2010

Seed rain and selected species germination and growth trials: implications for natural and augmented revegetation of post-dam Elwha River floodplain and reservoir sediments

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Recommended Citation

Michel, James T., "Seed rain and selected species germination and growth trials: implications for natural and augmented revegetation of post-dam Elwha River floodplain and reservoir sediments" (2010). *WWU Graduate School Collection*. 60.
https://cedar.wwu.edu/wwuet/60

SEED RAIN AND SELECTED SPECIES GERMINATION AND GROWTH TRIALS: IMPLICATIONS FOR NATURAL AND AUGMENTED REVEGETATION OF POST-DAM ELWHA RIVER FLOODPLAIN AND RESERVOIR SEDIMENTS

By
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Accepted in Partial Completion
of the Requirements for the Degree
Master of Science

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MASTER'S THESIS

James T Michel

May 19, 2010

SEED RAIN AND SELECTED SPECIES GERMINATION AND GROWTH TRIALS: IMPLICATIONS FOR NATURAL AND AUGMENTED REVEGETATION OF POST-DAM ELWHA RIVER FLOODPLAIN AND RESERVOIR SEDIMENTS

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

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ABSTRACT

The removal of Glines Canyon and Elwha dams from the Elwha River in Olympic National Park, Washington State is scheduled to begin in 2011. This undertaking is among the largest planned dam removals and ecosystem restoration projects in the world. One of the challenges associated with this restoration will be to understand processes influencing revegetation and invasive species colonization on the sediments exposed by dam removal. To help characterize post-dam vegetation succession within the Elwha River floodplain and dewatered reservoirs, we undertook field collections of reservoir sediments and seed rain during summer 2008. We then conducted two greenhouse experiments 1) to identify seed rain germinants upon fine reservoir sediments and 2) to explore effects of reservoir sediment texture on germination and growth of restoration candidate native species and potentially problematic invasive species. Measured summer seed rain was relatively low (<130 seeds/m^2) at three sites in the Elwha Valley. This suggests that, in the initial years following dam removal, colonization by seed rain may be slow, although the observed low seed rain density may have been a function of sampling method and timing. In the second seed sowing experiment, nearly all tested species (*Artemisia suksdorfii*, *Rubus parviflorus, Rubus spectabilis* and *Rubus discolor*) exhibited reduced capacity for germination and growth upon post-dam reservoir surfaces, while the invasive species *Cirsium arvense* was unaffected when compared to present-day river substrate. These results indicate a potential colonization advantage for *Cirsium arvense* on reservoir sediments in the years following dam removal. Depending on additional factors such as source population sizes, seed production, seed dispersal rates, and competition during establishment, this could allow for a relative increase in *Cirsium* *arvense* populations on the new post-dam substrates. These findings have implications for revegetation efforts directed at maintaining biodiversity and ecosystem functioning on floodplain and exposed reservoir surfaces following dam removal.

ACKNOWLEDGEMENTS

This research was funded in part by the North Coast and Cascades Research Leaning Network Grant. In addition to the guidance of my committee I am thankful for the advisement of Rebecca Brown, Joshua Chenoweth, Brian Bingham and Pat Shafroth. Olympic National Park staff provided experimental and permitting logistics. Sediment collection would not have been possible without the gracious assistance of Shawn Hintz and Gravity Environmental L.L.C. Greenhouse space was provided by the Biology department at Western Washington University. Field and greenhouse assistance were provided by Anton Clifford.

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INTRODUCTION

As dams in the US continue to age, dam removal has become an increasingly common management decision (Poff & Hart 2002). Most dams removed to date have been small, and the ecological response to the removal of large dams remains uncertain (Bednarek 2001, Poff et al. 2003, Gregory et al. 2002). The removal of Glines Canyon and Elwha dams from the Elwha River in Olympic National Park (ONP), Washington State is scheduled to begin in 2011 as part of the Elwha River Ecosystem and Fisheries Restoration Act (PL 102-495). Glines Canyon Dam is the largest dam scheduled for removal in the US (Woodward et al. 2008) and the Elwha is one of the largest river restoration projects in the US (McHenry & Pess 2008). The Elwha ecosystem presents a unique opportunity to study the ecological effects of large dam removal as 83% of the Elwha River watershed exists within ONP, a designated wilderness area, with limited interference from anthropogenic factors (Fig. 1).

One of the challenges associated with this restoration will be to understand processes influencing revegetation and invasive species colonization on the sediments exposed by dam removal. Approximately 21 million cubic meters of sediment are trapped behind these dams (Chenoweth et al. 2010). Some reservoir sediments will erode out of the system and into the Strait of Juan de Fuca, while other portions will remain behind in the former reservoirs or become deposited downstream in the floodplain. These newly exposed surfaces will be the substrate available for plant recolonization. To help characterize post-dam vegetation succession within the Elwha River floodplain and dewatered reservoirs, we undertook field collections of reservoir sediments and seed rain during summer 2008. We then conducted two greenhouse experiments to investigate plant growth from seed upon reservoir sediments.

Sediment Legacy

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 meters deep. Estimates made in 1994 indicated that of the 10.6 million m^3 of alluvium detained behind Glines Canyon dam, 48% was fine ($\leq$0.075 mm), 37% sand, 13% gravel and <2% cobble (USDOI 1996). The same analysis indicated that the 2.98 million m^3 of alluvial sediment detained behind Elwha dam was comprised of 66% fines ($\leq$0.075 mm), 28% sand, 4% gravel and <2% cobble (USDOI 1996). The volumetric projections of detained sediment will be almost two decades old by the time dam removal is projected to be completed in 2013. Recent estimates made by the Bureau of Reclamation indicate that the volume of sediment detained in both reservoirs will reach 21 million cubic meters by 2012 (Chenoweth et al. 2010).

Dam removal will be a staged gradual drawdown beginning in fall 2011, pausing for fish runs, and is projected to be completed by summer 2013 (Chenoweth et al. 2010). Computer models have projected that approximately 50% of fines and 15-35% of coarse sediments will be eroded downstream during & following dam removal (USDOI 1996). Although more than 50% of fine sediment is expected to erode out of the reservoirs, significant quantities will remain behind in the former reservoir beds, while other portions will become deposited downstream in the floodplain following flood events. Results from a study using a scale model of Lake Mills sediment movement 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 following dam removal (Bromley et al. 2005) (Fig. 2). Areas of fine sediments 1-2 m thick are expected to remain on valley wall landforms and 6-12 m thick terraces of mixed sediment will remain on the valley bottom in areas isolated from the active channel (Chenoweth et al. 2010). The exposure of these new sediments will be a significant factor influencing vegetation establishment and restoration.

