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Source: Northwest Science, 82(sp1) : 197-209

Published By: Northwest Scientific Association

URL: <https://doi.org/10.3955/0029-344X-82.S.I.197>

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Abstract

Hydrochory, the dispersal of seeds by water, is important for maintaining the diversity and genetic continuity of riparian plant communities. Dams may reduce levels of hydrochory to downstream reaches by trapping seeds within their impoundments. On Washington's Olympic Peninsula, we studied whether hydrochory in the Elwha River was affected by the Glines Canyon Dam. We also explored whether Lake Mills, the dam's impoundment, holds a hidden seed bank of trapped hydrochorous seeds, which may aid in revegetation after the dam is removed. Hydrochory levels were sampled during three time periods in July and August, 2005 using floating and submerged drift nets above and below Glines Canyon Dam. The Lake Mills seed bank was sampled along transects across Lake Mills. For all drift net samples there was a 90% reduction in seed abundance and 84% reduction in species richness below Glines Canyon Dam. The decline in seed abundance was seen at each of the three sampling times. Similar numbers of seeds were found in both floating and submerged nets, suggesting that buoyancy is not required for hydrochory in this system. Relatively few seeds germinated from the Lake Mills seed bank. There was no relationship between seed density and distance from the Lake Mills delta; however seed density declined with increasing water depth. Our results suggest that Glines Canyon Dam has reduced the rate of hydrochory in the Elwha River, which may cause fragmentation of the riparian flora and reduced diversity of riparian species below the dam.

Introduction

The role of rivers as dispersal corridors for migratory fish species such as a salmon has been extensively studied in the Pacific Northwest. Far less well-known is the role that rivers play as dispersers of other organisms such as plants or aquatic insects. The dispersal of plants by rivers is referred to as hydrochory, which is technically defined as the dispersal of seeds by water. Hydrochory is an important mechanism for dispersal of riparian plant species (Nilsson et al. 1991, Johansson et al. 1996, Andersson and Nilsson 2002, Gurnell et al. 2006) and has been shown by a variety of studies to significantly affect the structure of riparian vegetation (Hampe 2004, Jansson et al. 2005).

Long-distance hydrochory along river corridors can connect populations that would otherwise be isolated (Vogt et al. 2004). In cases where the genetic structure of riparian plant populations has been studied, it has been found to be consistent with long distance seed dispersal by hydrochory.

Populations located far apart from one another showed a higher degree of genetic similarity than predicted by models not factoring in a source of long-distance, directional dispersal (Kudoh and Whigham 1997, DeWoody et al. 2004, Jacquemyn et al. 2006, Kudoh et al. 2006).

Hydrochory can vary spatially and temporally along a river. Longitudinally, hydrochores tend to be more abundant further downstream within the watershed, as demonstrated by Andersson and Nilsson (2002). The volume and speed of water flow can further influence the spatial and temporal distribution of hydrochores. For example, Johansson and Nilsson (1993) found that the spatial distribution of hydrochorous propagules of a clonal aquatic plant was concentrated on river curves and obstacles (both of which had the highest populations of the species), and that temporal patterns of dispersal were related to water-level fluctuations. Rising water levels tend to entrain seeds, whereas declining water levels lead to deposition (Merritt and Wohl 2002). Hydrochore deposition is also related to sediment deposition (Goodson et al. 2003). Many riparian plants have floating propagules, which allows them to take advantage of hydrochory. In riparian zones in Northern Sweden, Johansson

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et al. (1996) found that species with longer seed floating times occurred more frequently. Temporal patterns of hydrochory are also influenced by species specific phenology, particularly the timing of seed maturity (Boedeltje et al. 2004).

Riparian zones are areas along rivers that are affected by flooding, and generally have high rates of exotic species invasion and high species diversity (Stohlgren et al. 1999, Levine 2000, Brown and Peet 2003, Stromberg 2007). Many riparian zones contain different species than surrounding habitats, which contributes to regional diversity even if the riparian zone itself is not diverse (Sabo et al. 2005). In riparian communities, hydrochorous seeds provide a source of immigrant species for the recolonization of flood disturbed sites and may help to maintain the relatively high species diversity often seen in riparian zones. MacArthur and Wilson (1967) suggested that species diversity represents a balance of immigration and extinction processes, with higher immigration associated with higher diversity. Thus sites with higher numbers of incoming seeds should have higher species diversity, a relationship that has been borne out in experimental studies (Levine 2000, Brown and Fridley 2003). In the case of riparian zones, hydrochory helps to maintain high rates of immigration, and thus high diversity. Indeed, patterns of riparian species diversity have been related to sites that receive high numbers of water dispersed seeds in Northern Sweden (Andersson et al. 2000b, Jansson et al. 2005). Hydrochory can also facilitate the rapid spread of invasive species along riparian corridors (Pysek and Prach 1994, Planty-Tabacchi et al. 1996, Brown and Peet 2003, Thomas et al. 2005).

