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PROJECT TITLE: **Colonization, succession and exotic species invasion on sediment deposits associated with dam removal, Olympic National Park**

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PROJECT OVERVIEW:

The removal of two dams on the Elwha River in Olympic National Park (ONP), scheduled to begin in 2011, will be among the largest planned dam removals in the world. Their removal presents a range of challenges for the science of river restoration. One of the challenges will be to understand processes controlling revegetation and invasive species colonization on sediments that are exposed by dam removal. It is not clear how quickly the sediment within the drained impoundments will become revegetated, or how sediment deposition will affect downstream riparian plant communities. To determine the trajectory of vegetation succession within the drained impoundments, the extent to which reservoir sediments will facilitate the colonization of invasive species, and how sediments will affect downstream riparian vegetation, we undertook a three part study including (1) a study of vegetation colonization and seed bank patterns related to temporal and physical gradients on the deltas of Lake Mills, (2) a field and greenhouse experiment assessing potential colonization of exposed reservoir sediments via seed rain, and (3) a greenhouse experiment assessing the relative abilities of selected native and invasive floodplain plant species to grow on fine reservoir sediments.

PART 1. Survey of Vegetation and Seed banks of Lake Mills Deltas

Introduction

Glines Canyon dam, 21.6 km upstream from the mouth of the Elwha river in Olympic National Park, Washington, was built in 1925 and is 64 m tall (Duda 2008). It impounds more than 10.55 million cubic meters of sediment and 51.2 million cubic meters of water forming Lake Mills (USGS 2000; Duda 2008). The redistribution of sediment within the impoundment following removal of Glines Canyon dam is of great concern (USDOI 1995; USGS 2000).

With the mass movement of sediment and hydrologic alteration expected following the removal of Glines Canyon dam it is uncertain how vegetation will colonize exposed reservoir sediment. Consequently, we investigated the existing vegetation and soil seed bank on currently exposed reservoir sediment on Lake Mills deltas (3.2 km upstream from Glines Canyon Dam) to provide insights into the revegetation process. Our research goals were to: 1) establish a baseline vegetation record for exposed reservoir sediment (deltas), 2) identify temporal and physical gradients correlated to patterns in vegetation colonization, and 3) determine the composition of the delta soil seed bank.

Examination of extant and soil seed bank species composition provided insight into native and exotic species revegetation potential. Investigating the relationship between temporal/physical gradients and vegetation colonization improved our understanding of the processes that control establishment of plant communities and the vegetation dynamics on exposed reservoir sediment. This research enabled a trajectory of vegetation recovery within the drained impoundment. Such knowledge will be useful in developing effective strategies for river restoration following dam removal (Palmer 2005).

Methods

In July and August 2007, 43 100 m^2 vegetation plots were established, including 31 plots on the Lake Mills deltas, four on Cat Creek deltas, and eight on Boulder Creek deltas (Table 1). Plots were stratified across gradients of time since sediment exposure (based on aerial photos), grain size, water availability, and plant species composition (Fig. 1). At each plot species composition, species cover, sediment grain size, soil depth, and ground cover were recorded following the methods of the Carolina Vegetation Survey (Peet et al. 1998). Species were identified using *Flora of the Pacific Northwest* (Hitchcock and Cronquist 1976) and updated using ITIS (ITIS 2008). Native and exotic species designations were assigned using *Flora of the Olympic Peninsula* (Buckingham et al. 1995).

Seed bank samples were pooled from eight samples taken in each plot, including a litter, surface 0 – 5 cm, and subsurface 5 – 10 cm layer. The seed bank samples were cold-stratified in preparation for planting in the greenhouse. Seed bank composition was determined by the seedling emergence method in the greenhouse following the methods of Ter Heerdt (1996).

A pooled surface soil sample was taken from each plot then dried, sieved and ~160 g of each was sent to Brookside Laboratories, New Knoxville, Ohio, where nutrients, texture, and density were analyzed. A topographic survey of vegetation plots was completed to determine the elevation of each plot above Lake Mills and the Elwha River. Piezometers were installed in 21 plots and ground water levels were recorded 3 times from 2007-2009. Percent canopy/ground cover, soil analysis, ground water, and grain size results per plot are attached (see Excel document: Soil Nutrient & Texture, % Cover, Ground H20, Grain Size Results). Full details of the study methods and data analyses are described in Hulce (2009).

Results

A total of 177 species were observed in extant vegetation and soil seed bank, 10 of which were only in the seed bank (Table 2). Extant vegetation consisted of 167 species, 141 native and 26 exotic. Native species with the greatest cover included: *Alnus rubra*, *Salix sitchensis*, *Equisetum arvense*, and *Petasites frigidus*. *Ranunculus repens*, *Mycelis muralis*, *Circium arvense*, and *Rumex crispus* were the exotic species with the greatest cover. Plot 36 was the only plot where no exotics were observed in the extant vegetation (Fig. 1). Native species richness and cover was significantly greater than that of exotic independent of time since sediment exposure (Fig. 4 and Fig. 5).

A total of 39 species were found in the soil seed bank, 29 native and 10 exotic (Table 3). The most abundant native species in the soil seed bank were *Agrostis exarata*, *Equisetum arvense*, *Mimulus guttatus*, and *Myosotis laxa*. *Arenaria serpyllifolia*, *Rumex crispus*, *Poa trivialis*, and *Leucanthemum vulgare* were the most abundant exotic species in soil seed bank, with *Arenaria serpyllifolia* making up 88% of all exotics. Native species richness was greatest in the litter layer and in more recently exposed sediment (Fig. 6), while exotic species richness was greatest in the surface and subsurface layers and in less recently exposed sediment (Fig. 7). Fifty-three percent of all seeds were found in the litter layer, 24% in the surface, and 23% in the subsurface. Native and exotics seed abundance throughout layers followed a similar pattern as overall seed abundance. Percent exotic species (26%) was proportionally higher in the seed bank than in extant vegetation (16%). No seeds were found in the soil seed bank of plots 3, 6, 7, 12, 15, 20, 28, and 33 (Fig. 1).

Results from a Mantel test (evaluated null hypothesis: no similarity between seed bank and extant vegetation composition) indicate that soil seed bank species composition had little similarity to extant species composition at all depths as hypothesized (litter, $P = 0.153$; surface, $P = 0.065$; subsurface, $P = 0.074$). However, species composition was similar ($P = 0.0001$) between layers.

Aerial photos and ground observations suggest that newly exposed reservoir sediment, if conditions in drained impoundment are similar to those currently observed on the deltas, will experience herbaceous revegetation within 1-4 years and shrub/forest within 10 years (Fig. 2 and Fig. 3). Vegetation succeeded from herbaceous on recently exposed sediment to shrub then tree on less recently exposed sediment.