Riparian Vegetation & Ecosystem Restoration

The sediments that will remain within the Elwha valley following dam removal will exist in dry reservoirs beds or downstream floodplain deposits. Some areas will be largely fine sediments and will be very poorly drained (Chenoweth et al. 2010). All newly exposed reservoir sediments will be limited in soil nutrients (DOI et al. 1994, Cavaliere 2010) and will lack fully developed microbial communities. Previous studies have cited the highly erosive nature of the fine sediments that will remain following dam removal (Mussman et al. 2008, Cook et al. 2009). An important focus of the Elwha Dam removal and associated ecosystem restoration is to improve habitat conditions for anadramous salmon

(*Oncorhynchus spp.*) populations. Dam removal will allow fish passage, but in order to provide optimal instream conditions, silt-laden runoff must be prevented. Pacific salmon egg-to-fry survival is negatively impacted by siltation. A review of the literature identified negative impacts on salmon egg survivorship when concentration of fine sediments (< 0.85 mm) surpasses 10% of riverbed substrate (Jensen et al. 2009). Vegetation is an effective means to control erosion and retain upland water and nutrients (Mussman et al. 2008, Whisenant 2003). In addition to controlling erosion and siltation, riparian vegetation also improves instream habitat through large wood inputs, channel and pool formation, bank stabilization, flood attenuation, stream temperature regulation and shading (Abbe & Montgomery 2003, Montgomery & Abbe 2006, Naiman et al. 2005, Apostol & Sinclair 2006**)**. Naiman and Latterell (2005) have made the assertion that vegetation health and diversity within the riparian zone is so important to salmonid health and survival that it is, in effect, fish habitat. Corenbilt et al. (2009) proposed that the control of sediment erosion by pioneering riparian vegetation provides key geomorphological and ecological functions in fluvial corridors, such that it defines fluvial ecosystem and landform organization. Accelerated succession of riparian vegetation will strongly influence all aspects of ecosystem recovery, both terrestrial and instream. The potential for invasive species to opportunistically colonize and persist upon reservoir sediments could significantly impair ecosystem function or delay restoration (D'Antonio & Vitousek 1992, Hood & Naiman 2000, Urgenson et al. 2009).

Visually and functionally this restoration project has the potential to be deemed successful or not based on factors inextricably linked to vegetation. By dissecting the interrelated webs of ecosystem processes, one common thread to successful ecosystem restoration of the Elwha River will be post-dam vegetation trajectory. Following dam removal, vast expanses of the former reservoirs will be a barren open canvas for plant colonization exposed to wind desiccation and full intensity sun, creating difficult conditions for plant establishment and succession. Reservoir sediments are limited in nutrients and organic matter (Chenoweth et al. 2010), while the seasonal extremes of drought and oversaturation will further challenge plant establishment. Texture of substrate impacts plant species germination and growth (Grubb 1986, Walker & del Moral 2003, Naiman 2005) and will be an important factor in determining which areas of the former reservoirs become colonized by different plant communities. In areas with large deposits of fine sediments, plants may struggle to germinate or properly develop root systems due to the small pore space, reduced capacity for oxygen exchange, and limited drainage (Walker & del Moral 2003). Experimental insight into differential plant growth by seed on differing textures of reservoir sediment will benefit restoration planning efforts.

Seed Dispersal and Vegetation Establishment

In riparian ecosystems plant seeds are dispersed by wind, water and animals (Goodson et al. 2001). Seeds released from vegetation can fall directly beneath the parent plant, be ejected over short distances by ‘ballistic’ distribution as seed pods explode, or may be transported by wind in a process called anemochory. Anemochorous seed dispersal distances can vary depending upon the density, aerodynamic properties of the seed, and wind patterns specific to the niche habitat (Sheldon & Burrows 1973, Greene & Johnson

1996, Tabacchi et al. 2005), with some seeds capable of distribution over several kilometers (Wood & del Moral 2000). In riparian zones, seeds may fall into the active river channel where water-facilitated dispersal (hydrochory) can transport seeds downstream. Hydrochory movement and deposition during flood events is the dominant seed dispersal mechanism in fluvial corridors (Goodson et al. 2003, Tabacchi et al. 2005), although wind distribution is especially important for riparian tree seed dispersal (Walker et al. 1986). Animals may facilitate the transport of seeds by brushing up against fruits and translocating seeds (epizoochory) or by consuming fruits and defecating in new locations (endozoochory). Seed rain refers to the combined aerial distribution of plant seeds, and includes: anemochory, zoochory and gravity. Additional seed sources specific to this restoration will be viable seeds (seedbank) contained within reservoir bottom sediments and the anthropogenic revegetation of dewatered reservoir sediments by ONP staff following dam removal.

Following dam removal the driving mechanisms for vegetation reestablishment in the Elwha watershed will be seed rain and active revegetation. Much of what will become floodplain habitat following dam removal is currently underwater behind the dams. Newly exposed lands will be far from seed sources for recolonization. This concern led to several studies which explored the seedbank contained within Lake Mills reservoir bottom sediments, delta deposits and lake hydrochory to assess the capacity of the seed repository within this system to contribute to the reestablishment of vegetation following dam removal. Brown and Chenoweth (2008) found the native seedbank of reservoir sediments limited and insufficient to facilitate rapid revegetation following dam removal.

The limited native seedbank will further be challenged by exotic species which are present in both hydrochory and reservoir bottom sediments (Brown & Chenoweth 2008). Hulce (2009) observed exotic species present in extant vegetation upon the Lake Mills delta and within the seedbank of delta sediments. In addition to the limited regrowth of vegetation from seedbank, seeds will not be delivered via hydrochory during flood events to the majority of newly exposed sediments. Approximately 70% of dewatered reservoir surfaces will be upland landforms outside the river's influence (Chenoweth et al. 2010). The park service has a mandate to preserve native plant species within park boundaries and is planning to replant 65% of the former reservoir beds over a seven or eight year period following dam removal (Chenoweth et al. 2010). Although active revegetation will be an important component of restoration, much of the dam-affected Elwha watershed will be subject to natural recolonization processes for several years prior to revegetation plantings. The seed rain that lands upon newly exposed reservoir sediments has the potential to germinate and influence post-dam vegetation trajectory. Collection of seed rain for identification of colonizing species has the potential to inform the restoration process and result in management plans tailored to specific site parameters.

This study focused on seed rain and active revegetation to acquire a pre-dam removal prognosis of competition between native and invasive species for establishment upon sediments to be exposed following dam removal. Invasive plants are often rapid colonizers capable of out-competing and impeding the growth and reestablishment of native vegetation (Tabacchi et al. 2005) on newly exposed substrates such as riparian zones following dam removal (Shafroth et al. 2002, Orr & Stanley 2006). Invasive species, even at small biomass, have been shown to alter riparian soil nutrients and biota (Bellingham et al. 2005, Peltzer et al. 2009), reduce growth of native species by altering soil microbial communities (Batten et al. 2007), reduce establishment and growth of native trees (Walker & Vitousek 1991) and are hypothesized to inhibit development of native understory and tree species in riparian systems (Fierke & Kauffman 2006). Stream restoration and salmon recovery cannot occur without a functional and diverse riparian zone harboring native riparian tree species (Lake et al. 2007). The establishment of persistent ecosystem-altering invasive plant communities upon newly disturbed substrates exposed by dam removal would be in direct contrast to the goals of the Elwha River Ecosystem Restoration Project. These experiments investigate the potential impact of seed rain and sediment texture on germination success of native and invasive species. Additional factors influencing successional trajectories following dam removal will include the relative abundance of source populations of potential colonizing species, as well as species specific differences in seed production, dispersal, predation and viability (Ferreras & Galetto 2010).

To address the concern for invasive species spread, ONP extensively mapped invasive plant communities with the potential to act as a vector for establishment into both reservoirs following dam removal (Chenoweth et al. 2010). Given that exotic seed sources will be present immediately following dam removal adds to the imperative to understand how native and invasive species establishment will be affected by reservoir sediments following the dam removal. Restoration efforts can be guided by the evaluation of candidate species' capacity for growth upon new substrates. Seed rain has the potential to contribute additional sources of seed to the revegetation of the dewatered reservoirs. This investigation into seed rain composition and abundance coupled with specific tests of target species will be important in characterizing the potential for invasive and/or native species recolonization.

Experimental Objectives

The specific objectives of this project are 1) to evaluate the potential for seed rain to contribute to post-dam vegetation recovery, 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 3) contribute to the understanding of processes shaping revegetation following dam removal, and 4) inform ONP revegetation and restoration efforts for the preservation of biodiversity and restoration of ecological processes within the Elwha River basin.