The reservoirs created by dams can trap sediment and seeds, affecting the ability of seeds to disperse downstream, thus fragmenting the biological connectivity of riparian zones (Jansson et al. 2000). For example, Merritt and Wohl (2006) found that dams reduced seed concentration in the water column by 70-94% on two rivers in the southern Rocky Mountains of Colorado. The effect of individual dams on seed dispersal is likely to depend on the hydraulic residence time of the dam (how long it takes water to move through the reservoir), the length of the impoundment (with more seeds possibly getting blown to the side in a longer impoundment), and for floating seeds, the prevailing wind speed. As deposition of hydrochores is often related to sediment deposition

(Goodson et al. 2003), one might speculate that more hydrochores are trapped behind dams that accumulate large amounts of sediment. In addition, dams can alter the flood regime of rivers, affecting the ability of seeds to disperse laterally from the aquatic to terrestrial environment. By reducing rates of hydrochorous dispersal to downstream riparian zones, dams may negatively affect downstream riparian species diversity and the resilience of riparian zones to major floods, as measured by their ability to rapidly revegetate following flood disturbance. This has been demonstrated in boreal systems where Andersson et al. (2000a) showed that both hydrochory and species richness were lower in the regulated Ume River, which is affected by multiple dams, as compared to the undammed Vindel River.

Dam removal is increasingly becoming a viable restoration option for rivers as dams constructed in the early 20th century age and no longer function as they were originally intended (Born et al. 1998, Bednarek 2002, Heinz Center 2002, Poff and Hart 2002, Pohl 2002, Doyle et al. 2003, Cui et al. 2006). Dam removal and the elimination of the seed-trapping impoundment should restore rates of hydrochory to pre-dam conditions. It is poorly understood whether seeds trapped by reservoirs remain viable. If so, reservoirs could serve as hidden seed banks, revegetating exposed sediments after dam removal (Shafroth et al. 2002). Seed banks in wetlands and lakes play an essential role in vegetation recovery after disturbance (Poiani and Johnson 1989, Baker 1994, de Winton et al. 2000, Richter and Stromberg 2005). Seed banks are also crucial in determining the presence of desirable and undesirable (e.g., invasive) species in any revegetation project (Baker 1994). For example, exotic species invasion has slowed restoration of natural stream bank conditions in dam removals in Wisconsin (Lenhart 2000). Despite their potential for restoration costs and benefits, reservoir seed banks have not been extensively studied.

In the near future, two dams on the Elwha River on the Olympic Peninsula, Washington (Glines Canyon Dam and the Elwha Dam) will be removed to restore the ecosystem and fisheries of the Elwha River Basin (Elwha River Ecosystem and Fisheries Restoration Act, PL 102-495). Glines Canyon Dam, which lies within Olympic National Park (ONP) and forms the Lake Mills Reservoir, will be one of the largest dams ever removed (Gregory et al. 2002). We studied the

effect of Glines Canyon dam on hydrochory of vascular plant species, and the role that Lake Mills plays as a reservoir of trapped seeds. We asked the following questions: 1) Will hydrochory be lower below Glines Canyon Dam compared to sites above the dam? And 2) How many viable seeds are contained in Lake Mills sediments, and what is the distribution of the seeds with water depth and distance from the mouth of the river? We hypothesized that seeds are trapped in the reservoir behind Glines Canyon Dam, which causes reduced species diversity and abundance of waterborne seeds in downstream reaches, and that many of the seeds in the reservoir remain viable. If the dams do not affect hydrochory then we would expect the same numbers or even more hydrochorous propagules downstream of the dam due to the tendency for hydrochores to be more abundant downstream in the watershed (Andersson and Nilsson 2002). We further expect to see more viable seeds closer to seed sources, e.g., closer to the Elwha River mouth in Lake Mills, and at shallower water depths. We also determined whether non-floating seeds are distributed hydrochorously by sampling hydrochory in submerged nets in addition to floating nets.

Study Area

The 64-m high Glines Canyon Dam, built in 1926, is furthest upstream (rkm 21.7) of two dams on the Elwha River, on the Olympic Peninsula, Washington. It forms Lake Mills, which has a capacity of around 49.3 million m³ and lies within ONP. Because the reservoir is kept full and operated largely as run-of-river, flow out of the reservoir is not regulated except for occasional late summer releases to support Chinook salmon populations in the lower river (Duda et al. 2008). As of 2000, Lake Mills had accumulated an estimated 10.5 m³ of trapped sediment (Childers et al. 2000). Glines Canyon Dam will be removed in the near future (Duda et al. 2008).

The average daily discharge of the Elwha River at the McDonald Bridge gauge (downstream from Glines Canyon Dam) from 1914 to 1994 was 42.3 m³sec⁻¹ (Childers et al. 2000) with annual minimum flows during summer around 8.5 to 14 m³sec⁻¹ and high flows (November to February) around 368 m³sec⁻¹ for a two year flood (BOR 1996). Information about the climate and geology of the Elwha watershed is described in Duda et al. (2008).

Methods

Hydrochory Sampling

We sampled hydrochorous seeds at two locations upstream and downstream from Lake Mills. The upstream sampling site was located at rkm 28.3, at the lower end of Geyser Valley around 400 m upstream from the geologic feature known as Goblins Gate and 1.6 km upstream from Lake Mills. The downstream sampling site was located at rkm 20.9, approximately 0.8 km downstream from Glines Canyon Dam. The two sites were selected to be as similar as possible in terms of flow volume and channel cross-section, while being safely accessible for sampling.