Plot elevation above Lake Mills ranged from 0-3.5 m, with increased tree basal area at higher elevations above the lake. Average ground water levels over 3 time periods ranged from 20-100 cm below the surface. Surprisingly, ground water, grain size, and soil nutrients were not strongly correlated to patterns in species composition or time since sediment exposure. Time since sediment exposure was based on aerial photos not actual sediment age, which may explain this lack of correlation. Actual sediment age was likely influenced by frequent flooding and further sediment deposition on the deltas after their formation.

Discussion

Exotic species were not a dominant component of Lake Mills Delta vegetation (16% of species; 16% of percent cover), which is encouraging for revegetation of the drained impoundment. However, 26% of seed bank species and 33% of all seeds were exotic, which could affect revegetation. Much of the delta sediment is inundated by water, which may substantially reduce viability of much of the seed bank (Chenoweth 2007, Brown and Chenoweth 2008). The 0.5 to 1 m of exposed sediment however, clearly carries a viable seed bank**.**

The rapid natural regeneration of vegetation (within 1-4 years) on exposed delta sediment may be duplicated in the drained impoundment if conditions are similar. However one obvious difference is the presence of a water table close to the surface of the exposed delta sediments, which will not be present in the drained reservoir. Gradual lowering of the water within the impoundment to maintain the water table, particularly at critical times of year for plant establishment may assist with rapid revegetation of the drained impoundment. For example cottonwood and willow have been shown to establish successfully only if declining water levels occur during the time of year when seeds are released (typically mid-spring; Rood 2005).

Native species such as *Alnus rubra*, *Salix sitchensis*, and *Petasites frigidus* may be useful for planting because they appear to be successful on the deltas. These species tend to produce larger amounts of shade than other natives, which may be beneficial in impeding light loving exotics. Planting of native grasses such as *Deschampsia elongata*, *Elymus glaucus var. jepsonii*, and *Agrostis exarata* (most successful grasses on deltas) might also be helpful in revegetating the impoundment.

PART 2. Seed Rain Experiment

Methods

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 were germinated in reservoir sediments. PVC funnel seed traps were deployed at three collection sites within the Elwha watershed. Collection sites were in the lower Elwha floodplain on the Lower Elwha S'Klallam Reservation (FP), on the north end of the Lake Mills delta (LM) and in Geyser Valley (GV). At each site, 20 seed traps were deployed from June through September 2008, with seeds harvested monthly. Harvested seeds were amalgamated by collection site and underwent cold, wet stratification at 4^{o}C for twelve weeks (Oct 2008 – Jan 2009) in preparation for experimental germination.

Reservoir sediments were collected in June 2008 from Lake Mills. A modified Van Veen grab sampler was used to collect approximately 125 L of fine sediments (d50 = 12.5 μm) at depths ranging from 7 – 10m. Sediments were stored in 5 gallon buckets and transported back to WWU where they were stored at 4^{o}C until the greenhouse experiments were initiated.

Greenhouse experiments were carried out at the WWU greenhouse for 12 weeks from January through March, 2009. Harvested seeds were sowed in 4" diameter pots representing five replicates of three seed treatments (FP, LM, and GV) and two sediment treatments (Lake Mills silt and a control growth medium of commercially available seed germinating peat and vermiculite), for a total of 30 pots. Each pot was filled with a 2cm layer of sterilized sand and gravel to ensure uniform water uptake, topped with a 10cm layer of the appropriate substrate per experimental treatment. Each pot was sowed with a density of seeds equivalent to the total surface area: seed ratio observed at the appropriate collection site. An additional 3 – 4 mm top covering of experimental substrate was added to cover the seeds.

During this experiment the greenhouse at WWU had a 16h light regimen and controlled temperature between 17^{o}C at night and 20^{o}C daytime. Pots were arranged in a randomized block configuration and were randomly shuffled weekly. Pots were placed in watering flats and watered predominantly from below with occasional overhead misting to maintain greenhouse humidity. Germinants were recorded weekly, with unknown germinants photographed and grown out to assist with identification.

Results

The number of seeds collected was surprisingly low, with all three trapping sites receiving fewer than 130 seeds/m^2. Seed collection occurred 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 does not explain the difference between our results and previous studies elsewhere fully. A likely explanation is that the sites we sampled within the Elwha watershed were further away from any nearby vegetation. We intentionally selected isolated unvegetated locations as a realistic representation of the large unvegetated expanses which will exist following dam removal. Our experimental design sought to characterize seed rain potential in areas isolated from nearby vegetation. 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. 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, which may have prevented seeds from settling down into traps or onto floodplain surfaces.

Of all the seeds collected and sown into experimental treatments, only two plants successfully germinated and became established. Both germinants grew on the Lake Mills fine sediment (L) and both were grasses. These germinants grew from seeds collected on the Lake Mills delta (LM) and the lower river floodplain (FP). These grasses have not yet been identified to species, but have undergone an eight-week outdoor vernalization to simulate a winter cycle and are presently growing in the greenhouse to encourage flowering during the second year of growth. Once both grasses have flowered they will be identified to species. At this point it is not known whether these grasses are native or exotic species. It is noteworthy that the only germinants on any substrate were observed on reservoir bottom fine sediments. From these experiments we can conclude that fine reservoir bottom sediments (L) are not completely inhospitable to plant growth.

PART 3. Selected Species Greenhouse Experiment

Methods

This experiment was designed to assess the relative abilities of selected native and invasive species to grow on fine reservoir sediments. The species chosen for this experiment were identified as priority species of interest through consultation with ONP Restoration Botanist Joshua Chenoweth. The native species chosen were coastal mugwort (*Artemisia suksdorfii*), thimbleberry (*Rubus parviflorus*) and salmonberry (*Rubus spectabilis*). These species were chosen because they are relatively fast growing and will provide shade quickly, they produce many seeds per plant, they are capable of spreading rapidly by seed and rhizome, and they already exist within the present riparian ecosystem and are growing relatively favorably on fine textured deposits. Invasive species chosen were Canada thistle (*Cirsium arvense*) and Himalayan blackberry (*Rubus discolor*). Both of these species spread aggressively by rhizome, produce large quantities of seed, create large monoculture stands and are known to be present in ONP.

Seeds of *A. suksdorfii* were obtained from the USDA Corvallis Plant Materials Center from among the stores of seeds to be utilized for post-dam restoration. Seeds of the other four species were collected by hand during summer 2008 from plants located in the Elwha watershed. *Rubus* fruits were macerated by hand and screened to separate seed from pulp and subsequently dried and stored for later use. *C. arvense* flower heads were dried and seeds hand separated from the pappus.

Collected seeds underwent cold, wet stratification at 4^{o}C for twelve weeks (Oct 2008 – Jan 2009) in preparation for experimental germination. *Rubus* seeds underwent additional scarification to promote germination success (see USDA 1974). *R. discolor* and *R. spectabilis* were immersed in 14% NaOCl in an ice bath for 24h (Wada and Reed, 2008). *R. parviflorus* has a considerably thinner endocarp and was immersed 14% NaOCl for 6h while stirring regularly to avoid damage to the embryo (procedure recommended by S. Wada, personal communication). Following scarification, seeds were rinsed for 1 h in running water and dried.

