

RESEARCH ARTICLE

Effects of Native Plant Species, Mycorrhizal Inoculum, and Mulch on Restoration of Reservoir Sediment Following Dam Removal, Elwha River, Olympic Peninsula, Washington

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Abstract

As dams across the country continue to age, successful restoration of dewatered reservoirs remains a critical factor in decisions regarding dam removal. Freshly exposed reservoir sediment may not support rapid reestablishment of native plant species due to poor fertility or absence of arbuscular mycorrhizal fungi propagules. This field study evaluated treatment effects involving combinations of native plants, mycorrhizal inoculum, and mulch on restoration of dewatered reservoir sediment over 20 months. Most plants, even those uninoculated, became mycorrhizal. In all treatments, sediment pH decreased, as did nitrogen and organic matter, compared to original reservoir sediment, while aggregate stability doubled from original anaerobic sediment. Revegetated plots with mulch had significantly greater vegetation cover and more native volunteer species compared to plots without mulch. The planted mulch

treatment also decreased plot runoff tenfold, reducing erosion to the same degree. Indicators suggest that the primary benefit of mulch resulted in increased moisture retention making the planted mulch treatment most successful for restoration of reservoir sediment due to extensive native plant growth, improved soil characteristics, and reduced runoff and erosion compared to nonmulched plots. While results from this plot-scale study suggest commercial mycorrhizal inoculum is unnecessary since natural inoculum sources sufficiently colonized plants, reservoir-scale restoration may require creation of additional source areas to encourage rapid reestablishment of native plants and mycorrhizal fungi.

Key words: arbuscular mycorrhizal fungi, dam removal, inoculum, native plant species, reservoir sediment, restoration.

Introduction

Less than a century after the modern dam engineering era began, construction of new dams in the United States has all but ceased, due, in part, to the growing awareness that dams dramatically affect river ecosystem processes. Once-useful economic benefits from dams are now critically examined in light of their ecological disruptions, including control of flow regime, alteration of water quality, interruption of sediment

transport, and severance of biological continuity (Ligon et al. 1995). Although dam removal as an ecological restoration tool continues to gain prominence in the eyes of scientists, managers, policy makers, and the public (Wunderlich et al. 1994; Hart & Poff 2002), ecological responses to dam removal remain uncertain (Bednarek 2001). Thus, successful execution of dam removal as a restoration tool requires a carefully planned restoration strategy. Such foresight and planning can ensure that dewatered reservoir sediment and riparian zones regain functionality and mitigate undesirable consequences such as soil erosion, exotic species invasion, or further degradation of water quality.

Mycorrhizas are symbiotic relationships between certain fungi and the roots of nearly all terrestrial plants; typically, both partners benefit. The fungus provides inorganic soil resources, particularly phosphorus and nitrogen, to a host plant in exchange for carbohydrates derived from photosynthesis (Allen 1991; Jeffries et al. 2003). Arbuscular mycorrhizal fungi (AMF), known to form symbioses with the majority of vascular plant families, are named for the dichotomously

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branched invaginations (arbuscules) formed around a penetrating fungus by the cell walls of plant roots. Because of the large surface areas where nutrient exchange occurs, AMF can be especially beneficial for the plant partner when soils are nutrient-poor.

Since soil disturbance such as reservoir dewatering can reduce the infectivity of native AMF propagules (Jasper et al. 1989), restoration strategies must consider the potential for reforming mycorrhizas. Only recently have restoration practitioners started reintroducing AMF propagules to disturbed or degraded soils to promote plant growth, accelerate plant succession, or attain desired species composition (Renker et al. 2004). AMF inoculation has been used to promote native plant growth and reestablishment in various ecosystems, including tallgrass prairies (Smith et al. 1998), natural and reclaimed sand dunes (Greipsson & El-Mayas 2000), and desertified Mediterranean ecosystems (Requena et al. 2001). In addition to directly benefiting plants, AMF hyphae physically bind microaggregates into macroaggregates (Tisdall 1991; Tisdall et al. 1997; Bearden & Petersen 2000) and produce glomalin (Wright & Upadhyaya 1996, 1998), a glycoprotein positively correlated with soil aggregate stability. Consequently, soil strength and structure are improved, resulting in reduced erosion and greater infiltration. Thus, in disturbed ecosystems, developing or maintaining AMF may be critical for successful reestablishment of predisturbance conditions.