We collected waterborne seeds using drift nets placed in a transect across the river at each sampling location during three sampling times: 6–8 July, 20 July, and 3–4 August, 2005 (Table 1). Except for 20 July, sampling efforts occurred over two days, with one day spent sampling the downstream reaches, and the second day spent sampling upstream reaches. Sampling dates were chosen based on logistical considerations and included medium and low flow conditions for the Elwha River ranging from around 10 to 24 m³sec⁻¹. At each sampling time, we placed six floating and four submerged nets across the river (Figure 1). Floating nets were 30.5 cm x 45.7 cm rectangular stream drift nets with a 243 µm mesh. We attached foam piping to the top of the net so the top of the opening remained above the surface of the water. Submerged sampling nets included plankton drift nets with a 20 cm diameter opening, 100 cm long, with 153 µm mesh attached to a 200 mL bucket with 147 µm mesh. We anchored nets in place for three hours. Samples were not taken if nets were moved or damaged during the collection period. During deployment, we avoided stirring up sediment upstream of the nets and traversed the transect downstream from nets at all times.

Discharge and turbidity data for the days when sampling occurred were obtained from USGS real-time data at the McDonald Bridge gauging station below Glines Canyon Dam (rkm 13.8) and from a gauging station above Lake Mills at rkm 26.1 (U.S. Geological Survey 2001).

Lake Mills Seed Bank Sampling

We established five perpendicular transects across Lake Mills, with each successive transect further

TABLE 1. Hydrochory sampling details from stations on the Elwha River above and below the Glines Canyon Dam. Discharge levels (Q, measured in $\text{m}^3\text{sec}^{-1}$) and turbidity are from USGS gauging station data from the McDonald Bridge (below dam) and above Lake Mills (above dam) gauges (U. S. Geological Survey 2001). The symbols **i** or **d** indicate the change in water discharge since the previous day (i = increasing, d = decreasing). Turbidity represents median unfiltered field turbidity in nephelometric turbidity units (NTU). In bold are the flow and turbidity either above or below the dam on the day that a reach was sampled.

Date Sampled	Above or Below Dam	Floating or Submerged	# samples	Above Lake Mills		Below Dam	
				Q	Turbidity	Q	Turbidity
6 July 2005	Below	Floating Submerged	4 4	22.4 i	13	25.1 i	1.5
8 July 2005	Above	Floating Submerged	6 4	23.0 i	3.8	22.8 i	1.5
20 July 2005	Below	Floating Submerged	6 5	13.2 d	1.5	15.2 d	1.2
20 July 2005	Above	Floating Submerged	4 5				
3 Aug. 2005	Below	Floating Submerged	6 3	10.1 d	0.7	12.1 d	0.9
4 Aug. 2005	Above	Floating Submerged	2 4	10.1 d	0.7	11.4 d	0.9

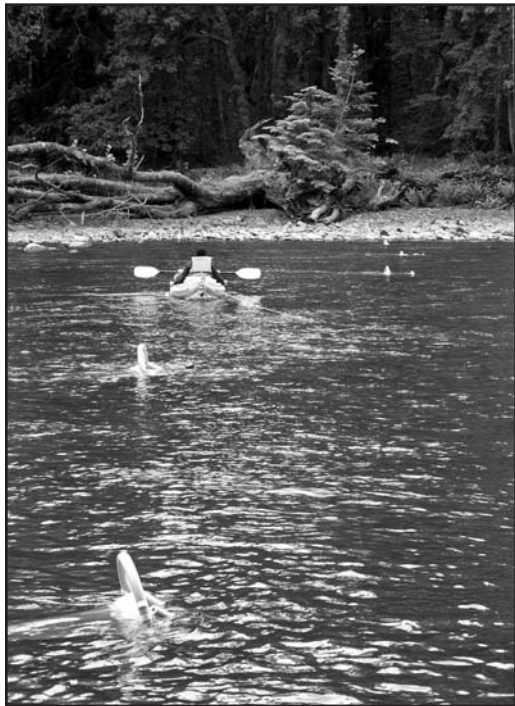


Figure 1. Surface drift nets in the transect located below Glines Canyon Dam.

away from the river delta. Along each transect, we sampled sediment across a range of water depth categories including: (1) shallow sites, at

0.8 m water depth; (2) middle sites, at 1.5 to 4.5 m; (3) lower sites at 5.5 to 10.6 m; and (4) deep sites at 13.5 to 34.0 m. The actual water depth of each sampling location along each transect was measured precisely using a plumb line. At each sampling location, we collected three samples, with samples separated by at least 7.5 meters (depth held constant), to capture potential variability in seed bank composition. Transects 1, 3 and 4 were sampled at all four depth categories, while transect two was sampled from all but the shallow depth category. Transect five was only sampled from the middle and lower depth categories on the western shores because steep bathymetry made it unsafe to collect on the eastern shores. Ten additional samples were collected directly from seasonally inundated delta deposits on the northern reach of the Elwha River delta. The location of each sampling site was recorded using a GPS.

The logistics of sampling sediment in Lake Mills required three depth-dependent collection methods. Each method was designed to capture the uppermost layer (top 12 cm) of sediment. Divers collected the samples from the lower and middle water depths using a 19 liter bucket. Divers dipped the lip of the bucket 12 cm deep into the sediments to fill it. Water depths below 12 m were too deep for available scuba divers, so a deep lake dredge was used to collect sediment from deep sites. Shallow sites were inundated with large woody

debris, requiring the use of a sharp-shooter shovel to extract the upper 12 cm of sediment at 0.8 m water depths. Using these methods we collected 18 shallow depth samples on 24 June 2005, 27 middle and 28 lower depth samples on 16 May 2005, 8 deep samples on 26 May 2005, and 10 river delta samples on 3 July 2005.