Prior to greenhouse sowing, we undertook a series of germination trials on representative samples of each of the selected species. The purpose of these germination trials was to assess the viability of seed stock used for each of the tested species seed stock and provide a point of reference for germination results seen on experimental substrates. Three replicate germination trials were conducted for each species (Baskin and Baskin, 2001). Each replicate consisted of 50 seeds placed onto moist filter paper and sealed in a zip-closure plastic bag. To enable comparisons across species, mean germination potential was calculated for each species and subsequent experimental results for each species were compared to the mean germination potential determined for that species.

Sediment treatments for this experiment consisted of (1) Lake Mills silt collected by grab samples as described above, (2) coarse surface deposits of river sand collected by shovel from the above water delta formation at the south end of Lake Mills, (3) an equal parts mixture of Lake Mills silt and river sand representing the expected homogenization of substrates following dam removal, and (4) a control growth medium of commercially available seed germinating peat and vermiculite. All five seed species were sowed in 4” diameter pots, along with an additional control treatment (i.e., no seeds sown) in five replicates of each of the four sediment treatments, for a total of 120 pots.

Each pot contained a 2 cm layer of sterilized sand and gravel for uniform water uptake, topped with a 10 cm layer of experimental sediment plus 50 seeds of a the experimental seed (or none in the case of the control), evenly spaced and covered with a 3 – 4mm covering of experimental substrate to prevent seed loss. Greenhouse experiments were carried out at the WWU greenhouse for 12 weeks from January through March, 2009, concurrent with the seed rain experiment, under the same greenhouse conditions, as described above.

Growth results were expressed in terms of percent germination, normalized percent germination and normalized percent cover. Percent germination was calculated as percentage of seeds that germinated successfully (i.e., the number of seeds germinated divided by the number of seeds sowed, multiplied by 100), expressed as a percentage of mean germination potential determined for that species. Normalized percent germination was the percent germination for any given treatment expressed as a percentage of the mean percent germination seen for that species in the river sand treatment (i.e., the natural floodplain substrate). Normalized percent cover was the percent cover in any given pot, expressed as a percentage of the mean percent cover seen for that species in the river sand treatment.

Results

Among the native species tested, growth rates were generally decreased on substrates containing reservoir silt. *R. parviflorus* was the only species that did not see a significant decrease in normalized percent growth on reservoir silt (Figure 8). Among the invasive species, *R. discolor* did not germinate upon either treatment containing reservoir silts, but *C. arvense* showed no significant decrease in normalized percent growth (Figure 9). These findings suggest that there is some potential for invasive species to gain a competitive advantage on fine sediments deposited after dam removal, but that *R. parviflorus* might be a suitable candidate for revegetation. However, it should be pointed out that *R. parviflorus* did show a significant decrease in normalized percent cover (Figure 10) on the full reservoir silt treatment, whereas *C. arvense* did not (Figure 11), which suggests that *R. parviflorus* might be less effective in shading out competing invasives.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS:

- Exotic species need to be managed as they currently represent 16% of extant vegetation (both richness and percent cover) and 33% of all seeds in the seed bank (26% of seed bank species) on Lake Mills Deltas.

- Gradual lowering of water in the impoundment, particularly at times of year crucial to plant establishment, may allow exposed sediments to revegetate as quickly as on the deltas.

- Rates of seed dispersal via long-range aerial transport are relatively low during the period between the spring freshet and fall rains. Consequently, remote areas of former reservoirs may be slow to colonize during the initial seasons following dam removal. In these areas, active revegetation with native species may be an effective strategy for forestalling colonization by invasive species.

- Germination and growth rates for many species may be decreased on fine sediments in the former reservoirs and/or downstream floodplains following dam removal.

- The potential exists for invasive species to thrive on fine sediments in the former reservoirs and/or downstream floodplains following dam removal. One species of potential concern is *Cirsium arvense*, which appears not to be hampered by fine reservoir sediments and may therefore have a competitive advantage over other species.

- Successful native species on the deltas that might be considered for planting include: *Alnus rubra*, *Salix sitchensis*, *Petasites frigidus*, *Deschampsia elongata*, *Elymus glaucus var. jepsonii*, and *Agrostis exarata.*

- One native species that shows promise for revegetation based on greenhouse experiments is *Rubus parviflorus*, which appears not to be hampered by fine reservoir sediments in terms of germination success.

- Greenhouse experiments have also shown that native grasses are capable of germinating successfully on fine reservoir sediments.

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Table 1. UTM coordinates for plots on Lake Mills Deltas.

South Island:		
Plot #	North	East
37	0455432	5314132
North Island:		
Plot #	North	East
38	0455479	5314222
39	0455382	5314324
40	0455395	5314263
West Delta:		
Plot #	North	East
35	0455404	5314017
32	0455424	5314018
36	0455478	5314002
33	0455533	5313869
34	0455383	5313926
29	0455501	5313813
East Delta:		
Plot #	North	East
27	0455483	5314099
26	0455510	5314122
21	0455517	5314083
25	0455553	5314125
24	0455550	5314103
20	0455613	5314111
15	0455685	5313870
17	0455680	5313806
18	0455663	5313874

Main Delta:		
Plot #	North	East
12	O455579	5313841
13	O455596	5313819
9	O455635	5313799
11	O455592	5313782
8	O455607	5313736
28	O455710	5313760
10	O455689	5313690
16	O455709	5313674
5	O455690	5313589
7	O455729	5313617
6	O455740	5313587
31	O455606	5313585
Cat Delta:		
Plot #	North	East
1	O455673	5313498
2	O455696	5313432
3	O455629	5313384
4	O455706	5313322
Boulder Delta:		
Plot #	North	East
57	O455007	5314487
56	O454984	5314430
55	O455046	5314442
53	O455088	5314396
51	O454999	5314377
50	O455066	5314365
48	O455031	5314341
49	O455014	5314399

Table 2: Elwha Delta Extant Vegetation and Soil Seed Bank Species (exotics in bold).