METHODS AND RATIONALE

Study Site

The Elwha River flows from its headwaters in the Olympic Mountains within ONP to the Strait of Juan de Fuca. In the process, it passes through two dams: the 64 m high Glines Canyon Dam (completed in 1927), which forms Lake Mills (~200 m elevation), and the 32 m high Elwha Dam (completed in 1913), which forms Lake Aldwell (~70 m elevation) (Figure 1). Both dams lack fish passage and inundate more than 9 km of river creating nearly 280 hectares of lakes. The Elwha watershed is a Pacific coastal forest dominated by Douglas fir (*Pseudotsuga menziesii*) upland and red alder (*Alnus rubra*) riparian forest (Shafroth et al. 2002).   Annual precipitation is orographically influenced and ranges between 350 cm at the headwaters to 75 cm at the mouth (Oregon State University 2005). A monitoring station 3 km downstream from Glines Canyon Dam receives 140cm of precipitation annually with 88% occurring October-April (WRCC 2009). This seasonality of rainfall and concomitant drought will influence vegetation recovery.

Experiment 1: Seed Rain Germination and Growth

Seed Rain Collection

To evaluate the potential for seed rain to contribute to post-dam vegetation recovery, we conducted a greenhouse experiment in which propagules captured from seed traps on the Elwha floodplain were germinated in reservoir sediments. Previous studies have utilized seed traps to characterize the seed rain of river ecosystems (Harmon & Franklin 1995, Gurnell et al. 2006, Page et al. 2002, Kollman & Goetz 1998, and Cottrell 2004). The trap design used in this study was similar to the tall funnel trap design utilized by Page et al. (2002) (Fig. 3). A foot-long length of PVC pipe was tapped into the floodplain, onto which a 100 mm diameter funnel was secured to the PVC pipe by two bungee cords. A plastic vial outfitted with a 100 μm mesh bottom (Research Nets Inc.) was secured to the outlet of the funnel by sliding over an o-ring. The 100 μm mesh enabled seeds entering the funnel to settle while also permitting water drainage to prevent premature germination of collected seeds.

Traps were deployed at three collection sites within the Elwha watershed (Fig. 4). Trap sites were located in the lower Elwha floodplain on the Lower Elwha Klallam

Reservation (FP), on the North end of the Lake Mills delta (LM) and in Geyser Valley (GV). 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. Trap sites were located on gravel bars 5-50 m from pioneering patches of willow (S*alix spp*.) and red alder (*A. rubra*) to reflect conditions on newly exposed sediments following dam removal (Fig. 5). In a previous study of seed rain on 3rd and 5th order streams in Oregon, minimally vegetated gravel bars were found to have a greater abundance and diversity of seeds than vegetated gravel bars (Harmon & Franklin 1995).

Seed rain traps were installed for 14 weeks from June 24, 2008 through September 28, 2008. This captured the growing season in between the spring freshet and the fall rains during which riparian plants have the greatest chance of establishment (Gurnell et al. 2006). Two transects of ten traps each, for a total of twenty traps at each site, were installed to maximize the potential for collection of species at a site (Kollman & Goetz 1998). Seeds were collected monthly and amalgamated by site for a total of three experimental seed sources (GV, LM & FP). Every month, collection vials were removed from each trap and replaced with new vials. Removed vials were placed in cold storage at 4^{o}C until experiment setup (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.

Sediment Collection

Lake Mills was chosen as the site for sediment collection since the majority of sediments are detained in this reservoir which is upstream of Lake Aldwell. Following dam removal, Lake Mills sediments will mobilize downstream toward and beyond Lake Aldwell. Sediments were collected in June 2008 from Lake Mills (Figs 6 & 7). 125 L of fine sediments were collected at a depth of 7-10 m using a 0.1 m^3 Van Veen sample grab from the prodelta formation at the northern end of Lake Mills. Fine sediments were analyzed at Western Washington University (WWU) for organic content and particle size by the loss on ignition standard method and on a Mastersizer particle size analyzer (Malvern Instruments Ltd., UK), respectively. Fine sediments had mean aggregate diameter (*D*50) of 12.5 um and were 98% inorganic, with a particle composition of 15% clay, 78% silt and 7% sand. All sediments were stored in 5 gallon buckets and transported to WWU where they were stored at $4^{o}C$ until experiments were initiated.

Experimental Design

The seed rain experiment was a blocked 2-factor ANOVA with 5 replicate pots for each seed trap by sediment combination. Three seed trap amalgamations (FP, LM and GV) plus a no seed control received two sediment treatments, Lake Mills reservoir bottom fine sediment (L) and a peat/vermiculite seed germinating mix (G) (Gardeners Supply Co.), yielding a total of 40 pots. The null seeding control tested for seeds contributed by the greenhouse or seed bank of sediments. The peat/vermiculite mix provided collected seeds the best potential for germination. By amalgamating seeds germination of all seeds collected over the 96 day field season were observed simultaneously.

Texture of substrate may be an important factor in determining which areas of the former reservoir become colonized by plants. We had hoped to test several texture treatments of sediment with seeds collected from each trap site to understand if different species responded differently to different textures of substrate, but the seed rain abundance was very low. We decided to evaluate growth on pure Lake Mills reservoir bottom fine sediment (L) and a peat/vermiculite seed germinating mix (G) rather than risk stretching a limited seed pool too far. Fine sediment was chosen as the most important experimental case to investigate due to the high volume of fine sediment contained in both reservoirs. The peat/vermiculite mix was selected as the second test case to provide the best possible growing conditions and encourage all trapped seeds to germinate.

For each soil and seed combination five replicate four inch square pots were filled with a 2 cm layer of sterilized sand and gravel for uniform water uptake across treatments. A 10 cm layer of appropriate substrate per the experimental design was followed by a density of seeds and trap detritus maintaining the surface area to seed ratio of the collection traps for each trap site in each replicate four inch square pot. This was achieved by weighing the amalgamated collection of seeds, scaling trap surface area to four inch pot surface area, subdividing and sowing identical masses into each replicate pot treatment. A 3-4 mm top covering of the pot’s experimental substrate covered the seeds to prevent seed loss.

Germination and Growth Procedures

After sowing of seeds all pots underwent cold, wet stratification at 4°C for twelve weeks (Oct 2008 – Jan 2009) to enhance the germination of all seeds collected (Baskin & Baskin 2001). In January 2009 all pots were transferred to the greenhouse. During this experiment the greenhouse at WWU had a 16 h 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 (Fig. 8). Germinants were recorded weekly, with unknown germinants photographed and grown out to assist with identification. Germinated grasses were removed from the greenhouse after eleven months and placed outdoors for eight weeks to vernalize and encourage flowering for further identification upon return to the greenhouse. These grasses did not flower, but were identified by vegetative key (Hitchcock et al. 1969).

