xeric conditions will prevent conifers from establishing and outcompeting slower-growing oaks.
5. Managers must ensure that Steller's jays continue to frequent Garry oak ecosystems in British Columbia. Occupancy of Garry oak ecosystems by Steller's jays is seasonal and our understanding of ecological factors influencing this occupancy is limited (Stewart and Shepard 1994). In particular, continued urbanization may result in declines of Steller's jays in the region.

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