This research was designed to study treatment effects involving combinations of native plant species, commercial mycorrhizal inoculum, and mulch on restoration of plots containing dewatered reservoir sediment. Over a 20-month period, we monitored biotic and abiotic parameters associated with beneficial AMF activity to determine treatment efficacy. Our hypotheses were: (1) plant roots and AMF will increase soil aggregate stability; (2) native plant biomass and vegetation cover will increase due to mycorrhizal associations that improve nutrient access; and (3) improved vegetation cover and soil aggregate stability will reduce plot runoff and sediment load. Understanding the effects of potential reservoir-scale treatments on vegetation establishment and other natural processes can guide restoration managers towards effectively subsidizing those processes and hastening reservoir recovery.

Methods

Study Area

Planned for 2012, the removal of the 64-meter-high Glines Canyon Dam along the Elwha River of Washington's Olympic Peninsula will comprise the country's largest dam removal to date. Restoring the 50 million cubic meters of storage capacity currently inundated by Lake Mills will be equally unprecedented. Coupled with the fact that many of the >2,000 dams within the Pacific Northwest are under review for potential removal (Graf 1999), successful reservoir restoration along the Elwha River will have far-reaching implications for future decisions regarding dam removal. Since construction in 1926–1927, nearly 11 million cubic meters of sediment

have accumulated behind the Glines Canyon Dam, much of which will remain following dam removal (USDI 1995). Previous soil analyses indicated low sediment fertility, with 1–2 ppm plant-available phosphate (Bray-P), 0.09–0.11% total Kjeldahl Nitrogen (TKN), and 1.5–1.8% organic matter (USDI et al. 1994). Preliminary growth trials with *Alnus rubra* (red alder) seedlings in reservoir sediment resulted in near-complete mortality (R. Olson 2004, Olympic National Park, Port Angeles, WA, personal communication). Consequently, mycorrhizal inoculation during planting and reseedling was considered to aid rapid establishment of native vegetation.

The study site is located in Olympic National Park (ONP) on the Boulder Creek Delta of Lake Mills (lat 47°58'48"N, long 123°35'59"W, elev 180 m), where a Douglas fir-dominated Pacific coastal forest covers most of the watershed. Annual average precipitation is 1,426 mm, with over 80% falling during October–March (WRCC 2007). While the 70 m² site consists of a boulder-cobble-gravel substrate, raised plots were constructed on a 15% southeast-facing slope and contained a fine sediment mixture of 75% silt, 15% sand, and 10% clay (USDI et al. 1994) collected from within the Lake Mills reservoir.

Experimental Design

The experimental design consisted of 12 plots to which we randomly applied 4 treatments, each with 3 replicates: (1) unplanted and uninoculated sediment (U); (2) native seeds and transplants with no inoculum (P); (3) native seeds and transplants with a commercial mycorrhizal inoculum (P + I); and (4) native seeds and transplants with mulch sacks of alder chips inoculated with saprophytic spores in addition to mycorrhizal inoculum (P + I + M). Original reservoir sediment (C), maintained in an anaerobic flooded state for the 20-month duration of the experiment, provided a control for final soil analyses. The 12 wooden, open-bottomed frames (2 × 0.5 × 0.25 m, L × W × H) were set onto a 5-cm-deep perimeter of bentonite clay chips to ease the transition between smooth frame sides and coarse delta substrate. Distance between plots was 1 ± 0.25 m, while distance from plots to surrounding native forest ranged from 5 to 10 m. Frames were internally lined with black plastic to eliminate lateral leakage. Each frame was equipped with a down-slope gutter and retention tank to monitor runoff and soil loss (Jackson et al. 1985). Lake Mills reservoir sediment was collected by scuba divers along underwater transects from a depth of 12 m.