Seedling Emergence Methods

Two general methods to estimate seed bank composition have been extensively studied: physical extraction (through a variety of methods including flotation, sieving, and air flow separation) and greenhouse seedling emergence methods (Simpson et al. 1989, Gross 1990, Brown 1991, TerHeerdt et al. 1996). Greenhouse seedling emergence methods detect only the readily germinable portion of seeds. Because our goal was to identify the ecologically active hydrochorous seeds and seed banks, we used the greenhouse emergence method.

Many temperate species require cold temperatures to break dormancy (Baskin and Baskin 1998). Before germination, drift net seeds were cold-stratified in a 4.4° C cold room from day of collection (via coolers at the field sites) until the first week in October, 2005, when they were planted in the greenhouse. The Lake Mills seed bank samples were not cold stratified because collecting in May ensured that most seeds within the sediments had at least six months exposure to cold temperatures while they were buried in the lake. Average river temperatures measured just upstream of Lake Mills ranged from 3.9° C in February 2005 to 6.2° C in April 2005 (U.S. Geological Survey 2001). Temperatures within the lake were not measured, but were unlikely to be more than a few degrees warmer than the river during the winter months.

We spread drift net samples over the surface of sterile Promix potting soil in 25.4 cm x 50.8 cm flats that were randomly placed in the Eastern Washington University greenhouse. Because the volume of drift seeds collected was relatively small for each sample, the surface depth of seeds over the potting soil was never greater than 1 mm. On every greenhouse table we placed a control flat (approximately one out of every eight flats) of untreated soil, to assess possible contamination by wind-borne seed from the greenhouse or seed in the potting soil. We watered flats from below as needed to keep the soil evenly moist, gener-

ally about every two days but varying seasonally, using an adjustable automated watering system. Osmocote slow release fertilizer was added as needed in the quantity recommended on the package. Greenhouse temperatures were regulated by a climate control system and ranged from 26.7° to 15.6° C. Samples were subjected to ambient light throughout the study.

We processed seed bank samples from Lake Mills in the ONP greenhouse within 48 hrs of collection. For all samples we used a constant volume of sediment (0.95 L) for seed germination. Each sediment sample was thinly spread into two 25.4 cm x 25.4 cm flats pre-filled with a 4 cm deep layer of a sterile, soilless mixture consisting of 70-80% aged Douglas fir bark, 10-20% sphagnum peat, 10% 9.5 mm Oregon white pumice, and trace bone meal. The target thickness for the samples was 4-5 mm, however there was variability due to consolidated clumps of silt/clay that were difficult to spread. Ultimately, the average thickness was 7.3 mm (0.95 liters/1290 cm²).

We scattered ten control flats filled with the soilless mixture among the flats to ensure that any contaminating seedlings from greenhouse weeds were identified. Samples were randomly redistributed throughout the study to minimize the possible influence of moisture or light variability on species germination. We watered all flats from below using capillary pads as needed to keep the samples moist. ONP greenhouse temperatures ranged from 32.2° to 15.6° C. Samples were subjected to ambient light throughout the study. For the Lake Mills samples, we allowed seeds to germinate and grow for six months, whereas seed drift samples were allowed to grow for 15 months because more time and greenhouse space were available.

For both the drift net and Lake Mills seed bank studies, we removed seedlings from flats as soon as they were identified. Removed seedlings were either destroyed or re-potted for use in future Elwha revegetation efforts. We identified plants using Hitchcock and Cronquist (1973) to the most precise taxonomic resolution possible. Botanical names were updated based on Kartesz (ITIS 2007). For Lake Mills seed bank samples, graminoids from the family Poaceae were identified to genus using (Hitchcock et al. 1969). We determined the native or exotic status for each species using Buckingham et al. (1995).

Data Analysis

For the seed drift samples, traditional parametric methods were not used because the data were heteroscedastic and not normally distributed due to the large numbers of net samples (53%) with no seeds, resulting in an inflated number of zero values. Data transformations did not improve the distribution. Thus, we used two group randomization tests (Manley 1997) to assess whether average seed species richness and average seed abundance of samples above Glines Canyon Dam were significantly different from samples taken below the dam. We tested for significant differences during each of the three periods and for all time periods together. Observations were randomized within the dam positions (above or below) and the difference between the two randomly assigned groups was calculated with 900 repeats to generate an empirical null distribution. Significance of the two-tailed test was assessed at the 95% confidence level. A Chi-square goodness-of-fit test was used to determine whether the frequency of nets with seeds present was different above the dam compared to below the dam for each of the three time periods. The above analyses were performed using SAS version 9.1 (SAS Institute 2003).

To determine if there were discernible spatial patterns in germinable seed densities in the sediments of Lake Mills, the relationship between measured sample depth and germinable seedling densities was analyzed using linear regression in SPSS 11.5 (SPSS 2003). The data were heteroscedastic and not normally distributed, so sample depth was log transformed, which improved the distribution as assessed by residual plots and normal quantile plots. The relationship between sample distance from the Elwha River delta and germinable seedling density was also analyzed using linear regression in SPSS. The measuring tool in ArcGIS (ESRI 2004) was used to determine the distance of each site from the Elwha River delta based on collected GPS points.

