

James T. Michel¹, James M. Helfield, Department of Environmental Sciences, Huxley College of the Environment, Western Washington University, Bellingham, Washington 98225-9181

and

David U. Hooper, Department of Biology, Western Washington University, Bellingham, Washington 98225-9160

Seed Rain and Revegetation of Exposed Substrates Following Dam Removal on the Elwha River

Abstract

Scheduled to begin in 2011, the removal of two dams on the Elwha River, Washington, will be one of the largest dam removal and river restoration projects undertaken in the United States. One challenge associated with this project is to understand how exposure and downstream deposition of sediments presently detained behind the dams will influence patterns of revegetation and invasive species colonization following dam removal. We conducted two greenhouse experiments assessing the potential effects of reservoir sediments on germination success and growth of (1) propagules dispersed naturally via seed rain, and (2) seeds of selected native and invasive species. Observed summer seed rain density was relatively low (<125 seeds m^{-2}). This suggests slow recolonization in the initial years following dam removal, although these results may have been influenced by sampling methods and timing. In the selected species experiment, four out of five tested species exhibited reduced germination and growth on fine reservoir sediments, while the invasive forb *Cirsium arvense* was unaffected. Though reduced compared to more typical alluvial sediments, germination and growth of the natives *Artemisia suksdorfii* and *Rubus parviflorus* were comparable to that of *C. arvense* on reservoir sediments. These native species may be useful for revegetating exposed sediments. However, depending on such factors as source population sizes, seed production and dispersal rates, growth rates, water availability and competition during establishment, control of *C. arvense* and other exotics in the years following dam removal may be necessary to prevent a relative increase in invasive species populations on the new post-dam substrates.

Introduction

Dam removal has become an increasingly common strategy for river restoration in the United States. This trend coincides with increasing costs associated with the maintenance of aging dam structures (Poff and Hart 2002), as well as shifting social values (Babbitt 2002) and increasing recognition of the adverse effects of dams on river ecosystems (Ward and Stanford 1979, Petts 1984, Collier et al. 1996). Most dams removed to date have been small, and the ecological response to the removal of large dams remains uncertain (Bednarek 2001, Gregory et al. 2002, Poff et al. 2003). The removal of Elwha Dam and Glines Canyon Dam from the Elwha River in Washington State, scheduled to begin in 2011 (DOI et al. 1994, DOI 1996a), will be one of the largest intentional dam removal and river restoration projects undertaken in the United States (McHenry and Pess 2008, Woodward et al. 2008). This project presents a unique opportunity to study the ecological effects of large dam removal, as the majority of the Elwha River watershed exists

within Olympic National Park (ONP) (Figure 1), a designated wilderness area with limited influence from anthropogenic stresses.

The scheduled removal of Elwha and Glines Canyon Dams from the Elwha River will expose large quantities of sediment which cover an area of nearly 325 hectares (Chenoweth et al. 2010). These sediment deposits have resulted as the downstream movement of alluvium has been halted by the installation and operation of both dams. For ~100 years alluvial sediment has been collecting behind both dams, and in areas of the Lake Mills reservoir deposits are nearly 25 m deep. One of the challenges associated with this restoration project will be to understand how the exposure and redistribution of reservoir sediments will affect patterns of vegetation establishment following dam removal. In this paper we present the results of two greenhouse experiments assessing germination and early growth success of floodplain plants on reservoir sediments. The objectives of this study are (1) to evaluate potential contributions of seed rain to post-dam vegetation regeneration, and (2) to assess the relative abilities of selected native and invasive understory species to grow from seed on fine reservoir sediments.

¹Author to whom correspondence should be addressed.
Email: michelj1t@gmail.com

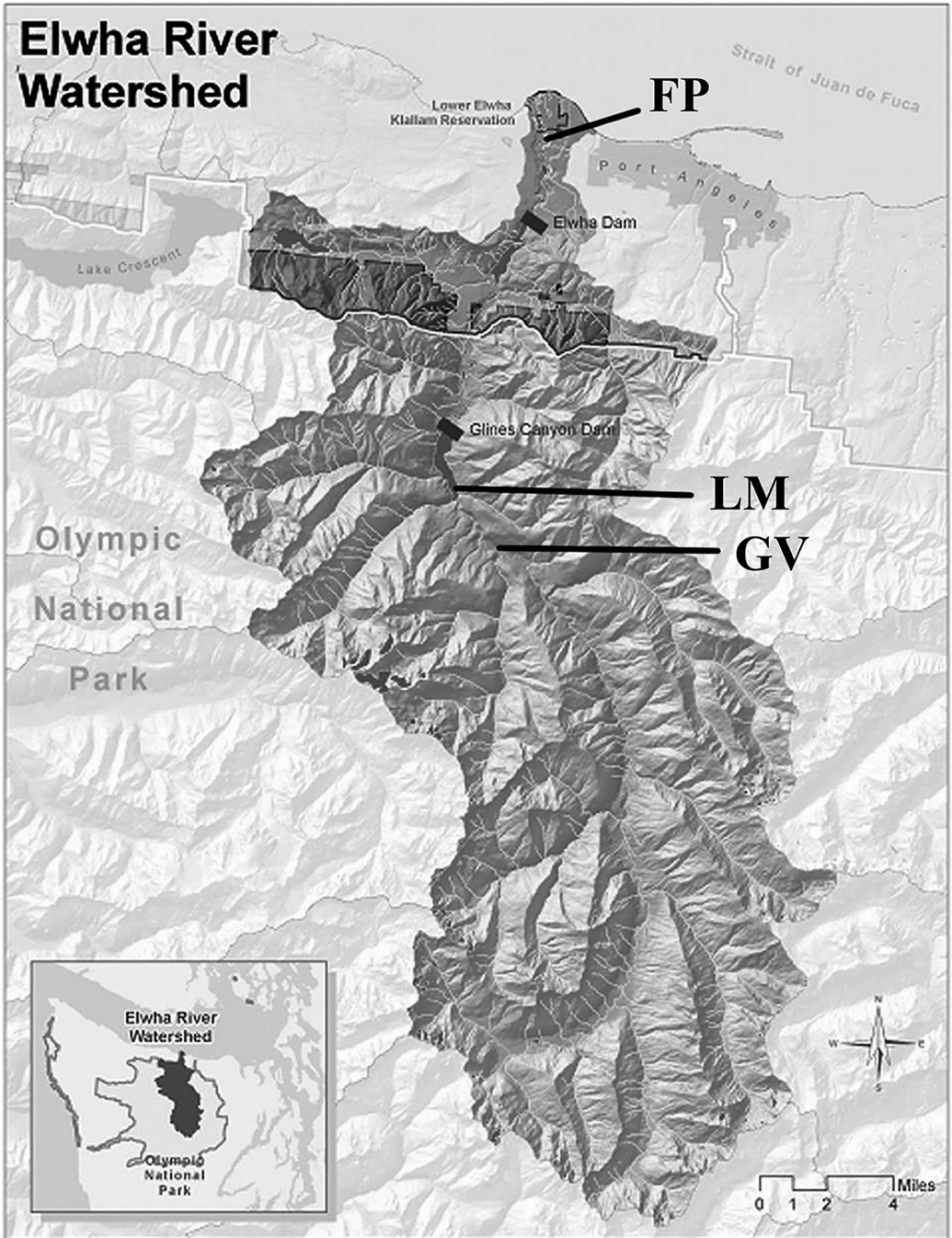


Figure 1. The Elwha River Watershed, including seed trap collection sites in the Geysers Valley (GV), on the Lake Mills delta (LM) and on the lower river floodplain (FP). (Map created by R. Knapp)

An estimated $10.6 \times 10^6 \text{ m}^3$ of sediment are retained behind Glines Canyon Dam, of which approximately 48% consists of fine ($\leq 0.075 \text{ mm}$)

particles (DOI 1996b). An additional $3 \times 10^6 \text{ m}^3$ are retained behind Elwha Dam, of which 66% consists of fine particles (DOI 1996b). The total

volume of sediment retained is likely to be greater by the time dam removal begins, as sediment accumulation has continued in the years since these values were reported. Following dam removal, some portion of these sediments will erode out of the system and into the Strait of Juan de Fuca, but a significant portion will be deposited in downstream floodplains or remain in the de-watered reservoirs. Computer models predict that approximately 50% of fines and 15 – 35% of coarse sediments will be eroded downstream during and following dam removal (DOI 1996b). Physical scale model simulations of Lake Mills predict downcutting and erosion of reservoir deposits along with a downstream progression of coarse sediment during dam removal. A new river channel will become established in the former reservoir, resulting in large expanses of terraced sediment during and following the two year removal process. In the de-watered reservoir behind Glines Canyon Dam fine sediment deposits will be 1 – 2 m deep along valley walls and coarse sediment terraces will be 6 – 18 m deep in areas isolated from the new active channel (Bromley et al. 2005, Chenoweth et al. 2010). These newly exposed surfaces will provide the substrate for plant recolonization and a basis for the development of post-dam floodplain soils.