Plant Species

Native perennial forbs were grown from seed in the ONP greenhouse, then transplanted in September 2005 for three treatments (P, P + I, and P + I + M). Prior to transplanting, plant roots were rinsed to remove potting soil. Species included *Achillea millefolium* L. (common yarrow, two transplants/plot), *Anaphalis margaritacea* (L.) Benth. & Hook. (pearly everlasting, one transplant/plot), *Artemisia suksdorfii* Piper. (Suksdorf's wormwood, four transplants/plot), and

Mahonia nervosa (Pursh) Nutt. (Oregon grape, two transplants/plot), all considered facultatively mycorrhizal. Additionally, we used a native graminoid seed mixture consisting of *Carex deweyana* Schwein. (Dewey's sedge, 1.5 g/plot), *Elymus glaucus* Buckley. (blue wildrye, 2.5 g/plot), and *Bromus pacificus* Shear. (Pacific brome, 1.3 g/plot) was spread within each planted plot and tamped into sediment at field capacity.

Mycorrhizal and Mulch Application

Inoculated seeds were weighed, then mixed with a commercial clay-based mycorrhizal seed inoculum (MycoGrow Micronized Endo/Ecto Seed Mix by Fungi Perfecti LLC) containing spore mass of both AMF (*Glomus aggregatum*, *G. intraradices*, and *G. mosseae*) and ectomycorrhizal fungi, (EMF) (*Pisolithus tinctorius* and four species of *Rhizopogon*). Transplant roots were dipped in a commercial mycorrhizal root dip gel inoculum (MycoApply Root Dip Gel by Mycorrhizal Applications, Inc.) containing *Glomus intraradices*, *G. mosseae*, and *G. aggregatum* (13,228 propagules of each AMF species per kg); *G. deserticola*, *G. clarum*, *G. monosporus*, *G. brasilianum*, and *Gigaspora margarita* (882 propagules of each AMF species per kg); *Rhizopogon villosulus*, *R. luteolus*, *R. amylogogon*, and *R. fulvigleba* (2.2×10^8 propagules of each EMF species per kg); and *Pisolithus tinctorius* (1.4×10^9 EMF propagules per kg). While both commercial inoculums contained EMF spores, all planted species were expected to form mycorrhizae with only AMF based on species mycorrhizal status identified through literature review.

Plots in the P+I+M treatment received two mulch sacks ($0.4 \times 0.25 \times 0.13$ m, L $\times$ W $\times$ H) in addition to native inoculated seeds and transplants. Hemp-burlap mulch sacks contained sawdust with alder chips (1:3 ratio) inoculated by Fungi Perfecti LLC, in June 2005, with the saprophytic fungus *Hypsizygus ulmarius* (100–300 spore-inoculated dowels per sack). Mulch sacks were placed on the sediment surface in both upper and lower halves of each plot. No adjustment to the standard planting configuration was necessary as it was designed to include space for the sacks.

Runoff and Erosion Analyses

An apparatus was constructed to gently but evenly distribute water across the upper plot width at approximately 0.25 L/s (90 cm/hr), for controlled overland flow from a 45-liter application. Water was applied within 24 hours of an actual rainfall event to transport sediment dislodged by raindrop kinetic energy. Runoff volume was measured and subsampled to determine sediment concentrations. Runoff samples (500 ml) were vacuum-filtered using glass-fiber filter disks (Whatman grade 934 AH). Total suspended solids (TSS, mg/L) were determined using standard methods (Norweco 1997).

Soil Analyses

After 20 months, brass-ring soil cores (4-cm diameter) were randomly collected from 6 locations within the upper 10 cm

of each plot. Samples were oven-dried (60°C), crushed to pass through a 2-mm sieve, and stored in airtight containers until analysis. Samples were analyzed for TKN, 0.001% N, pH (0.1 pH unit), plant-available phosphate (Bray-P, 0.5 ppm), and organic matter (OM, 0.1%) by the Division of Agricultural and Natural Resources Laboratory, University of California, Davis.

To determine aggregate stability, rapid immersion of 2 g oven-dried soil in 20 mL of double distilled H₂O produced a soil-water suspension to which ultrasonic energy was applied (Raine & So 1993). A titanium 13-mm probe was inserted to 19 ± 1 mm and operated at 40% capacity using a 130-watt ultrasonic processor (Cole-Parmer Instrument Company, Vernon Hills, IL, U.S.A.) from 15 to 2,250 seconds. The fraction of < 20 μ m material dispersed during sonication periods was determined using a laser diffraction particle size analyzer (Beckman Coulter, Inc., Fullerton, CA, U.S.A.).