Experiment 2: Targeted Species Germination & Growth Trials

Selection of Target Species

Following dam removal there will be a shift in the texture of substrates available for plant colonization, on both former reservoir beds and on downstream floodplain surfaces. It was our goal to contrast the ability of native and invasive species to colonize from seed on these new surfaces. Chenoweth (2007) evaluated growth and germination of one native grass and one native woody species on fine reservoir bottom sediments. Our seed sowing study built upon insight gained by Chenoweth (2007) and sought to understand the abilities of different riparian understory plant species to grow from seed on varying textures of Lake Mills sediment. Five priority species of interest were identified in communication with the Restoration Botanist at ONP (J. Chenoweth, personal communication 2008). Three native and two invasive species were chosen to test the hypothesis that woody and forb species are unlikely to colonize fine substrates (Grubb 1986). Native species evaluated were coastal mugwort (*Artemisia suksdorfii*), thimbleberry (*Rubus parviflorus*) and salmonberry (*Rubus spectabilis*). Tested invasive species were Canada thistle (*Cirsium arvense*) and Himalayan blackberry (*Rubus discolor*). More species than the handful selected and tested here will be important to the revegetation and restoration effort; however, we chose species fulfilling several important characteristics that we believed would inform restoration objectives. Selected native species were chosen because they are relatively fast growing and will provide shade quickly. They produce many seeds per plant, are capable of spreading rapidly by seed and rhizome, and are common in the Elwha riparian ecosystem. We identified two invasive species presently problematic within the Elwha watershed with the potential to colonize large expanses of nutrient-poor sediments exposed following dam removal. Both species of tested invasives spread aggressively by rhizome, produce large quantities of seed and can create monocultures. *Cirsium arvense* is capable of spreading laterally from rhizomes up to 5 m in one growing season (Boersma et al. 2006).

Seed and Sediment Collection

Seeds representing four of the five species of interest were collected by hand during summer 2008 from plants located in the Elwha watershed. Fruits of *Rubus* species were macerated by hand and screened to separate seed from pulp. The seeds were then dried and stored until later use. *Cirsium arvense* flower heads were dried and seeds hand separated from the pappus. Large quantities of clean dried *A. suksdorfii* seeds from the Elwha were sourced from the USDA Corvallis Plant Materials Center. Seeds in the *Rubus* genus have a robust endocarp and require scarification to elevate germination success (Baskin & Baskin 2001), (USDA 1974). *Rubus discolor* and *R. spectabilis* were immersed in 14% NaOCl in an ice bath for 24 h (Wada and Reed 2008). *Rubus parviflorus* has a considerably thinner endocarp and was immersed in 14% NaOCl for 6 h while stirring regularly to avoid damage to the embryo (procedure recommended by S. Wada, personal communication 2008). Following scarification, seeds were rinsed for 1 h in running water and dried. Lake Mills reservoir bottom fine sediments were collected as previously described for Experiment 1 and 125 L of coarse textured surface sand from new deposits was collected from the Lake Mills Delta at the South end of Lake Mills (Fig. 7) by shovel and stored in 5 gallon buckets. All sediments were transported to WWU where they were stored at 4^{o}C until experiments were initiated.

Experimental Design

The targeted species experiment was a blocked 2-factor ANOVA with 5 replicate pots for each species by sediment combination. To experimentally simulate the gradient of textures following dam removal we selected three experimental substrate treatments: pure lake bottom fine sediments from Lake Mills (L), coarse surface deposits of river sand (R), and an equal parts mixture of treatments L and R representing the expected homogenization of substrates following dam removal (LR). All five seed species plus a no-seed control (C) were crossed with the three sediment treatments, yielding a total of 90 pots. The null seeding control tested for seeds contributed by the greenhouse or experimental substrates. To test for germination method efficacy, each seed treatment was additionally sown into 5 replicate pots containing a commercially available peat/vermiculite seed germinating mix (G) (Gardeners Supply Co.), yielding 30 additional pots run parallel to the experiment. For each soil-seed combination, five replicate four inch square pots were filled with a 2 cm layer of sterilized sand and gravel for uniform water uptake across treatments. A 10 cm layer of appropriate substrate per the experimental design was followed by fifty seeds of a given species per pot evenly spaced and covered with a 3-4 mm top covering of the pot's experimental substrate to prevent seed loss.

Germination and Growth Procedures

To measure seed viability we ran a germination trial on a representative sample of three replicates of each species. Each replicate consisted of fifty seeds placed onto moist filter paper and sealed in a zip-closure plastic bag (Baskin & Baskin 2001**)**. Cold stratification and greenhouse conditions were as previously described in Experiment 1. Germination potential trials underwent simultaneous 12 week cold stratification with all experimental pots (Oct 2008-Jan 2009). Numbers of germinants were recorded weekly for germination trials, while germinants and percent cover were recorded weekly for all experimental and method validation pots for twelve weeks.

DATA ANALYSIS

The river sand (R) condition was a surrogate for the present riparian zone. Thus, we were able to observe changes in germination and growth trends upon predicted future substrate conditions (L, LR) relative to germination upon pre-dam removal floodplain substrate conditions (R). We measured germination success in terms of percent germination (PG) for a given species and treatment (equation 1).

$$(1)\ \text{Percent Germination (PG)} = \left(\frac{\text{\# germinants on experimental substrate}}{\text{\# seeds sown}} \right) \text{X } 100\%$$

Percent cover (PC) of plant growth was measured for each experimental and method validation pot in experiment 2 to assess growth rate as well as overall health of germinants. Percent cover was measured using a 10 cm x 10 cm piece of clear plastic with 1 cm gridlines. Each square of this grid was equivalent to 1% cover. The grid was placed above each pot with each square of the grid containing plant matter recorded and summed to determine PC for each pot.

Preliminary data analysis indicated germination and cover data were not normally distributed and did not exhibit homogeneous variance, and some treatments had zero germination. Further, block was not influential, and there was species by sediment interaction. Therefore, rather than a parametric blocked 2-way ANOVA analysis, a

Kruskal-Wallis one-way ANOVA by ranks was used to evaluate differences in germination and cover between sediment treatments for each species. After Kruskal-Wallis ANOVA, a post-hoc pairwise comparison of mean ranks was performed with $\alpha=0.05$ (Daniel 1990) (Stastix Software Inc.). Correlation analysis to compare germination trends to growth trends was performed using SPSS (SPSS Inc.).

RESULTS AND DISCUSSION

Experiment 1: Seed Rain Germination and Growth

Seed Rain Abundance

The number of seeds collected during June-September 2008 was surprisingly low with all three trapping sites receiving fewer than 130 seeds/m^2. Observed summer seed rain density on the Elwha was lower than the density of 340 seeds/m^2 observed at barren mid-elevation sites undergoing primary succession following the eruption of Mt. St. Helen’s (Wood & del Moral 2000). A previous study of seed rain on unvegetated gravel bars of 3rd and 5th order streams in the H.J. Andrews experimental forest, Oregon observed seed rain densities ranging from 316 – 3,798 seeds/m^2 over the course of one year (Harmon & Franklin 1995). Our study focused on seed collection during the three month window of time which riparian species are most likely to colonize newly exposed surfaces between the end of the spring freshet and the return of autumn high flows. This seasonal and temporal discrepancy helps to explain some of the low seed density we observed. Several key species of riparian tree species produce seeds near the time window during which we were capable of sampling (Burns & Honkala 1990) while others such as *A. rubra* slowly release seeds throughout the winter. We were interested in understanding the ability of long-range wind-dispersed seeds to provide source material for natural revegetation processes in remote areas of the watershed. Higher seed densities would likely have been observed if we were able to leave traps out for the full duration of a year; however, high water flows at trap sites would have eliminated traps. Alternative seed trap designs such as wet traps, turf mats or adherent paper may have collected more seeds and better quantified seed rain, however those trap designs would either have permitted seed predation by insects or would have damaged seeds and prevented experimental germination following seed collection. Another factor that may have contributed to the limited numbers of seeds collected is the strong afternoon catabatic winds that blow upstream in the Elwha Valley on sunny afternoons, (J. Michel, personal observation) which may have prevented seeds from settling down into traps or onto floodplain surfaces, resulting in patchy seed distribution concentrated in depositional zones near wood debris or standing vegetation.