Species	**Extant**	**Seed Bank**
Abies grandis (FACU)	x	
Acer circinatum (FACU)	x	
Acer glabrum (FAC)	x	
Acer macrophyllum (FACU)	x	
Achillea millefolium (FACU)	x	
Achlys triphylla (NI)	x	
Actaea rubra (NI)	x	
Adenocaulon bicolor (NI)	x	
Adiantum aleuticum (NI)	x	
Agrostis aequivalvis (NI)	x	
***Agrostis capillaris* (NI)**	x	
Agrostis exarata (FACW)	x	x
Agrostis exarata var. exarata (FACW)	x	
***Agrostis stolonifera* (FAC)**	x	
Agrostis humilis (NI)	x	
Alnus rubra (FAC)	x	x
Alopecurus geniculatus (FACW)	x	
Amelanchier alnifolia (FACU)	x	
Anaphalis margaritacea (NI)	x	x
Angelica sp. (elwha) (FAC)	x	
Antennaria howellii ssp. neodioica (NI)	x	
***Arenaria serpyllifolia* (FACU)**	x	x
Artemisia sp (elwha) (NI)	x	
Artemisia suksdorfii (NI)	x	
Aster chilensis var. chilensis (FAC)	x	
Athyrium filix-femina (FAC)	x	
Bromus carinatus (NI)	x	
***Bromus commutatus* (NI)**	x	
Bromus pacificus (NI)	x	
Bromus vulgaris (FACU)	x	
Campanula scouleri (NI)	x	
Cardamine occidentalis (FACW)	x	x
Cardamine oligosperma (FACW)	x	
Carex aurea (FACW)	x	
Carex deweyana (FAC)	x	
Carex nigricans (FACW)	x	

Cerastium beeringianum (FACU)	x	x
Chamerion angustifolium ssp. angustifolium (FACU)	x	
Chamerion latifolium (NI)		x
Circaea alpina (FACW)	x	x
***Cirsium arvense* (FACU)**	x	
***Cirsium vulgare* (FACU)**	x	
Claytonia sibirica (FACW)	x	
Clematis ligusticifolia (FACU)	x	
Collomia grandiflora (NI)	x	
Collomia heterophylla (NI)	x	x
Deschampsia elongata (FACW)	x	
Dicentra formosa (FACU)	x	
Elymus glaucus ssp. glaucus (FACU)	x	
Elymus glaucus var. jepsonii (FACU)	x	x
Epilobium anagallidifolium (FACU)		x
Epilobium brachycarpum (NI)	x	x
Epilobium ciliatum (FACW)	x	x
Epilobium ciliatum ssp. ciliatum (FACW)	x	
Epilobium ciliatum ssp. glandulosum (FACW)		x
Epilobium ciliatum ssp. watsonii (FACW)	x	
Epilobium lactiflorum (FACW)		x
Epilobium luteum (FACW)	x	x
Epilobium minutum (NI)	x	x
Equisetum arvense (FAC)	x	x
Equisetum hyemale var. affine (FACW)	x	
Equisetum sylvaticum (FACW)	x	
Equisetum telmateia var. braunii (FACW)	x	
Erigeron aliceae (NI)	x	
Erigeron philadelphicus (FACU)	x	
Eriophyllum lanatum var. lanatum (NI)	x	
Festuca occidentalis (NI)	x	
Festuca subuliflora (NI)	x	
Festuca subulata (FAC)	x	
Fragaria vesca (NI)	x	
Fragaria virginiana (NI)	x	
Galium sp. (Elwha delta) (NI)	x	
Galium sp. (Elwha, four leaves) (NI)	x	
Galium aparine (FACU)	x	x
Galium oreganum (NI)	x	

Galium trifidum (FACW)	x	
Galium triflorum (FACU)	x	
Geum macropyllum var. macropyllum (FACW)	x	x
Glyceria striata (OBL)	x	
Heracleum maximum (FAC)	x	
Heuchera micrantha var. diversifolia (NI)	x	
Hieracium albiflorum (NI)	x	
Hieracium gracile (NI)	x	
Hieracium gracile var. gracile (NI)		x
***Holcus lanatus* (FAC)**	x	
Holodiscus discolor (NI)	x	
***Hypericum perforatum* (NI)**		x
Hypochaeris sp. (elwha) (FACU)	x	
***Hypochaeris radicata* (FACU)**	x	
Juncus articulatus (OBL)	x	
Juncus bolanderi (OBL)	x	
Juncus bufonius (FACW)	x	x
Juncus covillei (FACW)	x	
Juncus effusus var. gracilis (FACW)	x	
Juncus nevadensis var. nevadensis (FACW)	x	x
Juncus tenuis (FAC)	x	x
***Leucanthemum vulgare* (NI)**	x	x
Lotus denticulatus (NI)	x	
***Lupinus arboreus* (NI)**	x	
Lupinus latifolius ssp. latifolius (NI)	x	
Lupinus albicaulis (FAC)	x	
Luzula parviflora ssp. parviflora (NI)	x	
Luzula piperi (NI)	x	
Mahonia nervosa (NI)	x	
Mimulus guttatus (OBL)	x	x
Mimulus lewisii (FACW)	x	x
Mimulus moschatus var. moschatus (FACW)	x	
Montia parvifolia ssp. parvifolia (FACW)	x	
***Mycelis muralis* (NI)**	x	x
***Myosotis arvensis* (FAC)**	x	
Myosotis laxa (OBL)	x	x
Nemophila parviflora var. parviflora (NI)	x	
Oemleria cerasiformis (FACU)	x	
Osmorhiza berteroi (NI)	x	

Oxalis oregana (NI)	x	
Petasites frigidus (FACW)	x	
Phacelia hastata (NI)	x	
Phleum alpinum (FAC)	x	
***Phleum pratense* (FACU)**	x	
Phlox gracilis (NI)	x	
***Plantago lanceolata* (FAC)**	x	
Plantago sp. (elwha) (NI)	x	
***Poa annua* (FAC)**	x	
***Poa compressa* (FACU)**		x
Poa laxiflora (NI)	x	
***Poa trivialis* (FACW)**	x	x
Polygonum minimum (FACU)	x	
Polystichum munitum (FACU)	x	
Populus balsamifera ssp. trichocarpa (NI)	x	
***Prunella vulgaris ssp. vulgaris* (NI)**	x	
Pseudotsuga menziesii var. menziesii (FACU)	x	
***Ranunculus repens* (FACW)**	x	x
Ribes sp. (elwha) (NI)	x	
Rosa gymnocarpa (FACU)	x	
Rubus leucodermis (NI)	x	
Rubus parviflorus (FACU)	x	
Rubus spectabilis (FAC)	x	
Rubus ursinus (FACU)	x	
***Rumex acetosella* (FACU)**	x	
***Rumex crispus* (FACW)**	x	x
Salix sp. (elwha) (FACW)	x	
Salix commutata (OBL)	x	
Salix sitchensis (FACW)	x	
Sambucus sp. (elwha) (FACU)	x	
Scirpus sp. (elwha) (OBL)	x	
Scirpus cyperinus (OBL)	x	
Sedum oreganum (NI)	x	
Sedum spathulifolium (NI)	x	
***Senecio vulgaris* (FACU)**		x
***Sonchus asper* (FAC)**		x
Stachys chamissonis var. cooleyae (NI)	x	
Stellaria calycantha (FACW)	x	
Stellaria longipes (FACW)	x	

***Stellaria media* (FACU)**	x	
Symphoricarpos albus (FACU)	x	
Symphoricarpos mollis ssp. hesperius (NI)	x	
Tellima grandiflora (NI)	x	
Thalictrum sp. (elwha) (FACU)	x	
Thuja plicata (FAC)	x	
Tiarella trifoliata (FAC)	x	
Tiarella trifoliata var. trifoliata (FAC)	x	
Tolmiea menziesii (FAC)	x	x
Trientalis borealis ssp. latifolia (FAC)	x	
***Trifolium hybridum* (FACU)**		x
***Trifolium repens* (FACU)**	x	
Trisetum canescens (NI)	x	
Tsuga heterophylla (FACU)	x	
Typha latifolia (OBL)	x	
Urtica dioica (FAC)	x	
Urtica dioica var. gracilis (FAC)	x	
Utricularia intermedia (OBL)	x	
Veronica americana (OBL)	x	x
***Veronica officinalis* (NI)**	x	
***Vicia hirsuta* (NI)**	x	
***Vicia sativa ssp. nigra* (NI)**	x	
***Vulpia myuros* (NI)**	x	
Xanthium strumarium var. canadense (FAC)	x	

Table 3. Soil seed bank species abundance at litter, surface, and subsurface layers (exotics in bold). Growth habit is indicated as herbaceous (H) or tree/shrub (T/S). Wetland status is indicated as OBL, FACW, FAC, FACU, or NI (no indicator).