Dispersion curves for the < 20 μ m material for each soil sample were fitted via nonlinear regression to the function:

$$D = c + b[1 - e^{-aE}] \quad (1)$$

where D = amount of dispersed material measured (g/g), E = energy applied using an ultrasonic probe (J/g), c = amount of dispersed material before sonication (g/g), and a and b are constants (Raine & So 1993). Soil dispersion characteristic curve parameters, which relate the energy consumed by ultrasonic aggregate dispersion to the quantity of <20 μ m material dispersed, were used to compare levels of aggregate stability.

Plant and Mycorrhizal Analyses

Vegetation cover was measured during spring, summer, and fall using a 0.25-m² quadrat; measurements were blocked by time for statistical purposes. Planted species were identified with assistance from J. Chenoweth, ONP restoration ecologist. Chenoweth also inventoried both native and exotic volunteer plants. During plant harvest in May 2007, root systems were rinsed and subsampled for mycorrhizal analysis. Root and shoot lengths were measured following separation at the crown; samples were then oven-dried (60°C) and weighed.

Subsamples of fine roots were stored in 50% ethanol until cleared (3% KOH, 10 minutes), rinsed, acidified (2% HCl, 30 minutes), and stained with Trypan Blue (0.05%, 20 minutes). Mycorrhizal colonization was determined (compound microscope, 400 $\times$ magnification) for 5-mm transects along slides using the gridline intersect method (Brundrett et al. 1996). Percent colonization was calculated as the number of root intersects containing mycorrhizal structures (hyphae, arbuscules, vesicles, or spores) relative to the total number of intersects.

Statistical Analyses

Treatments were randomly assigned to experimental plots, and parameters were analyzed using analysis of variance (ANOVA) following transformations to meet model assumptions (Kutner et al. 2005). Tukey's honestly significant difference (HSD) test ($p \leq 0.05$) was used to differentiate between means (SAS

Table 1. Arbuscular mycorrhizal colonization of planted species in experimental plots after 20 months.

Species	Intersects Root (#)	Mycorrhizal Colonization (%) ¹		
		P	P + I	P + I + M
<i>A. millefolium</i> ^c	109 ± 25	0.6 ± 0.6	0.0 ± 0.0	2.0 ± 2.0
<i>A. margaritacea</i> ^c	42 ± 12	18.9 ± 18.9	0.0 ± 0.0	14.8 ± 9.8
<i>A. suksdorfii</i> ^{bc}	145 ± 30	2.7 ± 2.7	10.0 ± 3.5	4.4 ± 2.7
<i>C. deweyana</i> ^c	61 ± 26	13.6 ± 9.9	0.5 ± 0.5	8.3 ± 6.6
<i>E. glaucus</i> ^a	65 ± 14	67.1 ± 24.3	69.2 ± 10.3	24.5 ± 14.8
<i>B. pacificus</i> ^{ab}	67 ± 19	13.6 ± 6.7	37.5 ± 2.4	30.4 ± 23.2
Species total	82 ± 29	19.4 ± 17.4	19.5 ± 15.8	13.4 ± 12.0

Data are expressed as mean ± standard error of the mean ($n = 3$). Species with different superscript letters are significantly different ($p \leq 0.05$, Tukey's HSD test).

¹Statistical analysis performed on square-root transformed values.

Institute, Inc. 2005, 2007). Vegetation cover, species richness, soil parameters, runoff, and erosion data were analyzed as balanced, completely randomized single-factor designs with equal sample sizes. A two-factor partially nested design was used to analyze individual plant and mycorrhizal data by accounting for plot-to-plot variability. Plots were nested within treatments to represent main plot error for determining treatment effects, in addition to determining plant species effects and treatment-species interaction effects.

Results

Mycorrhizal Colonization

Most plants in both uninoculated and inoculated plots became mycorrhizal after 20 months, demonstrating no effect of treatment on mycorrhizal colonization ($F_{2,6} = 0.01$, $p = 0.99$). Identified structures were primarily hyphae and vesicles with occasional spores—no arbuscules were observed. Colonization varied significantly between species, with native grass *Elymus glaucus* the only species always mycorrhizal and consistently the most highly colonized (Table 1). In every planted treatment, *Artemisia millefolium*, *Anaphalis margaritacea*, and *Carex deweyana* were completely nonmycorrhizal in at least one replicate plot.