Reservoir sediments differ from pre-dam floodplain soils in their physical and chemical properties, and these differences may influence patterns of vegetation establishment and invasive species colonization following dam removal. Reservoir sediments are relatively fine-textured, have low concentrations of available nutrients, and lack fully developed microbial communities (DOI 1996b, Cavaliere 2010, Chenoweth et al. 2010). Sediment texture may be especially important for plant germination and growth, as fine sediments are likely to inhibit root growth due to small pore spaces, poor drainage and reduced capacity for oxygen exchange (Grubb 1986, Walker and del Moral 2003, Naiman et al. 2005). De-watered reservoirs will also present a lack of canopy cover and greater exposure to sun and wind desiccation. Under these conditions, post-dam vegetation regeneration may be hindered, or may favor a different community of plants, with greater representation of opportunistic and ruderal species. Floodplain substrates are generally susceptible to invasion by opportunistic exotic species (Hood and Naiman 2000, Tabacchi et al. 2005), especially upon newly-exposed reservoir sediments follow-

ing dam removals (Shafroth et al. 2002, Orr and Stanley 2006).

Exotic species invasions in the years immediately following dam removal could have long-term consequences for the structure and dynamics of floodplain plant communities. Even small populations of exotic species can alter riparian soils and microbial communities (Bellingham et al. 2005, Batten et al. 2007, Peltzer et al. 2009) and inhibit the growth and establishment of native species (Walker and Vitousek 1991, D'Antonio and Vitousek 1992, Fierke and Kauffman 2006). Exotic species can thus alter patterns of succession to perpetuate lasting shifts in ecosystem processes as well as composition (D'Antonio and Vitousek 1992, Urgenson et al. 2009). In some cases these changes may be irreversible (Coblentz 1990).

Post-dam changes in floodplain regeneration and community dynamics would impinge not only on ONP's mission to preserve unimpaired native flora (Tolson 1933, Sellars 1997), but also on the restoration of habitat for anadromous Pacific salmon (*Oncorhynchus spp.*), a key objective of the Elwha dam removals (DOI et al. 1994, DOI 1996a). Dam removal will allow salmon access to spawning and rearing sites (McHenry and Pess 2008, Pess et al. 2008), but restoration of viable habitat will require a successional trajectory favoring the establishment of native vegetation. Once established, native riparian vegetation will stabilize stream banks and help minimize erosion and siltation (Gregory et al. 1991, Naiman and Decamps 1997, Corenblit et al. 2009). Siltation threatens the survival of salmon embryos and fry (Chapman 1988, Bjornn and Reiser 1991, Jensen et al. 2009), and will likely be exacerbated following dam removal due to the highly erosive nature of the fine sediments that will be exposed in the floodplain and de-watered reservoirs (Mussman et al. 2008, Cook et al. 2009). The ecological services provided by established riparian vegetation are essential to the growth and survival of salmonid fishes, such that a diverse community of native riparian vegetation is considered a vital component of stream habitat (Naiman and Latterell 2005, Lake et al. 2007). To the extent that post-dam changes in vegetation regeneration affect riparian diversity or river-riparian interactions, these changes would significantly compromise the success of the Elwha dam removals and associated ecosystem restoration.

Possible sources of colonizing vegetation on post-dam Elwha sediments include the seed bank present in reservoir sediments, water dispersed seeds (i.e., hydrochory), wind-blown seed rain (i.e., anemochory), and active revegetation by ONP personnel. Reservoir seed banks will likely be of limited influence, as recent greenhouse experiments suggest these sediments contain too few viable native propagules to facilitate revegetation (Brown and Chenoweth 2008). Hydrochory is frequently the dominant mechanism for seed dispersal in riparian zones (Goodson et al. 2003, Tabacchi et al. 2005, Nilsson et al. 2010), but it is also likely to be of limited influence on post-dam Elwha substrates, as most of the newly exposed reservoir area will be beyond the spatial influence of seasonal flooding (Chenoweth et al. 2010). Consequently, seed rain and active revegetation will likely be the most important colonization sources. ONP restoration plans call for the replanting of 65% of de-watered reservoir area over a period of 7 – 8 years following dam removal (Chenoweth et al. 2010). This leaves a potentially significant area and period of time for colonization via seed rain. Seed rain will likely include invasive propagules, as suggested by recent surveys confirming source populations of invasive species in established plant communities as well as in the sediment seed bank in the delta formed at the head of the upper reservoir (Hulce 2009). Improved understanding of which species are likely to colonize and germinate successfully on post-dam floodplain sediments would be helpful for informing strategies for revegetation and invasive species control.

In this paper we present the results of two greenhouse experiments assessing germination and early growth success of floodplain plants on reservoir sediments. The objectives of this study are (1) to evaluate potential contributions of seed rain to post-dam vegetation regeneration, and (2) to assess the relative abilities of selected native and invasive understory species to grow from seed on fine reservoir sediments. In so doing we hope to contribute to the understanding of processes shaping revegetation following dam removal, and to inform efforts for the preservation and restoration of biodiversity and ecological processes within the Elwha River basin. This study focuses on the influence of sediment texture on germination success and early growth. Additional factors likely to influence successional trajectories

and post-dam vegetation composition include the relative abundance of source populations as well as species-specific differences in seed production, dispersal and viability (Ferrerias and Galetto 2010).

Study Area

The Elwha River originates in the Olympic Mountains of northwestern Washington state, discharging into the Strait of Juan de Fuca approximately 72 km to the north (Figure 1). It drains a watershed of approximately 883 km², of which the upper 83% is protected within ONP (Duda et al. 2008). The watershed is a coastal temperate rainforest encompassing a range of microclimates and vegetation zones within the Olympic Peninsula Province physiographic classification of Franklin and Dymess (1988). Lower elevations are typically dominated by Douglas fir (*Pseudotsuga menziesii*) mixed with western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*). Valley bottoms, terraces and riparian zones are dominated by red alder (*Alnus rubra*) mixed with black cottonwood (*Populus trichocarpa*), willow (*Salix spp.*), grand fir (*Abies grandis*) and bigleaf maple (*Acer macrophyllum*) in varying proportions (Shafroth et al. 2002, Duda et al. 2008). Annual precipitation is orographically influenced and ranges from 550 cm at the headwaters to 100 cm at the mouth (Phillips and Donaldson 1972). A monitoring station 3 km below Glines Canyon Dam receives 140 cm of precipitation annually, with 88% occurring October-April (WRCC 2009).