Seed Rain Germinants

Only two individuals - four percent of seeds that were collected by seed trap and sown into experimental treatments - successfully germinated. The successful germinants were two grasses, which grew on the Lake Mills fine sediment (L). The native slender hairgrass (*Deschampsia elongata*) grew from seed rain collected on the Lake Mills delta (LM) and the invasive reed canary grass (*Phalaris arundinacea*) grew from seed rain collected in the lower river floodplain (FP). It is noteworthy that the only germinants observed on any substrate grew upon reservoir bottom fine sediments. Our results are consistent with a previous study (Chenoweth et al. 2010) in which the native grass

Elymus glaucus was found to grow successfully from seed on Lake Mills fine sediment. Our findings also support Grubb's (1986) hypothesis and other studies that have shown that fine sediments are preferentially colonized by grasses (Dolezal et al. 2008, Shiels et al. 2008). The limited number of species to germinate from seed rain is consistent with the work of del Moral and Wood (1993), which found that the best dispersing species often do not colonize well under stressful conditions.

Experiment 2: Targeted Species Germination and Growth Trials

Method Validation

Greenhouse germination and growth methods were validated by attaining comparable germination percentages between germination trials and seeds that were sown into the peat/vermiculite germinating mix (Table 1). Percent cover measurements further validated the experimental methods as 4 out of 5 species generated > 50% cover on the germinating mix (Table 1). Germination and growth on experimental substrates was considerably lower (Tables 2 & 3). From this we can conclude that our experimental methods were effective at germinating and growing experimental seeds and that experimental substrates collected from the Elwha watershed were far less optimal for the germination and growth of seeds than a commercially available seed germinating mixture.

Selected Species Trials

Germination and growth of *A. suskdorfii* and *R. parviflorus* were moderate, while germination and growth of *R. spectabilis, R. discolor* and *C. arvense* were limited on all experimental Elwha substrates. Of the native seeds sown into three different textures of Elwha reservoir sediment we saw greater than a five-fold decline in germination for *A. suksdorfii* (*p*=0.007) upon both treatments containing reservoir bottom sediments compared to germination on river sand. *Rubus spectabilis* did not germinate at all on either treatment containing reservoir bottom sediment. We did not observe differences in *R. parviflorus* growth between sediment treatments. Among tested invasive species, there was no detectable difference in the ability of the exotic *C. arvense* to germinate from seed on reservoir bottom sediments, while *R. discolor* did not germinate on either treatment containing reservoir bottom sediments. Despite the fact that *A. suskdorfii* experienced the greatest decrease in germination on future substrate conditions it still had the highest total germination rate of any species on fine reservoir sediments (Table 2).

Percent cover results were moderately correlated with germination trends (r=0.665, *p*<0.01). As with germination trials, *A. suskdorfii* saw greater than a three-fold decline in percent cover on both reservoir sediment treatments (*p*=0.007) when compared to percent cover on pre-dam removal substrate, but with this reduction *A. suskdorfii* still had comparable cover to the other germinating species. Since *R. spectabilis* did not germinate upon either treatment containing reservoir bottom sediment there was no comparison among substrates for percent cover. We did observe significant cover differences in *R. parviflorus* growth between the surface sand treatment (R) and the reservoir bottom treatment (L), however the mixture (LR) was not different from either treatment. There was no detectable difference in the percent cover of the exotic *C.*

arvense among texture treatments and *R. discolor* did not grow on either treatment containing reservoir bottom sediments.

Limitations

Results of these experiments have been considered in light of the following limitations. Germination and growth of seeds in this study occurred in the controlled environment of a greenhouse. Different germination and growth trends may be observed in the field where environmental conditions are more variable. It was not feasible to collect seed rain within the floodplain outside of the low flow season, thus the experimental design was not capable of capturing total seed rain potential of the Elwha watershed. High water flood events determined our sampling window and are the reason that hydrochory is the prevailing method of seed movement in riparian systems (Goodson et al. 2003, Tabacchi et al. 2005). The 2008 growing season offered a glimpse into seed rain of the Elwha, but not all species produce seed within a given year, particularly masting conifer species (Burns & Honkala 1990). High variance of germination and growth was observed for all experimental conditions and greater statistical power could have been achieved with increased replication. Despite these limitations, these results are a valuable preliminary indicator providing insight into factors that will influence the recovery of vegetation in the Elwha Valley following the removal of both dams.

Implications for Revegetation of the Elwha

These results indicate that reservoir bottom sediments may suppress or prevent the germination and growth of tested native species seeds. All tested native species showed declining trends with increasing reservoir bottom fine sediment. *Rubus parviflorus* showed promise with respect to germination upon reservoir sediments, but its limited percent cover observed on fine reservoir sediments (Table 3) suggests that it may not generate enough cover to shade out some invasive species. Although *A. suskdorfii* experienced the greatest declines in germination and growth on future sediment conditions, it still had the highest germination percentage and generated the highest percent cover among tested species on fine sediments. *C. arvense* germination was low in this experiment for all sediment treatments, but its germination and growth was not affected by future sediment conditions. The reduced germination and growth of tested native species on post-dam sediments suggests that *C. arvense* may be well adapted to take advantage of the increased quantity of fine sediment exposed following dam removal. In the dewatered reservoirs following dam removal, colonizing vegetation will be influenced not only by seed germination and growth, but also by source populations and seed production, dispersal, viability and predation (Ferreras & Galetto 2010). Vegetation trajectory will further be influenced by survivorship and growth rate of colonizers. Nonetheless, *C. arvense* should be actively managed during and following dam removal to prevent the potential for invasion of reservoir sediments. Grubb (1986) suggested that grasses will preferentially colonize fine substrates over forb and woody species. These results show that *C. arvense*, an invasive forb, is capable of colonizing fine and mixed reservoir substrates equally well with its ability to colonize coarser pre-dam removal surfaces. A test of species germination and growth on Mt St. Helens silts found several forb species that also colonized favorably on fine textured sediments (Tsuyuzaki et al. 1997). These results suggest that there may be other untested native or invasive forb and/or woody species with the capability to fare equally well on the post-dam fine sediment deposits.

Even though our seed trapping methods and timing did not capture the full range of seed rain within the Elwha watershed, and seed production fluctuates month to month and year to year, these results indicate that rates of seed input at remote unvegetated floodplain areas of the Elwha watershed are low. We observed seed rain at sites 5-50 m from pioneering vegetation. Following dam removal, the middle of dewatered reservoirs will be up to 400 m from source vegetation. The future floodplain in the former reservoir areas will be even further from intact vegetation, making it even more likely to be devoid of a significant anemochorous seed rain during the summer months following dam removal. On most of the newly exposed reservoir areas, seed rain, although limited, will be the driving process for natural revegetation. The reservoir sediment seed bank possesses limited quantities of viable seeds (Brown & Chenoweth 2008) and sediment terraces will be disconnected from flood dispersal of new seed, the prevailing method of seed dispersal in riparian zones (Goodson et al. 2003, Tabacchi et at. 2005). In this experiment, 4% of seed rain successfully germinated, which is comparable to germination rates observed for tested species on the Lake Mills reservoir bottom sediment treatments (Table 2). With a seed rain density of ~130 seeds/m^2, a 4% germination rate would yield approximately 5 germinants/m^2 in the first growing season following dam removal. Survivorship beyond establishment would likely not include all germinants. On the other end of the spectrum, if our measurements are low and seed rain is comparable to other Pacific Northwest sites (Harmon & Franklin 1995, Wood &

DelMoral 2000), a seed rain colonization rate of 4% at restoration sites could yield between 14 -150 germinants/m^2 in the first growing season following dam removal. Zoochorous seed rain has been increased at restoration sites by installing bird perches (Zanini et al. 2005), however birds have also been found to deliver invasive species to restoration sites (McKay et al. 2009). Without significant diversity or densities of wind-dispersed seed, sites far from intact vegetation may be slow to regenerate if no active revegetation is undertaken.