Results

Drift Net Measurements of Hydrochory

A minimum of 18 total species and 108 total seeds germinated from 53 total samples (average 2.04 seeds per net) over the three time periods including 23 samples above the dams and 30 below the dams (Table 2). Only three of the 18 species were

non-native (exotic) including *Mycelis muralis*, *Dactylis glomerata* subsp. *glomerata*, and *Stellaria media*. Only the exotic *D. glomerata* subsp. *glomerata* was found below but not above the dam, although it is common in the established riparian vegetation above the dam. Some of the species that were not positively identified (i.e., *Poaceae* sp.) may also include exotic species. We found 13 species in samples above but not below the dam compared with two species (*Agrostis* sp. and *D. glomerata* subsp. *glomerata*) found below the dam but not above the dam; however, there were many grasses that were not identified to species, and many *Agrostis* species were found in extant vegetation above the dam. Three species (including the low resolution *Poaceae* sp. as well as *Juncus effusus* and *Mimulus guttatus*), were found in both areas.

Of all nets sampled, 47% had germinating seeds. For the three time periods combined, a larger proportion of nets above the dam captured germinating seeds (78%) compared with nets below the dam (10%; $\chi^2 = 17.83$, $P < 0.0001$). The same pattern was observed during 6–8 July, 2005 (87.5% above, 0% below dam; $\chi^2 = 14.32$, $P < 0.001$) and 3–4 August, 2005 (66.7% above, 11.1% below dam; $\chi^2 = 5.00$, $P = 0.025$) time periods (Table 3). However, there was not a significant difference in proportion of nets with seeds on 20 July, 2005 ($\chi^2 = 2.16$, $P = 0.14$), although there was a greater proportion of nets with seeds above the dam (77.8% above, 45.5% below dam).

Two-group randomization tests showed that the average species richness and abundance of seeds per net (Figure 2) was significantly higher above Glines Canyon Dam (1.65 seeds per net) than below (0.27 seeds per net) for the combined sampling times (species richness $P = 0.001$; seed abundance $P = 0.001$) and for 6–8 July, 2005 (species richness $P = 0.002$; seed abundance $P = 0.002$) and 3–4 August, 2005 (species richness $P = 0.02$; seed abundance $P = 0.01$). On 20 July, there was a weaker relationship than the other sampling dates with greater seed abundance per net above the dam ($P = 0.028$), but not more species ($P = 0.058$). This represents an estimated 2.6 million seeds transported per year across the transect above the dam, and 660,000 seeds per year below the dam. This is a minimum estimate, based on the average river cross-sectional areas for times sampled recorded at the nearest USGS gauging stations; it assumes that the cross-sectional area at the

TABLE 2. Species of seeds trapped in drift nets by date, dam position, and net position. Number of nets refers to the number of net samples that a particular species was found within. A total of 18 species and 108 seeds were collected.

Date	Name	# Seeds	Dam Position	Net Position	# Nets	Origin
8 July 2005	<i>Asteraceae</i> sp.	2	Above	Floating	1	?
	<i>Cardamine oligosperma</i> var. <i>oligosperma</i>	5	Above	Floating	2	Native
	<i>Juncus effusus</i>	2	Above	Floating	1	Native
	<i>Mimulus moschatus</i> var. <i>moschatus</i>	2	Above	Floating	1	Native
	<i>Poaceae</i> sp.	1	Above	Floating	1	?
8 July 2005	<i>Juncus ensifolius</i>	1	Above	Submerged	1	Native
	<i>Mimulus lewisii</i>	1	Above	Submerged	1	Native
	<i>Poaceae</i> sp.	2	Above	Submerged	2	?
	<i>Veronica americana</i>	3	Above	Submerged	2	Native
20 July 2005	<i>Agrostis</i> sp.	2	Below	Floating	1	?
	<i>Juncus effusus</i>	1	Below	Floating	1	Native
	<i>Mimulus guttatus</i>	3	Below	Floating	1	Native
	<i>Poaceae</i> sp.	5	Below	Floating	3	?
20 July 2005	<i>Poaceae</i> sp.	1	Below	Submerged	1	?
20 July 2005	<i>Asteraceae</i> sp.	2	Above	Floating	2	?
	<i>Epilobium glaberrimum</i> subsp. <i>glaberrimum</i>	9	Above	Floating	2	Native
	<i>Mimulus guttatus</i>	3	Above	Floating	1	Native
	<i>Poaceae</i> sp.	6	Above	Floating	3	?
20 July 2005	<i>Carex</i> sp.	2	Above	Submerged	1	?
	<i>Epilobium glaberrimum</i> subsp. <i>glaberrimum</i>	3	Above	Submerged	2	Native
	<i>Galium aparine</i>	1	Above	Submerged	1	Native
	<i>Poaceae</i> sp.	3	Above	Submerged	2	?
	<i>Stellaria media</i>	16	Above	Submerged	2	Exotic
3 August 2005	<i>Dactylis glomerata</i> subsp. <i>glomerata</i>	1	Below	Floating	1	Exotic
4 August 2005	<i>Epilobium glaberrimum</i> subsp. <i>glaberrimum</i>	7	Above	Floating	2	Native
	<i>Mycelis muralis</i>	1	Above	Floating	1	Exotic
	<i>Myosotis</i> sp.	2	Above	Floating	1	?
	<i>Poaceae</i> sp.	3	Above	Floating	2	?
4 August 2005	<i>Epilobium glaberrimum</i> subsp. <i>glaberrimum</i>	15	Above	Submerged	2	Native
	<i>Poaceae</i> sp.	1	Above	Submerged	1	?
	<i>Tolmiea menziesii</i>	2	Above	Submerged	1	Native

TABLE 3. Summary data showing numbers of species (# Spp.) and seed abundance (# Seeds) from samples taken above and below Glines Canyon Dam in floating and submerged nets.