For more than 90 years, the Elwha River has been altered by two dams: At river kilometer (rkm) 7.9, the 32 m high Elwha dam, completed in 1913, forms the 1.08 km² reservoir Lake Aldwell. At rkm 21.6, the 64 m high Glines Canyon Dam, completed in 1927, forms the 1.68 km² Lake Mills (Duda et al. 2008). The dams are operated primarily as run-of-river impoundments. Both dams lack fish passage and thus prevent anadromous fish from accessing approximately 130 km of mainstem and tributary habitat above Elwha Dam (Duda et al. 2008, Pess et al. 2008). The 1992 Elwha River Ecosystem and Fisheries Restoration Act (U.S. Public Law 102-495) calls for restoration of the Elwha's native anadromous fish populations and their ecosystem, with dam removal subsequently identified as the most effective means to achieve this goal (DOI et al. 1994, DOI 1996a). The dams are scheduled to be removed incrementally via a

staged gradual drawdown beginning in fall 2011 and projected for completion by summer 2013, with pauses in the interim for salmon spawning migrations (Chenoweth et al. 2010).

Methods

Experiment 1: Seed Rain Germination and Growth

To evaluate the potential for seed rain to contribute to post-dam vegetation regeneration, we conducted a greenhouse experiment in which propagules captured from seed traps on the Elwha floodplain were germinated in reservoir sediments. Lake Mills was chosen as the source for experimental substrates because, as the upper reservoir, it retains the majority of the sediments that will be exposed and mobilized downstream following the dam removals (DOI 1996b). In June 2008 we collected 125 L of reservoir sediments at a depth of 7-10 m from the prodelta formation at the northern end of the reservoir, using a modified 0.1 m³ Van Veen grab sampler. Sediments were stored in 5 gallon buckets at 4 °C until greenhouse experiments were initiated. A random subsample was analyzed for organic content using the loss on ignition standard method (Ball 2006) and for particle size using a Mastersizer particle size analyzer (Malvern Instruments Ltd., UK). Reservoir sediments had mean aggregate diameter (*D*₅₀) of 12.5 µm and were 98% inorganic, with a particle composition of 15% clay, 78% silt and 7% sand.

Previous studies have utilized seed traps to characterize seed rain in river ecosystems (Harmon and Franklin 1995, Kollmann and Goetze 1998, Page et al. 2002, Cottrell 2004, and Gurnell et al. 2006). Our study used 100 mm diameter plastic funnel traps (for trap design see Page et al. 2002) positioned 2 cm above soil surface. Seed traps were deployed at three collection sites: Geyser Valley (GV), the Lake Mills delta (LM), and the lower river floodplain (FP) (Figure 1). These sites were chosen to represent, respectively, an upstream reference area unaffected by the dams (GV), a site within ONP (LM) directly affected by Glines Canyon Dam and a downstream site beyond the ONP Boundary (FP) where reservoir sediments are likely to be deposited following dam removal and source populations of invasive species are more abundant. Trap sites were located on minimally vegetated gravel bars 5-50 m from pioneering patches of willow (*Salix spp.*) and

red alder (*A. rubra*) to minimize local seed rain influence and focus collections on long-range seed rain. This placement was chosen to represent conditions on newly exposed sediments following dam removal, and because previous studies have demonstrated that abundance and diversity of seeds delivered via seed rain tend to be highest on minimally vegetated gravel bars (Harmon and Franklin 1995). At each site, we installed 20 traps arrayed in two transects of ten (parallel to river flow), for a combined sampling area of 0.16 m² (Kollmann and Goetze 1998). Seed traps were deployed for 14 weeks from June 24 through September 28, 2008. This period coincided with the growing season between the spring freshet and the fall rains, during which riparian plants have the greatest chance of establishment (Gurnell et al. 2006). Seeds were harvested monthly and amalgamated by site. Harvested seeds were kept in cold storage at 4 °C until sowing (Gurnell et al. 2006). We chose to utilize the emergence method to identify seed rain germinants, due to the difficulty of identifying seed to species.

Harvested seeds were sowed in a blocked 2-factor design with four site treatments and two substrate treatments. The four site treatments were GV, LM, FP and a control (i.e., no seeds sowed). The two substrate treatments were Lake Mills reservoir sediment and a commercially available peat/vermiculite germination mix (Gardeners Supply, Burlington, VT) representing an optimal growth substrate. It was not possible to include additional substrate treatments because of the low abundance of seeds harvested (see Results below). Seed amalgamations from each site were sowed into 5 replicate 10 cm x 10 cm square pots for each site-substrate combination (n = 40). Each pot was filled with a 2 cm layer of sterilized sand and gravel for uniform water uptake. This was topped with a 10 cm layer of experimental substrate, followed by a density of seeds and seed trap detritus approximating the density observed in seed traps at the site in question. Seeds were then covered with a 3 – 4 mm layer of experimental substrate to prevent seed loss.

After sowing, pots underwent cold, wet stratification at 4 °C for 12 weeks (Oct 2008 – Jan 2009) to enhance germination (Baskin and Baskin 2001). In January 2009, all pots were transferred to a greenhouse at Western Washington University (WWU) for 12 weeks of experimental germination (January – March 2009). During this experiment,

the WWU greenhouse had a 16 hr light regimen and controlled temperature between 17 °C at night and 20 °C daytime. Pots were arranged in a randomized block configuration and were randomly shuffled within each block weekly. Pots were placed in watering flats and watered predominantly from below with occasional overhead misting to maintain greenhouse humidity. Flats were permitted to dry out in between watering cycles to mimic the natural cycling of floodplain water availability. Germinants were counted and identified weekly, with unknown taxa photographed and grown out to assist with identification. Germinated grasses were removed from the greenhouse after 11 months and placed outdoors for eight weeks to vernalize and encourage flowering for identification to species. These grasses did not flower, but were identified by vegetative key (Hitchcock et al. 1969).

Experiment 2: Selected Species Germination and Growth

Chenoweth (2007) evaluated growth and germination of one native grass (*Elymus glaucous*) and one native woody species (*A. rubra*) on Lake Mills sediments, and found successful germination for *E. glaucous* while *A. rubra* was suppressed. Our greenhouse experiment sought to build upon insight gained by Chenoweth (2007) to assess the abilities of different native species to grow from seed on varying textures of post-dam sediment. Upon consultation with the Restoration Botanist at ONP (Joshua Chenoweth, ONP, personal communication), we selected species of interest to revegetation planning for which there were not established data about growth and colonization following riparian disturbance. Perennial species were chosen for study on account of persistent belowground root networks desirable for erosion control. Although knotweed (*Polygonum spp.*) and reed canary grass (*Phalaris arundinacea*) are well documented riparian invaders, (Orr and Stanley 2006, Urgenson et al. 2009) they were not chosen for this seed sowing study. *Polygonum spp.* are being aggressively managed prior to dam removal (Chenoweth et al. 2010) and *P. arundinacea* was not selected for testing because it is already known to colonize on dewatered reservoir surfaces (Orr and Stanley 2006). Thus, we identified five priority species of interest: coastal mugwort (*Artemisia suksdorfii*), thimbleberry (*Rubus parviflorus*), salmonberry (*Rubus spectabilis*), Canada thistle (*Cirsium arvense*) and Himalayan blackberry (*Rubus discolor*)

for which there was limited information available. Three of these (*A. suksdorfii*, *R. parviflorus*, *R. spectabilis*) are native species chosen because they (a) are relatively fast growing and provide shade or ground cover soon after planting, (b) produce many seeds per plant, (c) are capable of spreading rapidly by seed and rhizome, (d) are common in the Elwha riparian ecosystem, and (e) are consequently under consideration for application as part of post-dam revegetation work. The other two species (*C. arvense*, *R. discolor*) are invasives present within the Elwha watershed with potential to colonize large expanses of nutrient-poor sediments following dam removal. Both spread aggressively below the soil surface, produce large quantities of seed and are capable of creating monocultures via competitive exclusion. *C. arvense* can spread laterally up to 5 m in one growing season (Boersma et al. 2006).