The potential exists for aggressive invasive species to colonize post-dam floodplains and former reservoirs by multiple vectors. *C. arvense* is an example of an invasive species that is already mildly problematic to the watershed, produces large quantities of seed, and has the ability to disperse its seed by wind over long distances (Sheldon & Burrows 1973, Wood & del Moral 2000). Moreover, relative to other tested species, *C. arvense* germination and growth appears less likely to be reduced on post-dam sediments. In addition to germination, the colonization of pioneering species following dam removal will depend on factors such as the size of source populations and seed production, dispersal and viability. It is possible that *C. arvense* could spread from existing populations into restoration sites following dam removal, but its potential magnitude will depend on its abundance and distribution, as well as competitive interactions with other species. For example, the Park Service is considering applying *A. suskdorfii* seed to restoration sites (Chenoweth et al. 2010). Our data indicated higher germination and similar cover for this native species compared to *C. arvense*. However, whether naturally-seeding or planted native vegetation would achieve high enough densities to restrict spread of *C. arvense* will require further study.

Although the native forb (*A. suksdorfii*) and the two native and one invasive woody species (*R. spectabilis, R. parviflorus and R. discolor* respectively) we tested showed declines in germination and growth on future reservoir conditions, other species may perform better. Chenoweth (2007) found that *A. rubra* did not germinate effectively from seed on fine reservoir sediments; however, other nitrogen-fixing species such as legumes or other taxa w/ *Frankia* or ectomycorrhizal associations may be well suited to establish upon high stress reservoir sediments (Rodriguez et al. 2008, Hocher et al. 2009). We feel that this study provides guidance on the revegetation of Elwha reservoir fine sediments by seed and suggest future studies consider testing additional plant species to identify species with higher germination rates, and woody and forb species capable of colonizing from seed on fine reservoir sediments. It will also be valuable for active restoration to assess the ability of cuttings and transplanted species to grow on fine reservoir sediments.

Although only 4% of collected seed rain germinated and the species composition of seed rain was unknown, observed results indicate that grasses are likely to naturally colonize from seed rain on fine reservoir sediments. These findings are consistent with studies of primary succession following landslides and deglaciation, which have shown that grasses preferentially colonize fine textured sediments over woody and forb species (Dolezal et al. 2008, Shiels et al. 2008). Although grasses are not as effective as woody species with respect to shading out invasive species, grasses create dense root networks that will reduce erosion and may restrict the spread of invasive species. Grasses may therefore be beneficial for helping reduce sediment input that could disrupt salmon populations (Jensen et al. 2009). However, some species (e.g., *P. arundinacea*), have been shown to reduce plant diversity and establishment of woody species in riparian zones (Fierke & Kauffman 2006). Careful monitoring and early control of establishing populations of unwanted species will help minimize adverse effects.

We suggest that future experiments characterize the growth of early seral woody species on Elwha reservoir sediments as they have deep roots capable of providing slope stabilization, tall shoots capable of shading out disturbance-dependent invasives and will provide woody debris and leaf litter nutrient input (Naiman et al. 2005). Given the limited growth from seed we observed for tested species, it will be valuable to restoration planning to understand the capabilities of additional woody species to grow from seed and/or survive as transplants in reservoir bottom sediments following dam removal.
The findings of this research project suggest that proactive revegetation may be essential for maintaining riparian plant diversity and attenuating the erosion of reservoir sediments following the removal of the Elwha dams. Given the fact that floodplain ecosystems tend to support a disproportionate share of regional plant species (Naiman et al. 1993, Nilsson & Jansson 1995, Goebel et al. 2003), these efforts could have an important influence on biodiversity within the Elwha basin and ONP. Stream restoration and salmon recovery cannot occur without a functional and diverse riparian zone harboring native riparian tree species (Naiman & Latterell 2005, Lake et al. 2007). Whether brought about through natural colonization or active revegetation, recovery of native riparian vegetation on

surfaces exposed by dam removal will be necessary to accomplish the broader goals of the Elwha River Ecosystem Restoration Project.

CONCLUSIONS

In the Pacific Northwest, dam removal is often undertaken to enhance salmon recovery efforts. The ability to successfully restore salmon populations requires parallel restoration of a functional riparian ecosystem and prevention of excessive siltation. Vegetation trajectory following dam removal will shape ecosystem processes and will influence salmon recovery. In this specific case, the limited seed rain and seed bank of reservoir sediments suggests a delayed time course for plant recolonization. Vegetation monitoring following dam removal in Wisconsin has indicated that an invasive species observed in our seed rain germination study (*P. arundinacea*) has consistently invaded dewatered resevoirs and impaired vegetation recovery even when other species were planted (Orr & Stanley 2006). Growth of seeds and survival of transplanted seedlings on the post dam Elwha remains unknown, but this study combined with others (Brown & Chenoweth 2008, Chenoweth 2007) suggests that, without additional support in the form of active revegetation, this ecosystem at present may be incapable of regenerating sufficient vegetation to maintain biodiversity and ecosystem function in the first few years following dam removal. The exposure of sediments following dam removal may favor invasive species colonization. However, active revegetation of these sediments with native species well-suited to survive and compete with invasive species upon reservoir sediments may accelerate the rate of ecosystem recovery. Studies exploring native species growth and survival on reservoir sediments will provide valuable guidance to revegetation efforts. In order for dam removal to effectively restore an ecosystem and ensure salmon recovery, careful attention should be given to the restoration of functional and diverse native riparian habitat.

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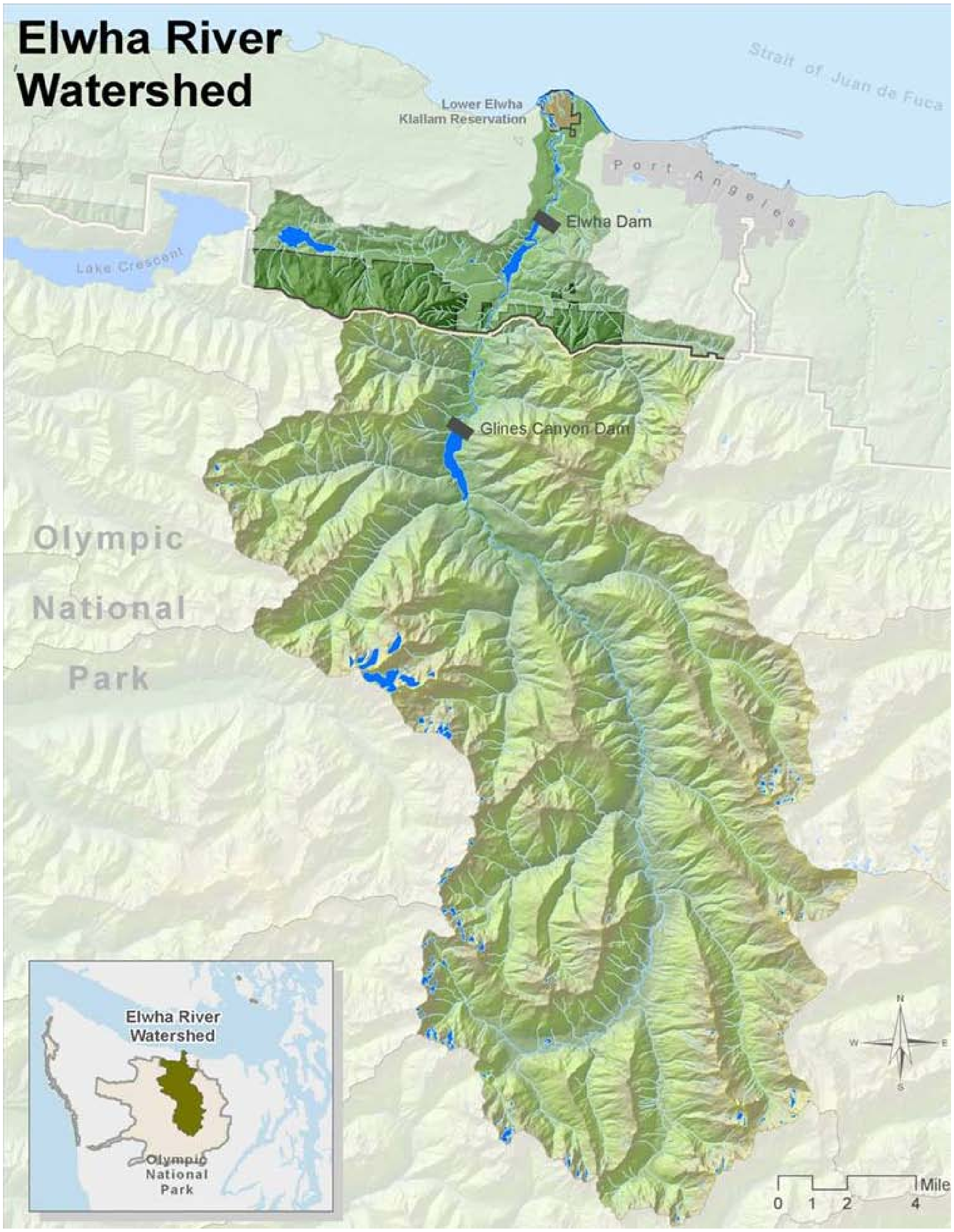