Plant Growth

Among planted species, results for root and shoot biomass and length, as well as root : shoot ratios, differed significantly

by species ($p < 0.001$) but not by treatment (root biomass [$F_{2,6} = 0.59$, $p = 0.58$]; shoot biomass [$F_{2,6} = 1.18$, $p = 0.37$]; biomass ratio [$F_{2,6} = 0.66$, $p = 0.55$]; root length [$F_{2,6} = 0.75$, $p = 0.51$]; shoot length [$F_{2,6} = 3.54$, $p = 0.10$]; length ratio [$F_{2,6} = 1.63$, $p = 0.27$]). However, root and shoot biomass tended to be greater in the P + I + M treatment than in P + I and P treatments (Table 2). Interaction effects between treatment and species were not significant. Due to high mortality, no *Mahonia nervosa* were collected for analysis.

Total vegetation cover of planted and volunteer species, less the area covered by mulch sacks, was significantly greater in the P + I + M treatment than in all other treatments, while the U treatment produced significantly less vegetation cover ($F_{3,52} = 113.88$, $p < 0.001$; Fig. 1). Vegetation cover in P and P + I treatments remained similar to each other throughout the 20-month experiment.

Not surprisingly, there were significantly more native volunteer species in unplanted plots ($F_{3,8} = 147.11$, $p < 0.001$) and, while not significant, more exotic volunteer species than in all other treatments ($F_{3,8} = 2.08$, $p = 0.18$; Fig. 2). Among preplanted plots, however, the P + I + M treatment had significantly more native volunteer species than P or P + I treatments while having fewer exotic volunteer species than the

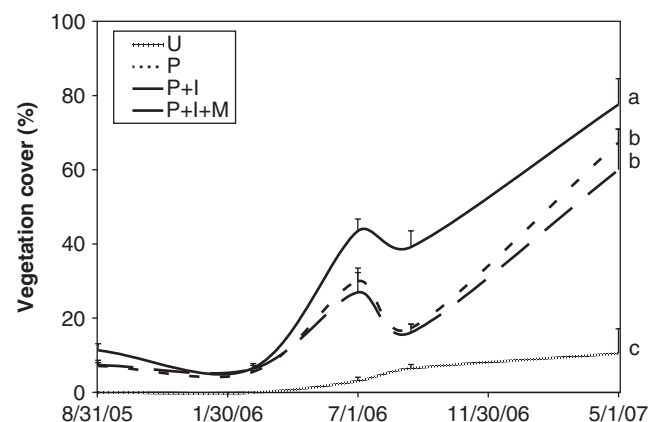


Figure 1. Effect of treatment on vegetation cover blocked by time over 20 months. Values are means ($n = 3$); bars represent standard error of the mean. Treatments with different letters are significantly different ($p \leq 0.05$, Tukey's HSD test) based on square-root transformed data. (U, unplanted and uninoculated; P, planted but uninoculated; P + I, plants with inoculum; P + I + M, plants with inoculum and mulch).

Table 2. Growth characteristics of planted species in experimental plots after 20 months.

Treatment	Biomass (g/seedling)			Length (cm/seedling)		
	Root ²	Shoot ¹	R/S ²	Root	Shoot ²	R/S ¹
P	1.60 ± 0.43	0.99 ± 0.26	1.64 ± 0.26	32.06 ± 3.64	16.18 ± 1.55	2.17 ± 0.24
P + I	1.31 ± 0.35	0.86 ± 0.28	1.87 ± 0.39	28.56 ± 3.02	14.17 ± 1.52	2.23 ± 0.25
P + I + M	2.13 ± 0.76	1.12 ± 0.36	2.04 ± 0.56	27.86 ± 3.84	16.82 ± 1.82	1.71 ± 0.20

Data are expressed as mean ± standard error of the mean ($n = 18$).

¹Statistical analyses performed on square-root transformed values.

²Statistical analyses performed on logarithmic transformed values.