Cleaned and dried seeds of Elwha-stock *A. suksdorfii* were acquired from the Department of Agriculture (USDA) Plant Materials Center in Corvallis, OR. *Rubus* and *Cirsium* seeds were collected by hand during summer 2008 from plants located in the Elwha watershed. *Cirsium* flower heads were dried and seeds hand-separated from the pappus. *Rubus* fruits were macerated by hand and screened to separate seed from pulp. The seeds were then dried and chemically scarified. Seeds of the *Rubus* genus have a robust endocarp and require scarification to increase germination success (USDA 1974, Baskin and Baskin 2001). *R. discolor* and *R. spectabilis* were immersed in 14% NaOCl in an ice bath for 24 h (Wada 2009). *R. parviflorus* has a considerably thinner endocarp and was immersed in 14% NaOCl for 6 hr while stirring regularly to avoid damage to the embryo (procedure recommended by Sugae Wada, Oregon State University, personal communication). Following scarification, seeds were rinsed for 1 hr in running water and dried.

Experimental substrates were collected from Lake Mills as described above (see Experiment 1 Methods). An additional 125 L of coarser alluvial sand (0.1-2 mm) was collected by shovel from the head of the Lake Mills delta. The alluvial sand was selected to represent the approximate texture of riparian substrates prior to dam removal and to represent the redistribution of delta sediments to the valley bottom following dam removal. All sediments were stored at 4 °C until the greenhouse experiment was initiated.

Seeds were sowed in a blocked 2-factor design with six species treatments (five species plus a control with no seeds sowed) and four substrate treatments (Lake Mills reservoir sediment, alluvial sand, an equal parts mixture of Lake Mills sediment and alluvial sand, and the commercially available germination mix). Seeds were sowed in 10 cm x 10 cm square pots with five replicate pots for each site-substrate combination (n = 120). Each pot was filled with a 2 cm layer of sterilized sand and gravel for uniform water uptake, topped with a 10 cm layer of experimental substrate, 50 seeds of the appropriate experimental species (or no seeds in the case of the no-seed control pots) and a 3–4 mm top layer of experimental substrate to prevent seed loss.

After sowing, pots underwent cold, wet stratification at 4 °C for 12 weeks (Oct 2008 – Jan 2009), followed by 12 weeks of experimental germination in the WWU greenhouse (Jan – March 2009; see Experiment 1 Methods for greenhouse conditions and procedures). In each pot, germinants were counted weekly, with germination and growth success measured according to percent germination and percent cover. Percent germination was calculated as

$$PG = (nG / nS) \times 100$$

where PG is percent germination, nG is the number of germinants observed, and nS is the number of seeds sown. Percent cover was measured using a 10 cm x 10 cm piece of clear plastic with 1 cm gridlines. The grid was placed above each pot and percent cover was calculated as the number of 1 cm² squares in which plant matter was visible.

We conducted a seed viability trial concurrently with the 12 week greenhouse experiment to assess differences in seed viability among tested species. Three replicate samples of each species

were tested. Each replicate consisted of 50 cold-stratified seeds placed onto moist filter paper and sealed in zip-closure plastic bags (Baskin and Baskin 2001). Numbers of germinants were recorded weekly.

Data Analysis

Preliminary analyses indicated germination and cover data were not normally distributed and did not exhibit homogeneous variance, with some treatments resulting in zero germination. Moreover, block was not influential, and there was a significant species by sediment interaction. Therefore, rather than use a parametric blocked 2-way ANOVA analysis, we used a Kruskal-Wallis one-way ANOVA by ranks followed by a post-hoc pairwise comparison of mean ranks (Daniel 1990) to evaluate differences in germination and cover between sediment treatments for each species (Stastix Software Inc., Tallahassee, FL). The relationship between germination trends and growth trends was evaluated using correlation analysis (SPSS Inc., Chicago, IL).

Results and Discussion

Experiment 1: Seed Rain Germination and Growth

The number of seeds collected was surprisingly low, with all three trapping sites receiving fewer than 125 seeds m⁻² (Table 1). Observed summer seed rain density on the Elwha was well below the range of values (316 – 3,798 seeds m⁻²) reported for unvegetated gravel bars on 3rd and 5th order streams in the H.J. Andrews Experimental Forest in Oregon (Harmon and Franklin 1995), and lower than the mean density (340 seeds m⁻²) observed at barren mid-elevation sites undergoing primary succession following the volcanic eruption of

TABLE 1. Seed rain collection and germination at three Elwha River sites. At each site, 20 funnel traps were deployed for a trapping area of 0.16 m²/site.

Collection Site	Number of Seeds Collected	Seed Rain Density (seeds m ⁻²)	Number of Seeds Germinated
Geyser Valley (GV)	20	125	0
Lake Mills Delta (LM)	14	87.5	1
Lower River Floodplain (FP)	16	100	1
Total	50	104.2	2

Mount St. Helens in southwestern Washington (Wood and del Moral 2000). The low seed densities observed in this study may be partly due to the timing and methods used for seed collection. We focused on the three month window of time between the end of the spring freshet and the onset of autumn high flows, during which plants are most likely to colonize newly exposed floodplain surfaces. Many riparian species produce seeds during this period of time, while others (e.g., *A. rubra*) slowly release seeds throughout the winter (Burns and Honkala 1990). Higher seed densities would likely have been observed if we had left traps out for the full duration of a year; however traps would have been eliminated by flood events. Similarly, alternative seed trap designs such as wet traps, turf mats or adherent paper (Page et al. 2002, Gurnell et al. 2008) may have been more effective for quantifying seed rain, but such trap designs would also have left captured seeds more vulnerable to granivory by insects or would have resulted in premature germination or destruction of the seed. Another factor that may have contributed to the limited numbers of seeds collected is the presence of strong afternoon catabatic winds blowing upstream in the Elwha Valley on sunny afternoons (J. Michel, personal observation), which may have prevented seeds from settling into traps or onto floodplain surfaces, resulting in patchy seed distributions concentrated in depositional zones near wood debris or standing vegetation. More detailed studies of spatial variability in seed distribution would help resolve this question. Nonetheless, our findings suggest that dispersal via seed might not be uniformly rapid during the summer months when floodplain sediments are most receptive to colonization. We observed seed rain at sites 5 – 50 m from established vegetation. Following dam removal, portions of the

de-watered reservoirs will be considerably farther from source vegetation, making colonization via seed rain even slower.

Of the seeds collected in seed traps, only two individuals (4%) germinated successfully (Table 1). The successful germinants were both grasses, and both grew on the Lake Mills reservoir sediment. The native slender hairgrass (*Deschampsia elongata*) grew from seed rain collected on the Lake Mills delta (LM) and the invasive reed canary grass (*P. arundinacea*) grew from seed rain collected in the lower river floodplain (FP). It is not clear if these grasses represent the species most abundant in the seed rain, or if they were merely the most successful germinants in the experimental substrates. The low germination of seed rain may indicate dormancy of some seeds collected. Seed rain dormancy could prolong germination of some species several years. Further investigation into seed rain dormancy may reveal higher viability and germination of wind dispersed seeds when observed over a multiple year timecourse. Studies of primary succession on volcanic soils indicate that well-dispersed species often lack the ability to establish successfully in physically stressful environments (del Moral and Wood 1993). In our experiments fine reservoir sediments were the only substrate to support germination from seed rain, suggesting that this new surface will not be wholly inhospitable to colonizing plants.

Experiment 2: Selected Species Germination and Growth

Percent germination results of seeds sown into the germination mix were comparable to seed viability measured on germination paper (Table 2). Moreover, four out of five species generated >50% cover on the germination mix (Table 2).

TABLE 2. Method validation for germination and growth procedures (mean \pm SD, n = 5)

Species	Measured Seed Viability (%)	% Germination Germinating Mix (G)	%Cover Germinating Mix (G)
<i>A. suksdorfii</i>	43 \pm 2.9	44 \pm 5.8	71 \pm 12
<i>R. parviflorus</i>	77 \pm 1.5	51 \pm 3.3	99 \pm 0.45
<i>R. spectabilis</i>	4.7 \pm 1.2	4.8 \pm 2.7	53 \pm 12
<i>C. arvensis</i>	60 \pm 5.6	56 \pm 10	98 \pm 1.5
<i>R. discolor</i>	3.3 \pm 0.6	2.8 \pm 1.8	5.6 \pm 8.8

TABLE 3. Effects of sediment type on percent germination (mean \pm SD, n = 5). For each species, differences among sediments were determined by Kruskal-Wallis one way ANOVA, followed by pair-wise comparison. Two values not followed by the same letter are significantly different ($\alpha = 0.05$).