Soil Seed Bank Species	Litter Abundance	Surface Abundance	Subsurface Abundance
Agrostis exarata (H) (FACW)	94	3	8
Alnus rubra (T/S) (FAC)	1	4	1
Anaphalis margaritacea (H) (NI)	1	2	2
***Arenaria serpyllifolia* (H) (FACU)**	92	49	25
Cardamine occidentalis (H) (FACW)	1	1	0
Cerastium beeringianum (H) (FACU)	1	1	1
Chamerion latifolium (H) (NI)	1	1	0
Circaea alpina (H) (FACW)	1	0	0
Collomia heterophylla (H) (NI)	0	1	1
Elymus glaucus var. jepsonii (H) (FACU)	1	1	0
Epilobium anagallidifolium (H) (FACU)	1	1	1
Epilobium brachycarpum (H) (NI)	0	1	0
Epilobium ciliatum (H) (FACW)	1	1	1
Epilobium ciliatum ssp. glandulosum (H) (FACW)	4	1	3
Epilobium lactiflorum (H) (FACW)	1	0	1
Epilobium luteum (H) (FACW)	0	1	0
Epilobium minutum (H) (NI)	11	2	1
Equisetum arvense (H) (FAC)	43	34	5
Galium aparine (H) (FACU)	0	0	1
Geum macrophyllum var. macrophyllum (H) (FACW)	0	0	1
Hieracium gracile var. gracile (H) (NI)	1	0	1
***Hypericum perforatum* (H) (NI)**	3	0	0
Juncus bufonius (H) (FACW)	0	0	14
Juncus nevadensis var. nevadensis (H) (FACW)	1	1	1
Juncus tenuis (H) (FACW)	1	0	3
***Leucanthemum vulgare* (H) (NI)**	1	1	2
Mimulus guttatus (H) (OBL)	23	2	33
Mimulus lewisii (H) (FACW)	1	1	1
***Mycelis muralis* (H) (NI)**	1	0	0
Myosotis laxa (H) (OBL)	7	18	14
***Poa trivialis* (H) (FACW)**	2	1	1
***Poa compressa* (H) (FACU)**	0	0	1

***Ranunculus repens* (H) (FACW)**	0	1	0
***Rumex crispus* (H) (FACW)**	3	2	5
***Senecio vulgaris* (H) (FACU)**	0	0	1
***Sonchus asper* (H) (FAC)**	0	1	0
Tolmiea menziesii (H) (FAC)	0	1	1
***Trifolium hybridum* (H) (FACU)**	0	0	1
Veronica americana (H) (OBL)	1	2	2
Total Abundance	**299**	**135**	**133**

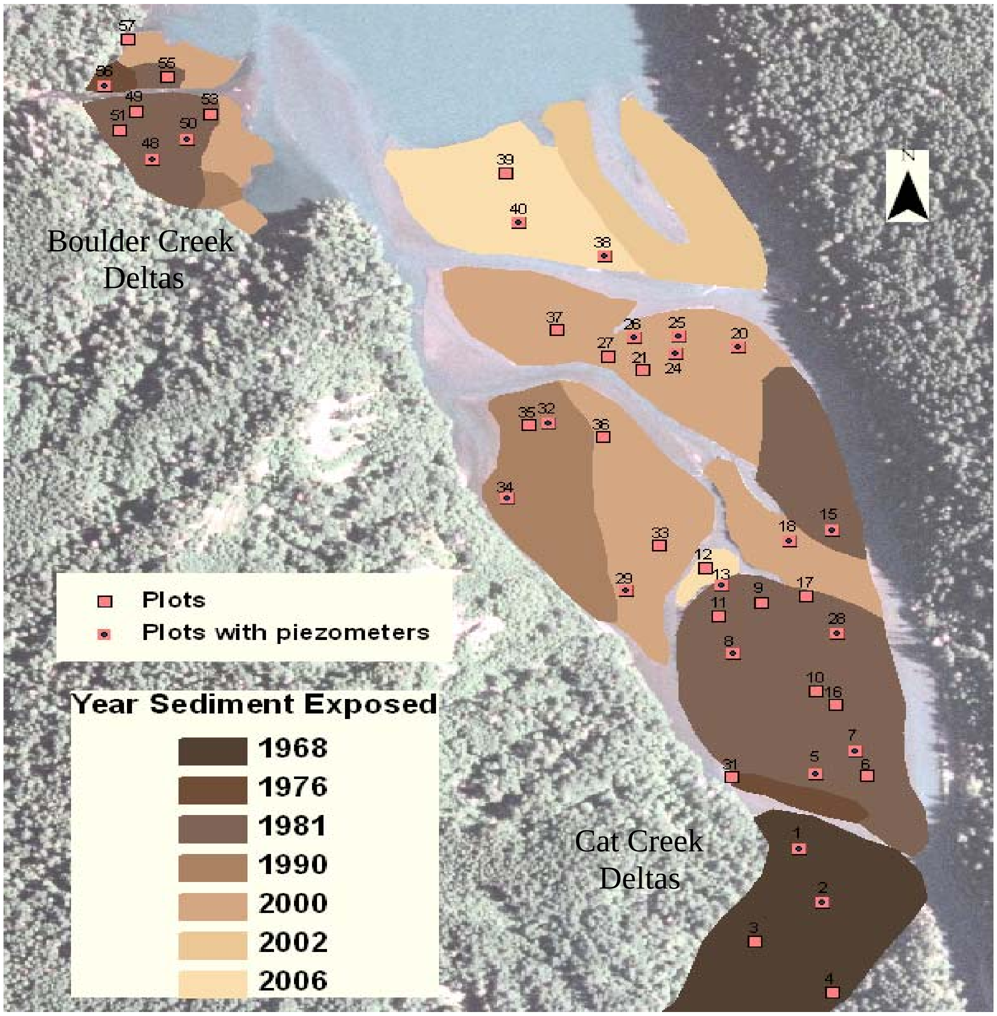

Fig. 1. Map of Lake Mills Deltas. Forty-three 100m^2 plots stratified by time since sediment exposure.