Date	Dam Position	Floating Nets		Submerged Nets		Total All Nets	
		# Spp.	# Seeds	# Spp.	# Seeds	# Spp.	# Seeds
8 July 2005	Above	5	12	4	7	8	19
6 July 2005	Below	0	0	0	0	0	0
20 July 2005	Above	4	20	5	25	7	45
20 July 2005	Below	4	11	1	1	4	12
4 Aug. 2005	Above	4	13	3	18	5	31
3 Aug. 2005	Below	1	1	0	0	1	1

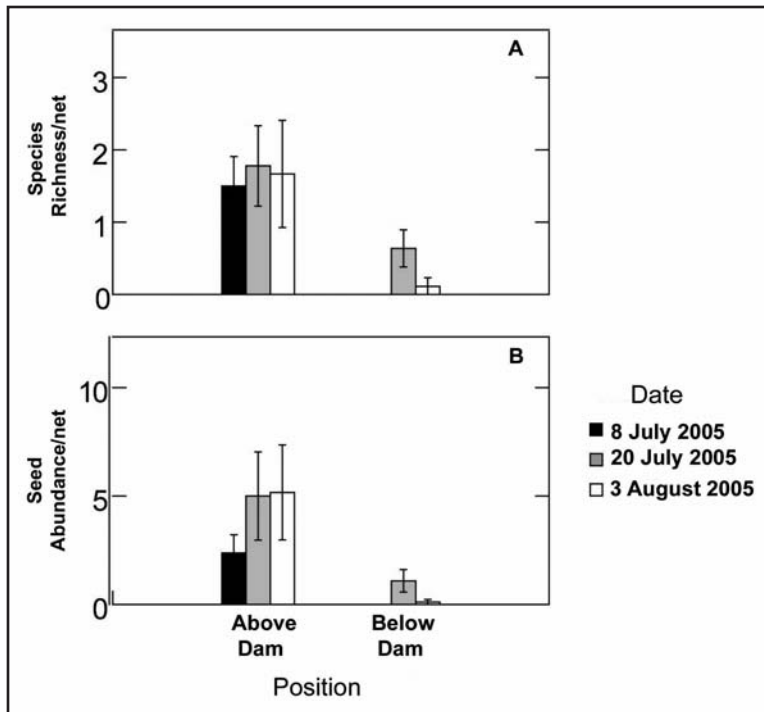


Figure 2. Seed species richness (A) and abundance (B) per net (SE) above and below Glines Canyon Dam on the three sampling dates (dates are given for one of the two days when sampling occurred).

gauging stations is similar to that at the transects, and that the number of seeds and cross-sectional area would remain constant year round (unlikely as our sampling occurred during a relatively low flow period; during much of the year cross-sectional area would be larger which would increase the counts). Similar numbers of seeds were found in both floating nets and submerged nets (Table 3, Figure 3), demonstrating that hydrochory occurs on the Elwha River with both floating and non-floating seeds.

During the first sampling period (6–8 July, 2005) river discharge below the dam ranged from 23.0 (above the dam) to 25.1 m³/s (below the dam) with higher turbidity above the dam (3.8 as compared to 1.5 NTU). Two weeks later (20 July, 2005)

the discharge was lower (13.2 and 15.2 m³/s above and below the dam respectively) with similar turbidity values above and below the dam (1.5 and 1.2 NTU, respectively). The third sampling period (3–4 August, 2005) saw the lowest discharge and turbidity levels (10.1 and 12.1 m³/s; 0.7 and 0.9 NTU, above and below the dam respectively; Table 1). One might expect that the higher discharge and turbidity levels in the first time period would result in greater numbers of hydrochorous seeds sampled due to higher flow rates of water and sediments through the nets, but this was not the case (Figure 2).

Lake Mills Seed Bank

A total of 104 seedlings germinated from the 91 sediment samples collected from Lake Mills in the summer of 2005, with a mean of 1.2 germinable seeds per liter. Half (52%) of the samples failed to germinate any seeds. No seeds germinated in the control flats. Individual samples germinated from 0 to 8.4 seeds per liter, with a total of 17 unique

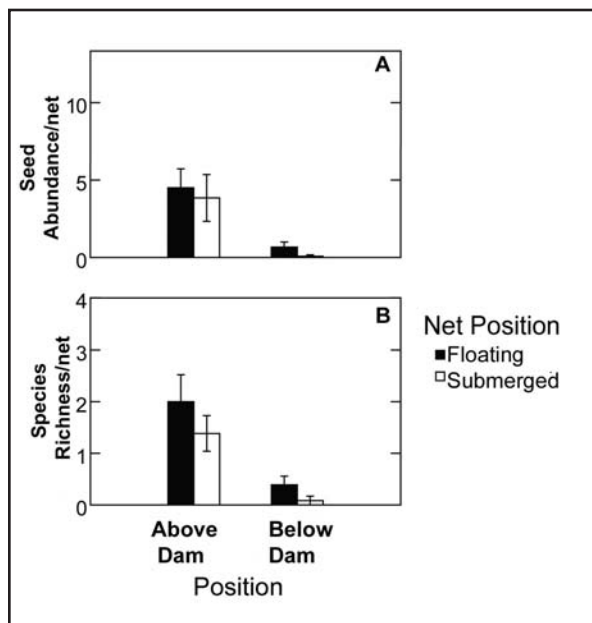


Figure 3. Seed species abundance (A) and richness (B) per net (SE) above and below Glines Canyon Dam in floating and submerged nets.