Species	100% Alluvial Sand	50% Alluvial Sand + 50% Reservoir Sediment	100% Reservoir Sediment	Kruskal Wallis (KW) test statistic	p
<i>A. suksdorfii</i>	26 \pm 1.7 ^a	4.8 \pm 1.1 ^b	3.2 \pm 3.0 ^b	9.96	0.007
<i>R. parviflorus</i>	13 \pm 10	14 \pm 15	2.0 \pm 3.5	4.34	0.114
<i>R. spectabilis</i>	1.2 \pm 1.1	0	0	7.00	0.030
<i>C. arvense</i>	1.2 \pm 1.8	0.4 \pm 0.9	1.2 \pm 1.8	0.775	0.679
<i>R. discolor</i>	1.6 \pm 1.7	0	0	6.92	0.031

These results suggest that sowing procedures and greenhouse conditions were effective and appropriate for germinating experimental seeds, and that observed differences in germination and growth success may be attributed to differences in experimental substrates. As expected, percent germination and percent cover values for all species were considerably greater on the germination mix than on the three experimental Elwha substrates (i.e., Lake Mills sediment, alluvial sand and the equal parts mixture).

Among experimental Elwha substrates, the effects of fine reservoir sediments on germination success varied with species (Table 3). Of the native species tested, *A. suksdorfii* had the highest germination rate in alluvial sand, but also showed more than a five-fold decline in percent germination on substrates containing reservoir sediments relative to alluvial sand. *R. spectabilis* had low germination on alluvial sand and did not germinate at all on reservoir sediments. In contrast, *R. parviflorus* showed no significant decline in germination success, likely because of high variability among replicates. Both the tested invasive species had low germination success on alluvial sand; *R. discolor* did not germinate on either treatment containing reservoir sediments, but *C. arvense* showed no significant decline in germination success. Despite *A. suksdorfii* having experienced the greatest decrease in germination success on fine reservoir sediments, it still had the highest percent germination on Lake Mills sediment of any species. No native or invasive species showed significantly increased germination suc-

cess on substrates containing reservoir sediments when compared to germination on alluvial sand.

Percent cover results were correlated with percent germination ($r = 0.665$, $p < 0.01$). Most species followed similar trends for cover as for germination, but *R. parviflorus* showed a significant decline in percent cover on pure Lake Mills sediment relative to alluvial sand (Table 4). This suggests that *R. parviflorus* might be hampered in terms of early growth, if not germination, on post-dam substrates. Cover was low for *C. arvense*, but did not differ significantly among substrates. As with percent germination, no species showed increased percent cover on substrates containing reservoir sediments when compared to germination on alluvial sand.

Implications for Post-Dam Revegetation

Colonization via seed rain may be relatively slow during summer months following dam removal. Nonetheless, even if the rates of dispersal we observed are representative of conditions on the Elwha (i.e., not an artifact of sampling methods or timing), seed rain will be an important mechanism for post-dam revegetation. Observed rates of seed rain germination (4%) were comparable to germination rates observed in seeds sown in reservoir sediments (Table 3). With a seed rain density of 125 seeds m^{-2} , a 4% germination rate would yield approximately 5 germinants m^{-2} in the first growing season following dam removal. If post-dam seed rain densities are more comparable to values reported at other Pacific Northwest

TABLE 4. Effects of sediment type on percent cover (mean \pm SD, n = 5). For each species, differences among sediments were determined by Kruskal-Wallis one way ANOVA, followed by pair-wise comparison. Two values not followed by the same letter are significantly different ($\alpha = 0.05$).

Species	100% Alluvial Sand	50% Alluvial Sand + 50% Reservoir Sediment	100% Reservoir Sediment	Kruskal Wallis (KW) test statistic	<i>p</i>
<i>A. suskendorfii</i>	10 \pm 2.2 ^a	3.0 \pm 3.0 ^b	1.6 \pm 1.5 ^b	9.90	0.007
<i>R. parviflorus</i>	4.8 \pm 1.3 ^a	5.4 \pm 4.8 ^{ab}	1.0 \pm 1.4 ^b	6.98	0.031
<i>R. spectabilis</i>	1.0 \pm 1.0	0	0	6.92	0.031
<i>C. arvense</i>	0.2 \pm 0.45	0.8 \pm 1.8	1.2 \pm 1.8	0.801	0.670
<i>R. discolor</i>	1.4 \pm 1.7	0	0	6.90	0.032

sites (e.g., Harmon and Franklin 1995, Wood and del Moral 2000), this rate of germination could yield 14 – 150 germinants m². Given the limited potential for colonization via hydrochory or reservoir seed banks (Brown and Chenoweth 2008, Chenoweth et al. 2010), even relatively slow rates of dispersal via seed rain are likely to make important contributions to post-dam revegetation.

For vegetation colonizing post-dam floodplains and de-watered reservoirs, patterns of establishment and competitive interactions could be influenced by the physicochemical character of post-dam sediments. All of the native species we tested were less successful on reservoir sediments than on the alluvial sand currently present in the riparian zone (Tables 3 and 4), indicating that at least some native species will be at a comparative disadvantage for establishment on post-dam substrates. In contrast, some invasive species might be unaffected by the change in sediment texture and may therefore be at a competitive advantage. *C. arvense* is an example of an invasive species that is already present in the Elwha watershed (Brown and Chenoweth 2008, Chenoweth et al. 2010), produces large quantities of seed, and has the ability to disperse its seed by wind over long distances (Sheldon and Burrows 1973, Wood and del Moral 2000). *C. arvense* was the only tested species to be unaffected by sediment type in both percent germination and percent cover (Tables 3 and 4), suggesting that it may be capable of taking advantage of post-dam decreases in germination or growth experienced by its potential competitors.

It should be recognized that post-dam vegetation colonization will be influenced not only by sediment texture and its effects on germination success, but by a range of factors including source population sizes and species-specific differences in seed production, dispersal and intrinsic germination potential (Ferreris and Galetto 2010). For example, the relatively high seed viability seen in *A. suskendorfii* (Table 2) is likely the reason that, despite suffering significant declines in percent germination on reservoir sediment relative to other substrates, this species maintained the highest rates of germination success on reservoir sediment of any tested species (Tables 3 and 4). Similarly, species that produce copious amounts of seed may colonize more effectively than do less fecund competitors, despite having lower rates of germination success. Our observations during the 2008 growing season may or may not be representative of future seed rain abundance or species composition, as some species, particularly masting conifers, may produce significantly different amounts of seed from year to year (Burns and Honkala 1990). Over longer periods of time following dam removal, patterns of succession and species composition will be further influenced by differences in growth rate, herbivory, mortality and competitive dynamics among seedlings. It is noteworthy that although tested *C. arvense* seed was highly viable and *C. arvense* populations are well established on sand deposits in the Elwha floodplain, we observed a very low percentage of seed germination on all Elwha substrates including alluvial sand. This discrepancy suggests that

although *C. arvense* produces thousands of seeds per plant, it may be more effective at spreading by creeping roots following the establishment of a single seed-dispersed colonizer.