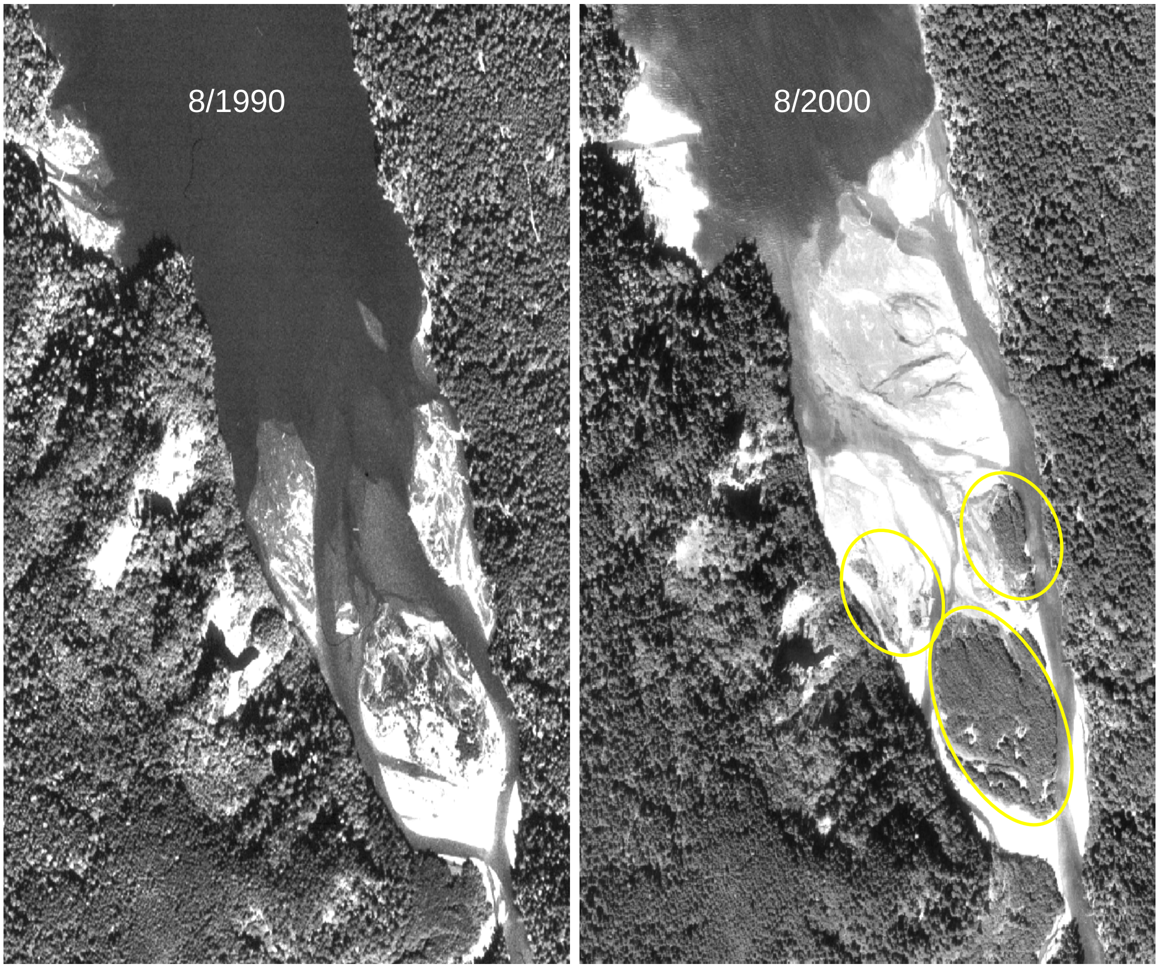

Fig. 2. Aerial photos showing changes in vegetation over time. Forest and shrub vegetation formation on delta sediment (indicated by circles) from August 1990 (left) to August 2000 (right).

Fig. 3. Aerial photos showing changes in vegetation over time. From August 2002 (left) to September 2006 (right) forest and shrub vegetation filled in on the east main, west main, and Boulder creek deltas. Herbaceous vegetation is also present on much of the sediment that became exposed over the 4 year period (indicated by circles).

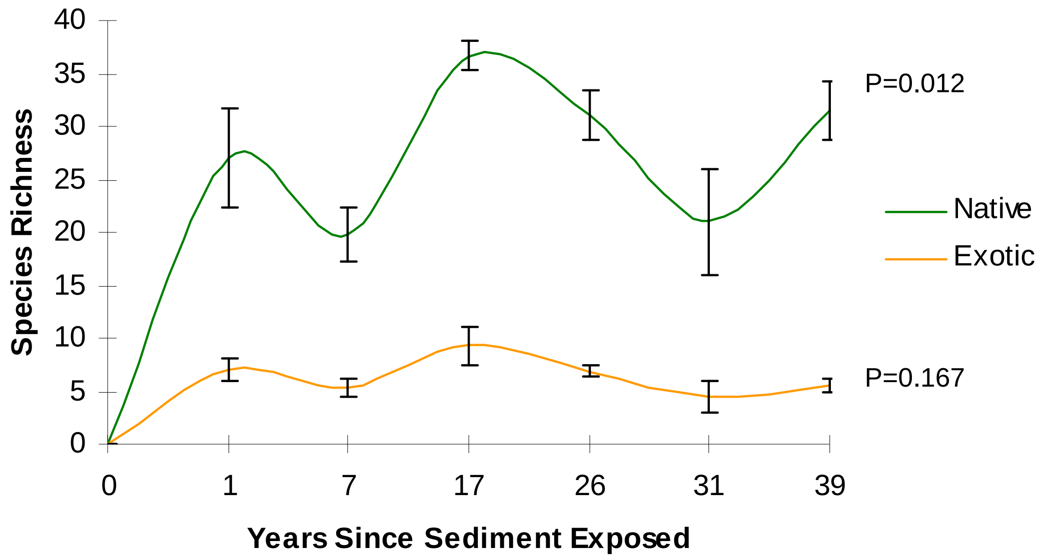

Fig. 4. Species richness vs. years since sediment exposed. Native species richness was greater than exotic species richness independent of when sediment was exposed.