TABLE 4. Total seedlings to germinate from 91 summer 2005 Lake Mills sediment samples. Origin was determined using Buckingham *et al* (1995). Wetland status was determined using Reed (1988).

Species	Count	Origin	Dispersal	Wetland status [†]
<i>Juncus</i> sp.	25	Unknown	Wind, water	
<i>Carex deweyana</i> var. <i>deweyana</i>	18	Native	Water	OBL
<i>Mycelis muralis</i>	11	Exotic	Wind	Not listed
<i>Alnus rubra</i>	10	Native	Wind	
FAC				
<i>Epilobium ciliatum</i> subsp. <i>ciliatum</i>	9	Native	Wind	FACW-
<i>Equisetum</i> sp.	7	Native	Wind, water?	OBL
<i>Agrostis</i> sp.	5	Unknown		
<i>Sagina procumbens</i>	3	Exotic	Water?	FAC
<i>Mimulus lewisii</i>	3	Native	Water	FACW+
<i>Senecio vulgaris</i>	2	Exotic	Wind	FACU
<i>Stellaria crispa</i>	2	Native	Unknown	FAC+
<i>Galium trifidum</i>	2	Native	Animal	FACW+
<i>Carex deweyana</i>	3	Native	Unknown	FACU
<i>Veronica americana</i>	1	Native	Water?	OBL
Unknown forb 1	1	Unknown		
Unknown forb 2	1	Unknown		
<i>Carex obnupta</i>	1	Native	Water	OBL

[†]OBL = obligate wetland species, FAC = facultative wetland species, FACU = species usually occurs in uplands but is occasionally found in wetlands, and FACW = species usually occurs in wetlands but is occasionally found in uplands. See Reed (1988) for additional detail.

species (Table 4). Of the seedlings that germinated, 52 were graminoids represented by five species; 42 were forbs represented by ten species; and ten were *Alnus rubra*, the only woody species to appear in the lacustrine sediment samples.

Juncus, *Agrostis*, and *Carex* were not identified to species if they did not flower. Two forbs died shortly after their cotyledons formed, preventing identification. The *Juncus* species was likely *J. balticus*, a FACW+ species (Reed 1988), but some may have been *J. effusus*. In a trial sample collected from Lake Mills in February 2005, several *Juncus* seedlings emerged, flowered and were identified as *J. balticus*. The foliage was similar and *J. balticus* is common along the shoreline of Lake Mills.

Fifteen percent of the seedlings identified were known exotic species. The three species not native to the Olympic Peninsula were *Mycelis muralis* (wall lettuce), *Sagina procumbens* (bird-eye pearlwort) and *Senecio vulgaris* (common groundsel). *M. muralis* was the most abundant exotic species

to germinate in the samples and represented 10% of all the seedlings observed during the study (11 seedlings). There are no exotic species from the genus *Carex* or *Equisetum* known to occur on the Olympic Peninsula, so they are considered native for this study.

Seventy-six percent of all seedlings that germinated from the sediments were native species. The most abundant germinable seeds were from the genus *Juncus*, producing ~24% of all germinable seeds. 20 (~19%) of the seedlings belonged to the genus *Carex*. *A. rubra* made up 10% of the total species, while the pioneering forb *Epilobium ciliatum* subsp. *ciliatum* represented 9% of the total. Fifty-six percent of the species were facultative or obligate wetland species (assuming the *Juncus* sp. 1 is *J. balticus*) (Reed 1988).

As predicted, seed density was negatively related to water depth, with highest seed densities (3.0 seeds per liter, 59% of germinated seeds) in shallow areas closest to the shoreline (seed density = $2.23 - 0.76 \times \log \text{ water depth}$; $P < 0.001$; $R^2 =$

0.21). The adjusted R^2 from this regression was low, leaving significant unexplained variation. The relationship between germinable seed densities and distance for the Elwha River delta was not statistically significant ($P = 0.48$, $R^2 = 0.01$).

Of the 29 total species that germinated, only six were found in both the Lake Mills seed bank samples and the drift net samples. These included *M. muralis*, *Mimulus lewisii*, and *Veronica americana* as well as three which were imprecisely identified and could possibly be the same species: *Agrostis* sp., *Carex* sp., and *Juncus* sp. All of the species identified in drift net and Lake Mills seed bank samples are present in established riparian vegetation along the Elwha River, but the 29 species represent only a small fraction (< 20%) of the established riparian flora (R. Brown, unpublished data).

Discussion

Our results support the hypotheses that Glines Canyon Dam is reducing the rate of hydrochorous seed transport to downstream reaches on the Elwha River and that viable seeds are present in Lake Mills sediments. This is consistent with findings from other studies on dammed rivers (Andersson et al. 2000a, Merritt and Wohl 2006), and may be responsible for lower riparian species richness downstream from dams on the Elwha River (R. Brown, unpublished data). When Glines Canyon Dam is removed, we would expect natural levels of hydrochory in downstream reaches to be restored. The presence of numerous seeds in both floating and submerged nets suggests that hydrochorous seed dispersal is not restricted to floating seeds in the Elwha River.