In addition to the five species tested here, various other native and non-native taxa may be capable of colonizing post-dam substrates. For example, the forbs *Anaphalis margaritacea*, *Hypochaeris radicata*, *Lupinus lepidus* and *Epilobium angustifolium* were the most abundant species to colonize barren sediments deposited by the eruption of Mount St. Helens, with seedling colonization strongly influenced by ground surface microtopography and particle size (Wood and del Moral 1988, Tsuyuzaki et al. 1997). Greenhouse experiments conducted on these species demonstrate that germination of *Anaphalis* and *Epilobium* does not differ with soil texture, while a higher percentage of *Hypochaeris* seeds germinate on silt than on sand or gravel (Tsuyuzaki et al. 1997). Similarly, although previous studies have found that *A. rubra* does not germinate effectively from seed on Elwha reservoir sediments (Chenoweth 2007), other nitrogen-fixing species or species with ectomycorrhizal associations (e.g. *Lupine*, *Ceanothus*) may be capable of establishing on fine, nutrient-poor substrates under stressful growth conditions (Rodriguez et al. 2008, Hoher et al. 2009).

Grasses might play a particularly important role in post-dam revegetation. The results of our seed rain germination experiment support Grubb's (1986) hypothesis that grasses will colonize fine substrates more readily than will forb or woody species. These findings are also consistent with previous work on the Elwha, in which the native grasses *E. glaucus*, *Bromus vulgaris*, and *D. elongata* were found to germinate and grow successfully from seed on Lake Mills sediment (ONP 2003, Chenoweth 2007). Other recent studies have also demonstrated that grasses are dominant over woody and forb species in recolonizing fine sediments following deglaciation and landslides (Dolezal et al. 2008, Shiels et al. 2008). Although only two grasses germinated in this study, the germination of the invasive species *P. arundinacea* reveals that it is present and viable in the seed rain and is capable of germinating on the reservoir sediments. Studies of smaller-scale dam removals in Wisconsin have found that *P. arundinacea* consistently invades de-watered reservoirs, even where other species have been seeded (Orr and

Stanley 2006). Pioneering invasive grasses can inhibit the establishment of woody species and reduce overall plant diversity in riparian zones (Fierke and Kauffman 2006).

To the extent that invasive species such as *C. arvense* and *P. arundinacea* will be present in seed rain and capable of germinating on post-dam substrates, the results of this study point to the need for monitoring and maintenance of colonizing species in the months and years following dam removal. In keeping with the goals of the dam removals and associated ecosystem restoration (DOI et al. 1994, DOI 1996a), the objectives of post-dam vegetation management should be to supplant invasive species with natives so as to maintain riparian plant diversity, and to restore and maintain riparian functions affecting habitat for salmonid fishes. Among the species tested here, *R. parviflorus* may be a suitable candidate for seed application due to its ability to germinate on fine reservoir sediments. However, since early growth and percent cover appear to be hampered on post-dam sediments *R. parviflorus* might be less effective at shading out invasive competitors initially. Multi-year studies exploring the growth rates of species in the de-watered reservoirs during and following dam removal would provide valuable understanding of longer-term impacts of fine sediments on plant colonization, growth and survivorship. Other potential candidates for seed application include *A. suksdorfii*, due to its high seed viability, and native grasses such as *D. elongata*, *E. glaucus*, and *B. vulgaris* which appear to be capable of germinating and spreading effectively on fine reservoir sediments. Among riparian plants, grasses and forbs are generally not as effective as woody species with regard to generating shade for forestalling invasives or moderating stream temperatures. Moreover, woody species are more likely to provide allochthonous litter and LWD. Initially, grasses will create dense root systems that may inhibit the spread of invasives and help stabilize banks to reduce surficial erosion and instream siltation affecting spawning salmon. This may be especially important for post-dam salmon populations, given the erosive nature of the fine sediments that will be exposed following dam removal. With time, grasses will facilitate soil development and the subsequent establishment of forbs and woody species.

Given the limited growth from seed observed for all tested species on reservoir sediments,

revegetation efforts may be enhanced by use of cuttings or transplants, particularly of woody species. Further research is necessary to determine the extent to which cuttings and transplants will survive on fine reservoir sediments. Revegetation might also be supplemented through zoochory, which may be encouraged through installation of bird perches at project sites (Zanini et al. 2009), although it should be recognized that zoochory may also deliver invasive propagules (McKay et al. 2009).

Due to the high cost of revegetation, it will not be feasible to plant the entire area of sediments that will be exposed following dam removal. Considering the potential widespread influence of seed rain, the success of post-dam revegetation efforts will likely require active monitoring and control of invasives, including reductions of source populations prior to dam removals (Chenoweth et al. 2010). The results of this study suggest that *C. arvense* and *P. arundinacea* should be given particular attention in this regard.

Conclusions

The results of this study demonstrate that sediments exposed following the Elwha dam removals may impede germination and growth of some plants. This could create a competitive advantage for some invasive species, although competitive dynamics and patterns of succession will be influenced by a range of factors including water availability, growth rates, source population size, seed production and dispersal ability. It should also be noted that our results were observed in a greenhouse microcosm study. This study provides an indication of potential outcomes within the post-dam Elwha Valley, however growing conditions, temperature fluctuations, substrate depth, herbivory and water availability will be different *in situ*. Seed rain will likely be the primary source of colonizing vegetation, but the seed rain at sites far from seed sources are not likely to receive high quantities or a significant diversity of seed. In addition, seed rain might not be uniformly abundant during the summer months when riparian substrates are most receptive to colonization. Consequently, active revegetation and management may be essential and effective for forestalling exotic plant invasions and maintaining

post-dam riparian plant diversity. Of the invasive species we tested, *C. arvense* showed the potential to germinate on coarse or fine post-dam substrates. Of the native species we tested, *R. parviflorus* and *A. suksdorfii* are potentially suitable candidates for revegetation. Although these species are less successful on fine reservoir sediments than on coarser alluvial substrates, they may still be relatively successful in comparison with other tested species. This study did not provide definitive evidence regarding grass establishment, but our results indicate the presence of *D. elongata* in Elwha seed rain and the ability of *D. elongata* to colonize fine reservoir sediments. *D. elongata* and other native grasses may be particularly effective in helping to attenuate erosion and siltation affecting post-dam salmon habitat. Given the importance of native riparian vegetation for salmon habitat (Naiman and Latterell 2005, Lake et al. 2007), revegetation of post-dam substrates will play an essential role in the success of the Elwha dam removals and associated ecosystem restoration. Since floodplain ecosystems tend to support a disproportionate share of regional plant species (Naiman et al. 1993, Nilsson and Jansson 1995, Goebel et al. 2003), revegetation might also have an important influence on regional biodiversity within the Elwha basin and ONP.

Acknowledgements

We thank Rebecca Brown, Joshua Chenoweth, Pat Shafroth, Ed Schreiner, Peter Homann and Brian Bingham for their valuable contributions to the development of this project. We also thank Anton Clifford for field and lab assistance. Sediment collection would not have been possible without the gracious assistance of Shawn Hinz and Gravity Environmental L.L.C. Greenhouse space and logistic support was provided by the Department of Biology, Western Washington University. We are also grateful to the Northwest Science editorial staff and two anonymous reviewers for assistance with the refinement of this manuscript. This project was funded by a grant from the National Park Service North Coast and Cascades Research Learning Network (H8W07060001), and by Western Washington University.