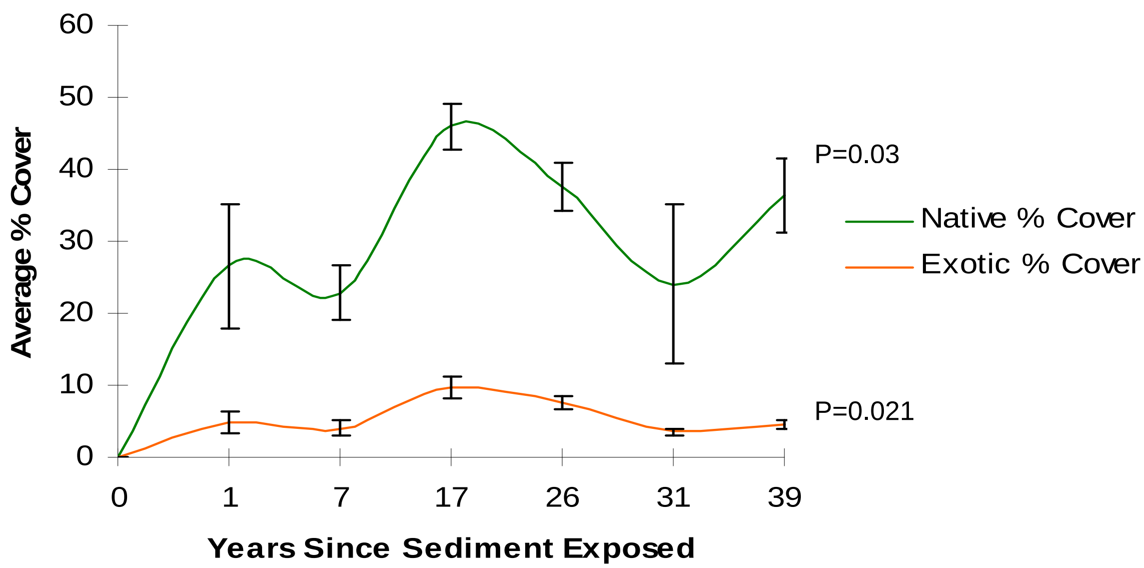

Fig. 5. Average percent cover vs. years since sediment exposed. Native percent cover was greater than exotic percent cover independent of when sediment was exposed.

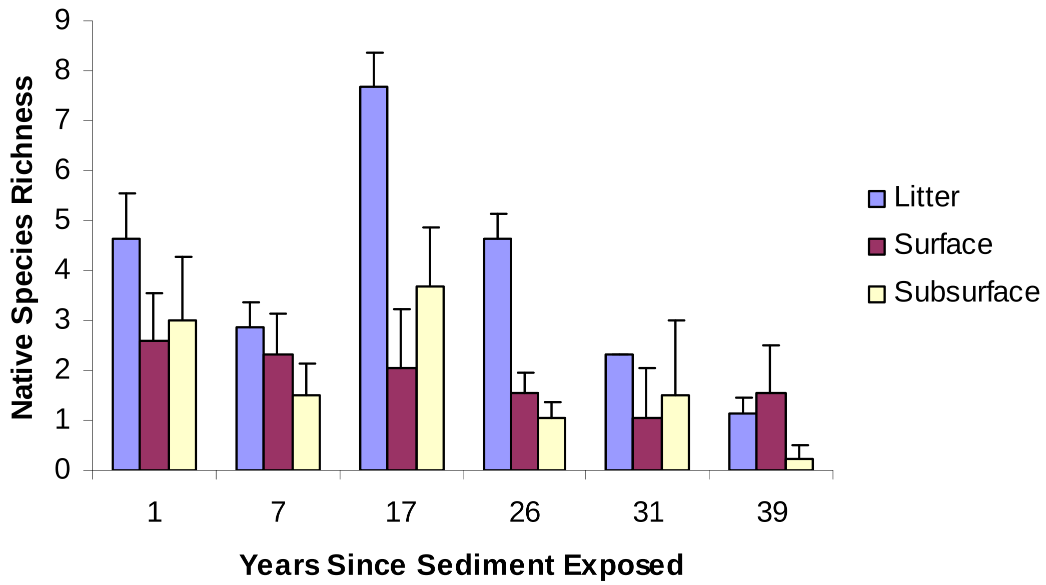

Fig. 6. Seed bank native species richness vs. years since sediment exposed. Native species richness was greatest in the litter layer and in more recently exposed sediment.

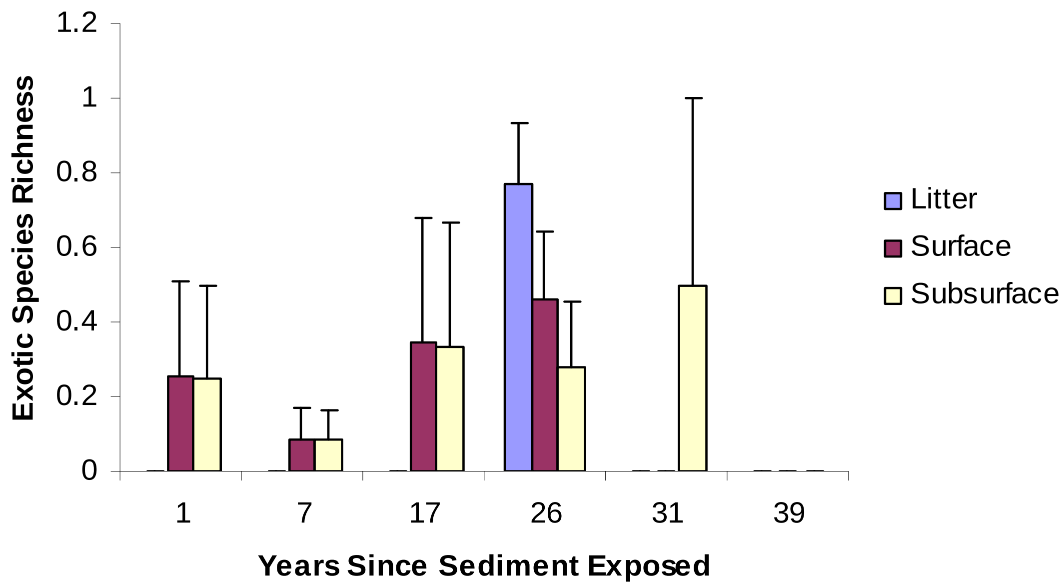

Fig. 7. Seed bank exotic species richness vs. years since sediment exposed. Exotic species richness was greatest in the surface and subsurface layers and in less recently exposed sediment.