FIGURE 1. Overview of Elwha Watershed (Map created by R. Knapp)

FIGURE 2. Scale model of Lake Mills depicting terracing of sediments left behind following dam removal (Reproduced with permission of C. Bromley).

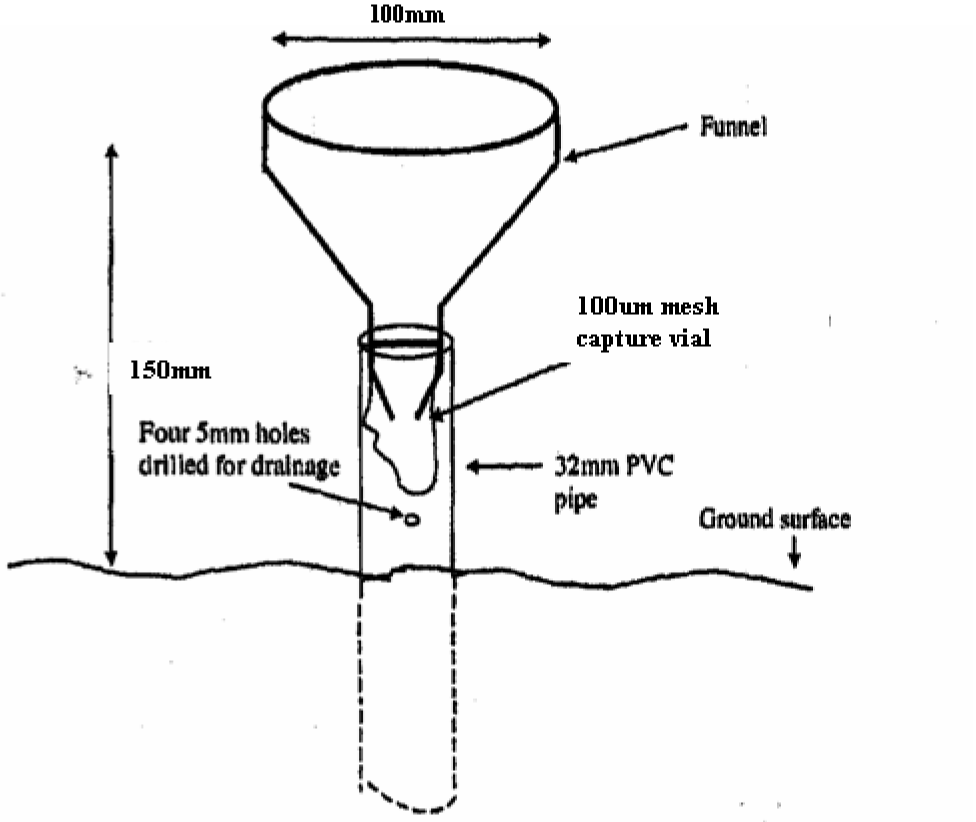

FIGURE 3. Cut-away view of funnel seed trap. High density polyethylene funnel is held by bungee to PVC pipe. Small o-ring attaches 100µ–mesh vial to funnel. (Reproduced with permission of M. J. Page)