The relatively small numbers of seeds in the Lake Mills seed bank suggest that either the number of hydrochores arriving in Lake Mills is small compared to the volume of sediment being deposited, or that many of the seeds trapped in Lake Mills lose viability over time. Assuming this might be the case, we expected recently deposited seeds located closer to the mouth of the Elwha River to have higher viability. However, there was no trend in seed density with distance to the mouth of the Elwha in Lake Mills. There are several possible explanations. Many hydrochorous riparian plant species, such as cottonwoods and willows, are adapted to set seed in conjunction with seasonal river flows and quickly lose

viability once the seed becomes wet (Leck and Schütz 2005, Naiman et al. 2005). In addition, patterns of seed dispersal related to hydrochory in lakes may be largely governed by surface wind patterns (Nilsson et al. 2002), limiting the effective dispersal distance of floating seeds entering the lake from river currents.

As we expected, seed density was negatively related to water depth in Lake Mills, consistent with other studies along stable shorelines (Haag 1981, Nicholson and Keddy 1983, Poiani and Johnson 1989, Collins and Wein 1995, Abernethy and Willby 1999). This may also be caused by surface winds, which tend to blow floating seeds to the sides of lakes (Nilsson et al. 2002). In addition, high seed densities near the shore may reflect windblown or hydrochorous seed inputs from lake shore vegetation. 63.7 % of the species that germinated from the Lake Mills sediments have structures adapted for wind dispersal, including *Alnus rubra*, *Epilobium ciliatum* subsp. *ciliatum*, *Senecio vulgaris* and *Mycelis muralis*. Wind dispersal does not preclude a seed from being rafted into a site by water; many species are known to be dispersed by multiple vectors (e.g., polychory, Ozinga et al. 2004). Seeds of wind-dispersed riparian species are light and readily float in water. Some riparian species, such as *Populus balsamifera* subsp. *trichocarpa*, disperse wind-blown seed in spring as flood waters recede, and likely combine wind and water dispersal to maximize dispersal and colonization sites (Naiman et al. 2005, Rood et al. 2005).

The only purely hydrochorous species that germinated in the Lake Mills seed bank samples was *Mimulus lewisii* with three seeds, including one from the seasonally inundated Elwha River Delta, one from 218 m north of the delta, and the third from approximately 1733 m away from the delta on the western shore of the lake in a small, tranquil bay. Although it is possible the seed came from the river and managed to raft into the bay, *M. lewisii* has been observed growing on floating logs that collect in the tranquil bays of Lake Mills (personal observation).

The drift net results should be interpreted with caution because they represent a limited number of sampling times and sites. Greater numbers of sampling sites are needed to assess the spatial variability in hydrochory along the Elwha River. In particular, it would be interesting to examine

how far downstream the hydrochory effects of dams extend. In addition, hydrochory varies temporally in riparian systems with increased rates of hydrochory during high flow events. Studies have shown hydrochory to be lowest during summer months (Boedeltje et al. 2004), when sampling for our study occurred. Future studies assessing whether Glines Canyon Dam removal causes increased hydrochory to downstream reaches will need to occur during the same time of year as this study for a realistic comparison. If hydrochory increases following dam removal, there would be further evidence that the patterns we observed are related to the presence of the dam.

In addition, we did not measure variability in flow rate in each net, which would have allowed us to better assess the source of variation in seed supply. In general, we would expect a higher amount of flow through the net to bring greater numbers of seeds (Johansson and Nilsson 1993, Merritt and Wohl 2002). In both transects, the nets were distributed across the river including areas with differing flow rates within each transect. However, that variation was not explicitly controlled. Another possible source of error could arise from not sampling above and below the dams on the same day. Changes in water level and turbidity from day to day could potentially influence our results. High, rising water levels and turbidity levels are likely to be correlated with higher numbers of hydrochores (Johansson and Nilsson 1993, Merritt and Wohl 2002). However, there was not a consistent variation in flow level or turbidity in which upstream nets were always sampled on days with higher flow rates and turbidity levels. For example, during the first sampling period, which had the highest flow rates, we found the lowest numbers of seeds sampled above or below the dam. Finally, it is possible that for both the drift net and seed bank studies that some viable seeds did not germinate due to dormancy or germination requirements not being met.

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To conclude, hydrochory is an important mechanism for the dispersal of riparian plant species (Nilsson et al. 1991, Johansson et al. 1996, Andersson et al. 2000b). Our study provides evidence that dams on the Elwha River reduce levels of hydrochory, and that some of these seeds become trapped in Lake Mills where few remain viable. Reduced levels of hydrochory may be the cause of lower riparian diversity in reaches downstream from the dam. Our results suggest that dam removal will restore levels of hydrochory downstream of Glines Canyon Dam. However, the seed bank within Lake Mills may not be sufficient to allow rapid revegetation of impoundment sediments when the dam is removed. Finally, the presence of exotic species in both drift net and Lake Mills seed bank samples suggests that hydrochorous dispersal and seed banking of this invasive species could be a concern for revegetation efforts following dam removal.

Acknowledgements

This research would not have been possible without the help of our field assistants Malcolm Havis, Jeremiah Dung, and Moose Sanders. Malcolm Havis in particular was instrumental in setting up and managing the experiment and designing the floating seeds traps. We would also like to acknowledge Jerry Freilich and Steve Acker of Olympic National Park, who provided logistical support. Jeff Duda and two anonymous reviewers provided valuable comments which greatly improved the manuscript. Funding was provided by a Faculty Research Grant provided to Rebecca Brown through The Eastern Washington University Foundation, a Research Learning Network Grant provided to Joshua Chenowith from the National Park Service, and a Gunnar and Frances Fagerlund Research Fellowship to Malcolm Havis from the Dungeness River Audubon Center supported by the River Foundation.

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