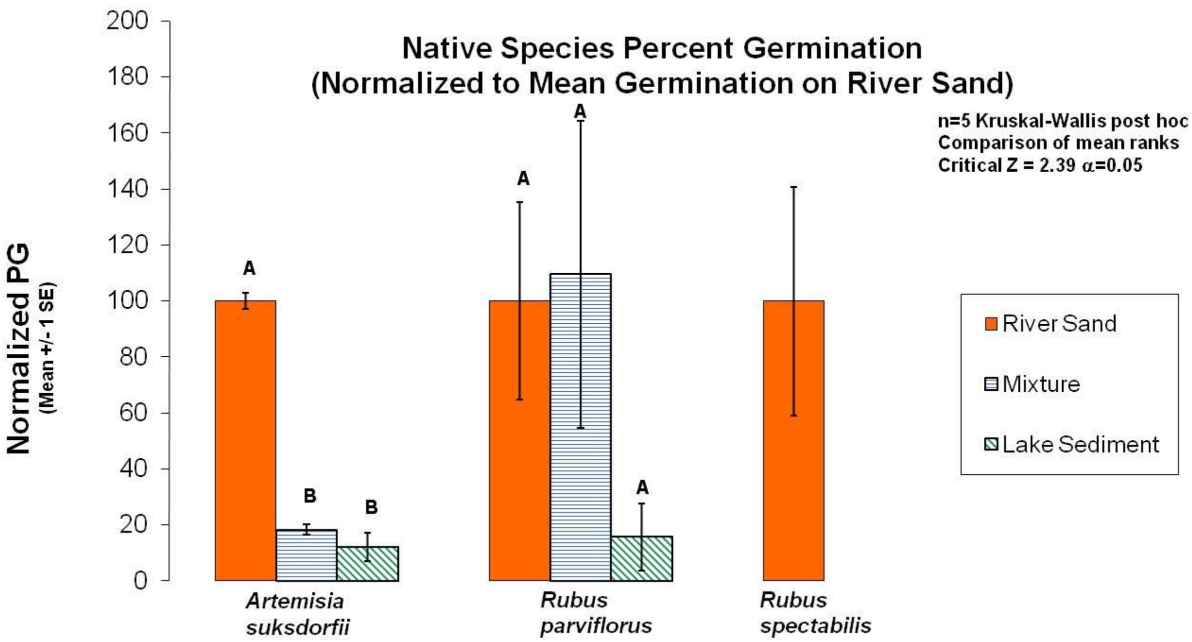

Fig. 8. Normalized percent germination for native species on experimental substrates.

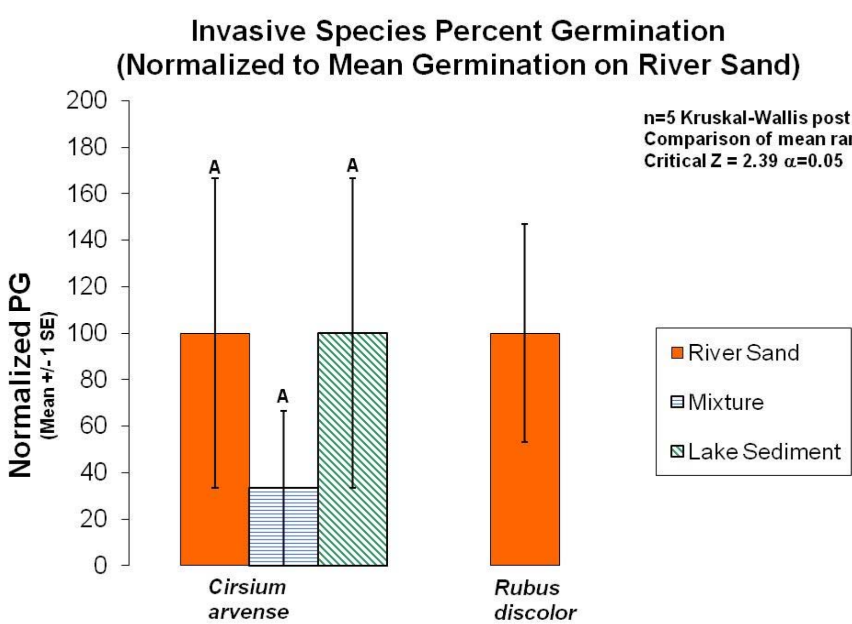

Fig. 9. Normalized percent germination for invasive species on experimental substrates.

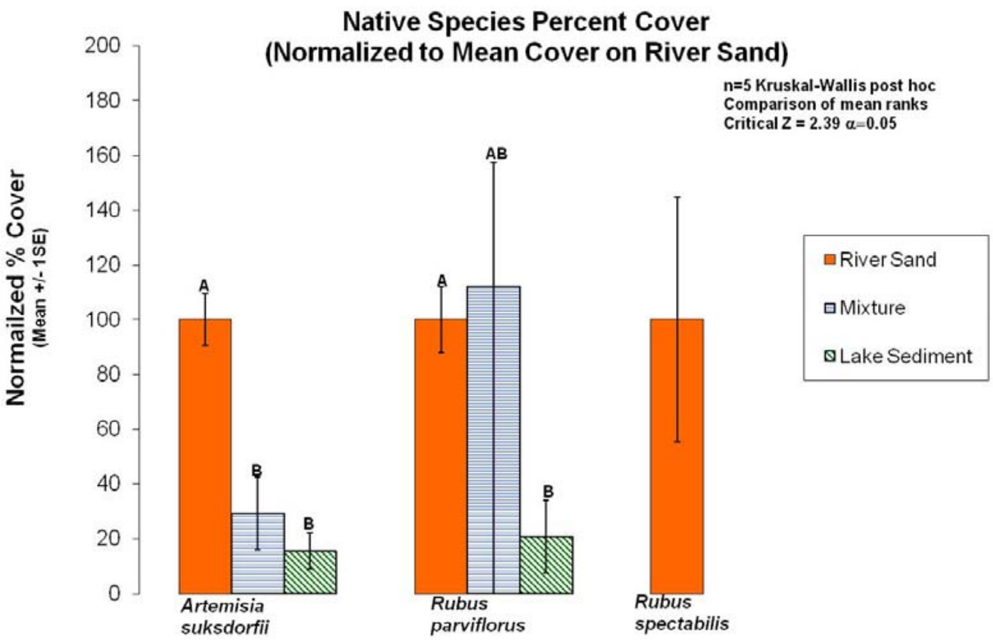

Fig. 10. Normalized percent cover for native species on experimental substrates.

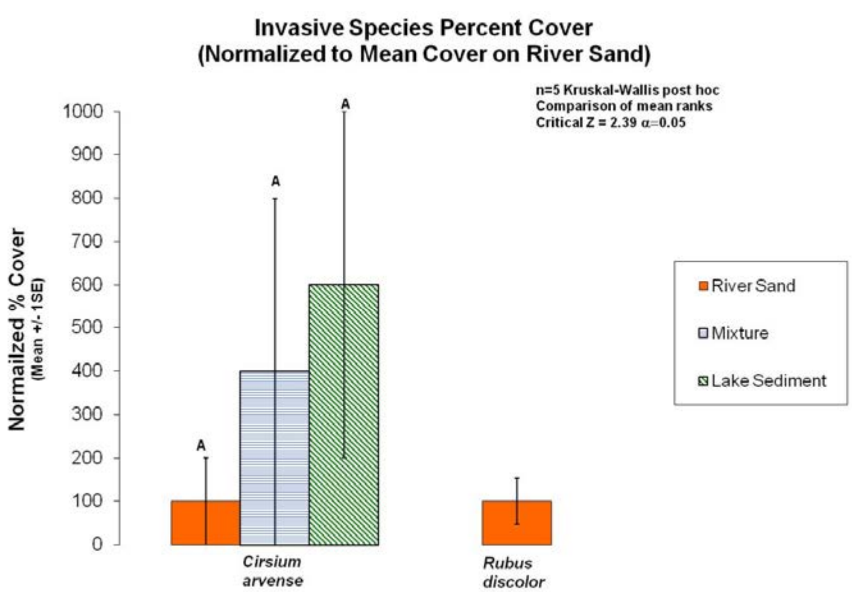

Fig. 11. Normalized percent cover for invasive species on experimental substrates.