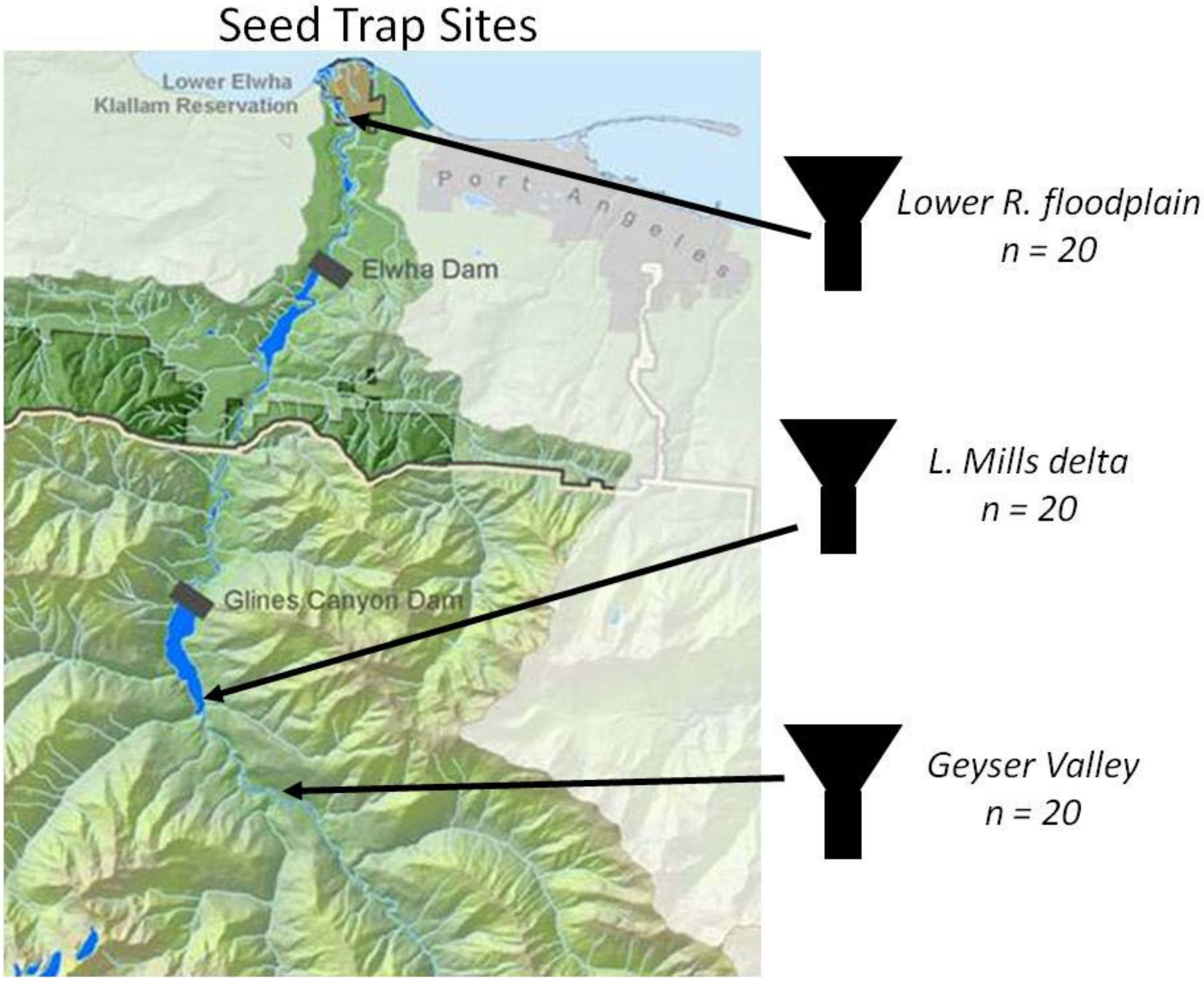

FIGURE 4. Seed trap locations within the Elwha Valley
(Map created by Robert Knapp)

FIGURE 5. Floodplain placement of seed traps.

FIGURE 6. Fine sediment collection from Lake Mills by Van Veen sample grab.

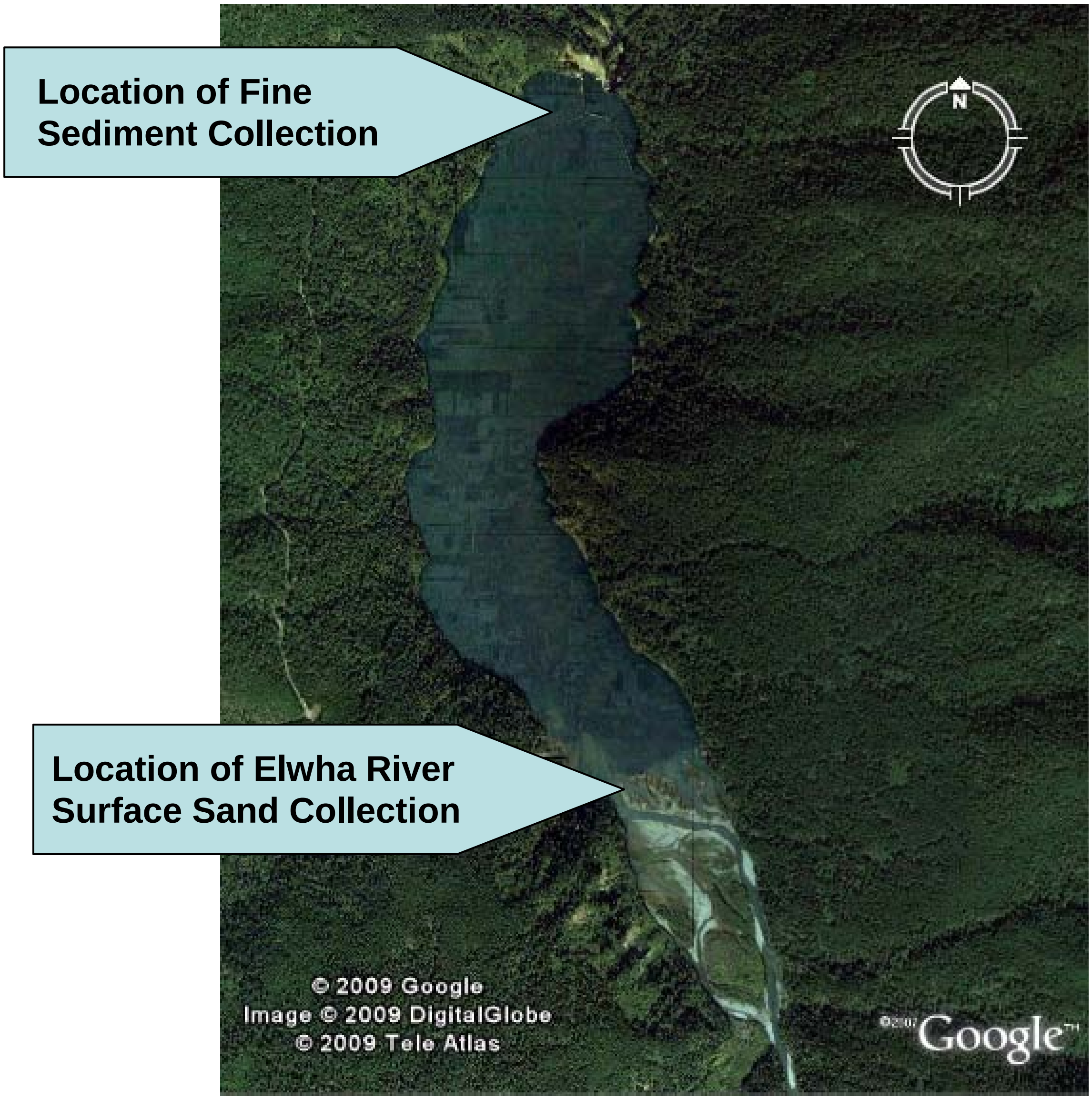

FIGURE 7. Detail of Lake Mills sediment collection sites.

FIGURE 8. Layout of growing flats in the greenhouse at week 10.

TABLE 1. Method validation for germination and growth procedures (mean ± SE) n=5

Species	% Germination Germination Trial	% Germination Germinating Mix (G)	% Cover Germinating Mix (G)
A. suksdorfii	43 ± 1.7	44 ± 2.6	71 ± 5.4
R. parviflorus	77 ± 0.9	51 ± 1.5	99 ± 0.2
R. spectabilis	4.7 ± 0.7	4.8 ± 1.2	53 ± 5.4
C. arvense	60 ± 3.2	56 ± 4.4	98 ± 0.7
R. discolor	3.3 ± 0.3	2.8 ± 0.8	5.6 ± 3.9

TABLE 2. Effect of sediment texture treatment on % germination (mean ± SE) n=5

Species	River Sand (R)	50/50 Mix (LR)	Lake Sediment (L)	*KW*	*p*
A. suksdorfii	26 ± 0.75^{a}	4.8 ± 0.5^{b}	3.2 ± 1.4^{b}	9.96	0.007
R. parviflorus	13 ± 4.5	14 ± 7.0	2.0 ± 1.5	4.34	0.114
R. spectabilis	1.2 ± 0.49	0	0	7.00	0.030
C. arvense	1.2 ± 0.8	0.4 ± 0.4	1.2 ± 0.8	0.775	0.679
R. discolor	1.6 ± 0.75	0	0	6.92	0.031

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 different at α=0.05.
KW=Kruskal-Wallis statistic

TABLE 3. Effect of sediment texture treatment on growth (% cover) (mean ± SE) n=5

Species	River Sand (R)	50/50 Mix (LR)	Lake Sediment (L)	*KW*	*p*
A. suksdorfii	10 ± 1.0 ^{a}	3.0 ± 1.3 ^{b}	1.6 ± 0.7 ^{b}	9.90	0.007
R. parviflorus	4.8 ± 0.6 ^{a}	5.4 ± 2.2 ^{ab}	1.0 ± 0.6 ^{b}	6.98	0.031
R. spectabilis	1.0 ± 0.45	0	0	6.92	0.031
C. arvense	0.2 ± 0.2	0.8 ± 0.8	1.2 ± 0.8	0.801	0.670
R. discolor	1.4 ± 0.7	0	0	6.90	0.032

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 different at α=0.05.

KW=Kruskal-Wallis statistic