Literature Cited

- Babbitt, B. 2002. What goes up, may come down. *BioScience* 52:656-658.
- Ball, D. F. 2006. Loss on ignition as an estimate of organic matter and organic carbon in non-calcareous soils. *European Journal of Soil Science* 15:84-97.
- Baskin, C. C., and J. M. Baskin. 2001. *Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination*. Academic Press. San Diego, CA.
- Batten, K. M., K. M. Scow, and E. K. Espeland. 2008. Soil microbial community associated with an invasive grass differentially impacts native plant performance. *Microbial Ecology* 55:220-228.
- Bednarek, A. T. 2001. Undamming rivers: A review of the ecological impacts of dam removal. *Environmental Management* 27:803-814.
- Bellingham, P. J., D. A. Peltzer, and L. R. Walker. 2005. Contrasting impacts of a native and an invasive exotic shrub on flood-plain succession. *Journal of Vegetation Science* 16:135-142.
- Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. In W.R. Meehan (editor), *Influences of Forest and Rangeland Management of Salmonid Fishes and their Habitats*. American Fisheries Society, Bethesda, MD.
- Boersma, P. D., S. H. Reichard, and A. N. VanBuren. 2006. *Invasive Species in the Pacific Northwest*. University of Washington Press, Seattle.
- Bromley, C., T. Randle, G. Grant, and C. Thorne. 2005. Physical modeling of the removal of Glines Canyon Dam and Lake Mills from the Elwha River, WA. Proceedings of the 2005 Watershed Management Conference, July 19-22, 2005, Williamsburg, VA., ASCE.
- Brown, R. L., and J. Chenoweth. 2008. The effect of Glines Canyon Dam on hydrochorous seed dispersal in the Elwha River. *Northwest Science* 82(Special Issue):197-209.
- Burns, R. M., and B. H. Honkala. 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Agriculture Handbook 654 vol 2. U.S. Department of Agriculture, Forest Service, Washington, DC.
- Cavaliere, E. 2010. *Elwha River sediments: phosphorus dynamics under diverse environmental conditions*. M.S. Thesis, Western Washington University, Bellingham.
- Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society* 117: 1-21.
- Chenoweth, J. 2007. Predicting seed germination in the sediments of Lake Mills after the removal of Glines Canyon Dam on the Elwha River. M.S. Thesis, University of Washington, Seattle.
- Chenoweth, J., S. A. Acker, and M. McHenry. 2010. Revegetation and restoration plan for Lake Mills and Lake Aldwell. Elwha River ecosystem restoration project. Lower Elwha Klallam Tribe and the National Park Service. Port Angeles, WA.
- Coblentz, B. E. 1990. Exotic organisms: a dilemma for conservation biology. *Conservation Biology* 4: 261-265.
- Collier, M., R. H. Webb, and J. C. Schmidt. 1996. *Dams and Rivers: Primer on the Downstream Effects of Dams*. U.S. Geological Survey Circular 1126, U.S. Geological Survey, Reston, VA.
- Cook, K. L., W. W. Wallender, C. S. Bledsoe, G. Pasternack, and S. K. Upadhyaya. 2009. Effects of native plant species, mycorrhizal inoculums, and mulch on restoration of reservoir sediment following dam removal, Elwha River, Olympic Peninsula, Washington. *Restoration Ecology*. Published online 6 August 2009, doi: 10.1111/j.1526-100X.2009.00559.x
- Corenblit, D., J. Steiger, A. M. Gurnell, E. Tabacchi, and L. Roques. 2009. Control of sediment dynamics by vegetation as a key function driving biogeomorphic succession within fluvial corridors. *Earth Surface Processes and Landforms* 34:1790-1810.
- Cottrell, T. R. 2004. Seed rain traps for forest lands: Considerations for trap construction and study design. *BC Journal of Ecosystems and Management* 5:1-6.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.
- Daniel, W. W. 1990. *Applied Nonparametric Statistics*. 2nd ed. PWS-Kent.
- del Moral, R., and D. M. Wood. 1993. Early primary succession on the volcano Mount St. Helens. *Journal of Vegetation Science* 4:223-234.
- Department of Agriculture (USDA). 1974. *Seeds of Woody Plants in the United States*. U.S. Forest Service, Agriculture Handbook No. 450, Washington, DC.
- Department of the Interior (DOI), Department of Commerce and Lower Elwha S'Klallam Tribe. 1994. *The Elwha Report: Restoration of the Elwha River Ecosystem and Native Anadromous Fisheries*. Report submitted pursuant to Public Law 102-495, Port Angeles, WA.
- Department of the Interior (DOI). 1995. *Alluvium distribution in Lake Mills, Glines Canyon Project and Lake Aldwell*. Elwha Technical Series PN-95-4. Bureau of Reclamation, Pacific Northwest Region, Boise, ID.
- Department of the Interior (DOI). 1996a. *Elwha River ecosystem restoration, final environmental impact statement*. NPS D-271A. Department of the Interior, National Park Service, Olympic National Park, Port Angeles, WA.
- Department of the Interior (DOI). 1996b. *Sediment analysis and modeling of the river erosion alternative*. Elwha Technical Series, PN-95-9. Bureau of Reclamation, Pacific Northwest Region, Boise, ID.
- Dolezal, J., K. Homma, K. Takahashi, M. P. Vyatkina, V. Yakubov, V. P. Vetrova, and T. Hara. 2008. Primary succession following deglaciation at Koryto Glacier Valley, Kamchatka. *Arctic Antarctic and Alpine Research* 40:309-322.
- Duda, J. J., J. E. Freilich, and E. G. Schreiner. 2008. Baseline studies in the Elwha River ecosystem prior to dam removal. *Northwest Science* 82 (Special Issue):1-12.
- Ferreras, A. E., and L. Galetto. 2010. From seed production to seedling establishment: Important steps in an invasive process. *Acta Oecologica-International Journal of Ecology* 36:211-218.
- Fierke, M. K., and J. B. Kauffman. 2006. Invasive species influence riparian plant diversity along a successional