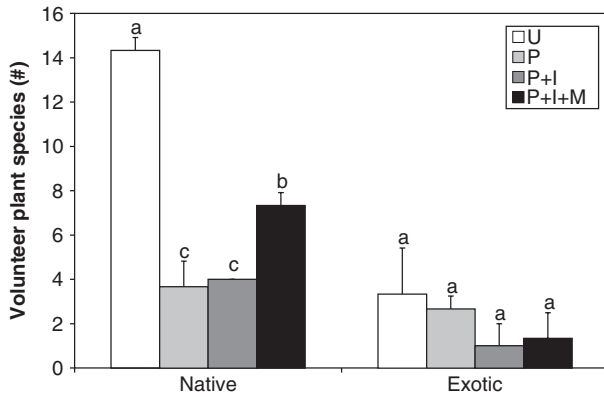


Figure 2. Species richness of native and exotic volunteer plant species in experimental plots. Values are means ($n = 3$); bars represent standard error of the mean. For each plant type (native or exotic) treatments with different letters are significantly different ($p \leq 0.05$, Tukey's HSD test). (U, unplanted and uninoculated; P, planted but uninoculated; P + I, plants with inoculum; P + I + M, plants with inoculum and mulch).

P treatment. Exotics thus accounted for 23% of total species in the U treatment, 25% in the P treatment, and only 9% in P + I and P + I + M treatments.

Soil Analyses

Application of ultrasonic energy to soil-water suspensions increased aggregate breakdown until all aggregates were completely dispersed under the given energy intensity (Fig. 3). Dispersion curve parameters were compared to assess differences in aggregate stability (Table 3). Parameter a , which partially quantifies the rate of aggregate breakdown with increasing energy application, was more than twice as great for C than for any treatment, indicating significantly less stability under ultrasonic energy application ($F_{4,8} = 18.93$, $p = 0.0004$). Parameter b , the contribution of $> 20 \mu\text{m}$ fraction to the $< 20 \mu\text{m}$ fraction due to aggregate breakdown, was not significantly different between any sediment tested ($F_{4,8} = 2.96$, $p = 0.09$).

Table 3. Effect of treatment on soil characteristics.

Parameter	Treatment				
	C	U	P	P + I	P + I + M
Soil pH ¹	5.7 ^a	5.2 ^b $\pm$ 0.1	5.2 ^b $\pm$ 0.0	5.3 ^{ab} $\pm$ 0.1	5.2 ^b $\pm$ 0.1
Total Kjeldahl nitrogen (%)	0.125 ^a	0.098 ^b $\pm$ 0.002	0.093 ^b $\pm$ 0.004	0.093 ^b $\pm$ 0.002	0.097 ^b $\pm$ 0.001
Organic matter (%) ²	2.95 ^a	2.12 ^b $\pm$ 0.12	1.97 ^b $\pm$ 0.10	2.06 ^b $\pm$ 0.07	2.17 ^b $\pm$ 0.04
Phosphate-Bray (ppm)	6.0 ^a	5.6 ^a $\pm$ 0.1	5.5 ^a $\pm$ 0.1	5.5 ^a $\pm$ 0.1	4.6 ^b $\pm$ 0.3
Dispersion curve parameter a	0.0034 ^a	0.0012 ^b $\pm$ 0.0001	0.0011 ^b $\pm$ 0.0001	0.0012 ^b $\pm$ 0.0001	0.0015 ^b $\pm$ 0.0002
Parameter b	25.91	25.02 $\pm$ 0.27	25.77 $\pm$ 0.71	25.50 $\pm$ 0.25	26.89 $\pm$ 0.06
Parameter c	34.9 ^a	25.30 ^{ab} $\pm$ 0.44	23.33 ^b $\pm$ 2.18	25.17 ^{ab} $\pm$ 1.82	23.32 ^b $\pm$ 1.14
Runoff (L) ³	—	14.7 ^a $\pm$ 3.6	5.5 ^{ab} $\pm$ 4.0	5.8 ^{ab} $\pm$ 1.0	1.5 ^b $\pm$ 0.9
Total suspended solids (mg/L) ³	—	11.5 $\pm$ 3.9	8.6 $\pm$ 4.2	20.5 $\pm$ 3.6	8.8 $\pm$ 1.1

Data are expressed as mean $\pm$ standard error of the mean ($n = 3$, unless stated in text). For each parameter, values within rows with different letters are significantly different ($p \leq 0.05$, Tukey's HSD test).

¹Statistical analysis performed on inverse transformed values.

²Statistical analysis performed on square-root transformed values.

³Statistical analyses performed on logarithmic transformed values.