- gradient, Willamette River, Oregon. *Natural Areas Journal* 26:376-382.
- Franklin, J. F., and C. T. Dyrness. 1988. *Natural Vegetation of Oregon and Washington*. Oregon State University Press, Corvallis.
- Goebel, P. C., B. J. Palik, and K. S. Pregitzer. 2003. Plant diversity contributions of riparian areas in watersheds of the northern Lake States, USA. *Ecological Applications* 13:1595-1609.
- Goodson, J. M., A. M. Gurnell, P. G. Angold and I. P. Morrissey. 2001. Riparian seed banks: structure, process and implications for riparian management. *Progress in Physical Geography* 25:301-325.
- Goodson, J. M., A. M. Gurnell, P. G. Angold, and I. P. Morrissey. 2003. Evidence for hydrochory and the deposition of viable seeds within winter flow-deposited sediments: the river Dove, Derbyshire, UK. *River Research and Applications* 19:317-334.
- Greene, D. F., and E. A. Johnson. 1996. Wind dispersal of seeds from a forest into a clearing. *Ecology* 77: 595-609.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones: focus on links between land and water. *BioScience* 41:540-551.
- Gregory, S. V., H. Li, and J. Li. 2002. The conceptual basis for ecological responses to dam removal. *Bioscience* 52:713-723.
- Grubb, P. J. 1986. The ecology of establishment. *In* A. D. Bradshaw, D. A. Goode, and E. H. P. Thorpe (editors), *Ecology and Design in the Landscape*. Blackwell Scientific Publications, Oxford. Pp. 83-95.
- Gurnell, A. M., A. J. Boitsidis, K. Thompson, and N. J. Clifford. 2006. Seed bank, seed dispersal and vegetation cover: Colonization along a newly-created river channel. *Journal of Vegetation Science* 17:665-674.
- Gurnell, A. M., K. Thompson, J. Goodson, and H. Moggridge. 2008. Propagule deposition along river margins: linking hydrology and ecology. *Journal of Ecology* 96:553-565.
- Harmon, J. M., and J. F. Franklin. 1995. Seed rain and seed bank of 3rd-order and 5th-order streams on the western slope of the Cascade range. USDA Forest Service Research Paper. Pacific Northwest Research Station, Corvallis, OR.
- Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson. 1969. *Vascular Plants of the Pacific Northwest*. University of Washington Press, Seattle.
- Hocher, V., F. Auguy, D. Bogusz, P. Doumas, C. Franche, H. Gherbi, L. Laplaze, M. Obertello, and S. Svistoonoff. 2009. Actinorhizal nitrogen fixing symbiosis: An example of adaptation against soil abiotic stresses. *Cahiers Agricultures* 18:498-505.
- Hood, W. G., and R. J. Naiman. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. *Plant Ecology* 148:105-114.
- Hulce, C. 2009. Vegetation colonization and seed bank analysis of Lake Mills deltas: pre-dam removal analysis for post-dam removal insight. M.S. Thesis. Eastern Washington University, Cheney.
- Jensen, D. W., E. A. Steel, A. H. Fullerton, and G. R. Pess. 2009. Impact of fine sediment on egg-to-fry survival of Pacific salmon: A meta-analysis of published studies. *Reviews in Fisheries Science* 17:348-359.
- Kollmann, J., and D. Goetze. 1998. Notes on seed traps in terrestrial plant communities. *Flora* 193:31-40.
- Lake, P. S., N. Bond, and P. Reich. 2007. Linking ecological theory with stream restoration. *Freshwater Biology* 52:597-615.
- McCay, T. S., D. H. McCay, and J. L. Czajka. 2009. Deposition of exotic bird-dispersed seeds into three habitats of a fragmented landscape in the northeastern United States. *Plant Ecology* 203:59-67.
- McHenry, M. L., and G. R. Pess. 2008. An overview of monitoring options for assessing the response of salmonids and their aquatic ecosystems in the Elwha River following dam removal. *Northwest Science* 82(Special Issue):29-47.
- Mussman, E. K., D. Zabowski, and S. A. Acker. 2008. Predicting secondary reservoir sediment erosion and stabilization following dam removal. *Northwest Science* 82(Special Issue):236-245.
- Naiman, R. J., H. Décamps, and M. M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3:209-212.
- Naiman, R. J., and H. Décamps. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* 28:621-658.
- Naiman, R. J., and J. J. Latterell. 2005. Principles for linking fish habitat to fisheries management and conservation. *Journal of Fish Biology* 67:166-185.
- Naiman, R. J., H. Décamps, and M. E. McClain. 2005. *Riparia: Ecology, Conservation and Management of Streamside Communities*. Elsevier Academic Press, Burlington, MA.
- Nilsson, C., and R. Jansson. 1995. Floristic differences between riparian corridors of regulated and free-flowing boreal rivers. *Regulated Rivers: Research and Management* 11:55-66.
- Nilsson, C., R. L. Brown, R. Jansson, and D. M. Merritt. 2010. The role of hydrochory in structuring riparian and wetland vegetation. *Biological Reviews* 85:837-858.
- Orr, C. H., and E. H. Stanley. 2006. Vegetation development and restoration potential of drained reservoirs following dam removal in Wisconsin. *River Research and Applications* 22:281-295.
- ONP (Olympic National Park). 2003. Lake Mills growing trials. National Park Service, Department of the Interior. Internal report on file at Olympic National Park, Port Angeles, WA.
- Page, M. J., L. Newlands, and J. Eales. 2002. Effectiveness of three seed-trap designs. *Australian Journal of Botany* 50:587-594.
- Peltzer, D. A., P. J. Bellingham, H. Kurokawa, L. R. Walker, D. A. Wardle, and G. W. Yeates. 2009. Punching above their weight: low-biomass non-native plant species alter soil properties during primary succession. *Oikos* 118:1001-1014.
- Pess, G. R., M. L. McHenry, T. J. Beechie, and J. Davies. 2008. Biological impacts of the Elwha River dams and potential salmonid responses to dam removal. *Northwest Science* 82(Special Issue):72-90.

- Petts, G. E. 1984. *Impounded Rivers: Perspectives for Ecological Management*. John Wiley and Sons, New York.
- Phillips, E. L., and W. R. Donaldson. 1972. Washington climate for Clallam, Grays Harbor, Jefferson, Pacific, and Wahkiakum counties. Cooperative Extension Service Publication EM 3708. Washington State University, Pullman.
- Poff, N. L., and D. D. Hart. 2002. How dams vary and why it matters for the emerging science of dam removal. *Bioscience* 52:659-668.
- Poff, N. L., J. D. Allan, M. A. Palmer, D. D. Hart, B. D. Richter, A. H. Arthington, K. H. Rogers, J. L. Meyers, and J. A. Stanford. 2003. River flows and water wars: emerging science for environmental decision making. *Frontiers in Ecology and the Environment* 1:298-306.
- Rodriguez, R. J., J. Henson, E. Van Volkenburgh, M. Hoy, L. Wright, F. Beckwith, Y. O. Kim, and R. S. Redman. 2008. Stress tolerance in plants via habitat-adapted symbiosis. *The ISME Journal* 2:404-416.
- Sellars, R. W. 1997. *Preserving Nature in the National Parks: A History*. Yale University Press, New Haven, CT.
- Shafroth, P. B., J. M. Friedman, G. T. Auble, M. L. Scott, and J. H. Braatne. 2002. Potential responses of riparian vegetation to dam removal. *Bioscience* 52:703-712.
- Sheldon, J. C., and F. M. Burrows. 1973. The dispersal effectiveness of the achene-pappus units of selected compositae in steady winds with convection. *New Phytologist* 72:665-675.
- Shiels, A. B., C. A. West, L. Weiss, P. D. Klawinski, and L. R. Walker. 2008. Soil factors predict initial plant colonization on Puerto Rican landslides. *Plant Ecology* 195:165-178.
- SPSS v. 16.0. 2007. SPSS for Windows. SPSS Inc.
- Statistix v. 9.0. 2008. Analytical Software Inc.
- Tabacchi, E., A. M. Planty-Tabacchi, L. Roques, and E. Nadal. 2005. Seed inputs in riparian zones: Implications for plant invasion. *River Research and Applications* 21:299-313.
- Tolson, H. A. 1933. *Laws Relating to the National Park Service, the National Parks and Monuments*. Department of the Interior, Washington, DC.
- Tsuyuzaki, S., J. H. Titus, and R. del Moral. 1997. Seedling establishment patterns on the Pumice Plain, Mount St. Helens, Washington. *Journal of Vegetation Science* 8:727-734.
- Urgenson, L. S., S. H. Reichard, and C. B. Halpern. 2009. Community and ecosystem consequences of giant knotweed (*Polygonum sachalinense*) invasion into riparian forests of western Washington, USA. *Biological Conservation* 142:1536-1541.
- Wada, S. 2009. Evaluation of *Rubus* seed characteristics: seed coat morphology, anatomy, germination requirements and dormancy breaking. Ph.D. Dissertation, Oregon State University, Corvallis.
- Walker, L. R., J. C. Zasada, and F. S. Chapin. 1986. The role of life history processes in primary succession on an Alaskan floodplain. *Ecology* 67:1243-1253.
- Walker, L. R., and P. M. Vitousek. 1991. An invader alters germination and growth of a native dominant tree in Hawaii. *Ecology* 72:1449-1455.
- Walker, L. R., and R. del Moral. 2003. *Primary Succession and Ecosystem Rehabilitation*. Cambridge University Press, Cambridge, UK.
- Ward, J. V., and J. A. Stanford. 1979. *The Ecology of Regulated Streams*. Plenum Press, New York.
- Western Regional Climate Center (WRCC). 2009. Period of record monthly climate summary. Elwha Ranger Station, Washington (452548). <http://wrcc.dri.edu/> (accessed 10 December 2009).
- Wood, D. M., and R. del Moral. 1988. Colonizing plants on the pumice plains, Mount St. Helens, Washington. *American Journal of Botany* 75:1228-1237.
- Wood, D. M., and R. del Moral. 2000. Seed rain during early primary succession on Mount St. Helens, Washington. *Madrono* 47:1-9.
- Woodward, A., E. G. Schreiner, P. Crain, S. J. Brenkman, P. J. Happe, S. A. Acker, and C. Hawkins-Hoffman. 2008. Conceptual models for research and monitoring of Elwha dam removal—management perspective. *Northwest Science* 82(Special Issue):59-71.
- Zanini, L., and G. Ganade. 2005. Restoration of Araucaria forest: The role of perches, pioneer vegetation, and soil fertility. *Restoration Ecology* 13:507-514.

Received 17 October 2010

Accepted for publication 29 December 2010