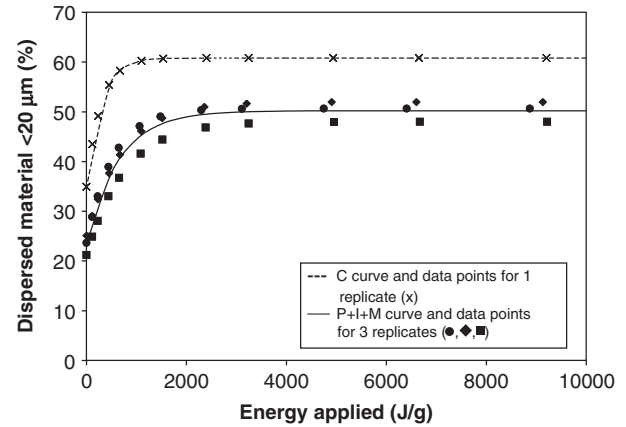


Figure 3. Experimental data points and dispersion curves calculated using Equation 1 (see text). Y-axis indicates volume of $< 20 \mu\text{m}$ material for increasing levels of ultrasonic energy applied to original reservoir sediment (C) and sediment in the P + I + M treatment (3 replicate samples). The P + I + M curve and data are characteristic of all treatments (no significant differences).

The original fraction of $< 20 \mu\text{m}$ material prior to energy application, represented by parameter c , ranged from a high of 34.9% in C to a low of 23.3% in the P + I + M treatment, while no other treatment was significantly different from P + I + M ($F_{4,8} = 4.02$, $p = 0.04$).

Original sediment (C) had lower acidity ($F_{4,8} = 4.43$, $p = 0.04$) and greater TKN ($F_{4,8} = 11.89$, $p = 0.002$), Bray-P ($F_{4,7} = 15.95$, $p = 0.001$), and OM ($F_{4,8} = 7.06$, $p = 0.01$) than all treatment sediments (Table 3). Sediments in the U, P, and P + I treatments were not significantly different from each other for any lab-measured soil characteristic, although pH in the P + I treatment was also not significantly different from C. Sediment in the P + I + M treatment was not significantly different from other treatments except for values for Bray-P, which were significantly reduced, possibly due to increased plant uptake.

Runoff and Erosion

Runoff volume was significantly reduced in the P + I + M treatment by an order of magnitude over the U treatment, while runoff was intermediate in P and P + I treatments ($F_{3,8} = 4.07$, $p = 0.0499$; Table 3). While low concentrations of total suspended solids measured in runoff samples varied greatly between treatments, variation within treatments precluded statistical significance ($F_{3,6} = 1.38$, $p = 0.34$; Table 3). However, similar sediment concentrations coupled with significant runoff differences resulted in a 10-fold decrease in P + I + M treatment erosion (i.e., sediment concentration) over the unplanted treatment (U). Two plots (one each from P + I + M and P treatments) were excluded from analyses because they developed deep cracks or cavities, preventing runoff measurements.

Discussion

Despite controlled inoculation of seeds and transplants, most uninoculated and inoculated plants became mycorrhizal after 20 months. Some mycorrhizal colonization of uninoculated plants is typical for multiyear field experiments when plant species are facultatively mycorrhizal and spores are present in the environment (Allen & Allen 1988; Titus & del Moral 1998). Potential vectors for spore transmittance include strong winds, which are common along Lake Mills and can disperse AMF spores over distances up to 2 km (Warner et al. 1987), or animals, which regularly consume, transport, and then defecate viable spores within coniferous forest ecosystems (Maser et al. 1978).

Given the proximity of experimental plots to spore-rich Pacific coastal forests, plot-scale mycorrhizal colonization of uninoculated planted species is not surprising. Following the eruption of Mount St. Helens, Allen et al. (2005) found that isolated patches of surviving vegetation or reestablished plants served as critical sources initiating both plant and fungal recovery in severely disturbed areas similar to the Lake Mills reservoir. After 10 years of natural recovery, pumice plains more than 1 km from intact vegetation exhibited 60–70% of their 22-year total postdisturbance species richness, although vegetation was composed primarily of facultatively mycotrophic species that remained nonmycorrhizal (del Moral et al. 2005). Reservoir-scale restoration will require mycorrhizal dispersal over distances similar to those analyzed during the Mount St. Helens studies, but the large-scale source area surrounding the severely disturbed reservoir should encourage even more rapid invasion of fungi and plants by both wind and animals. Furthermore, islands of densely planted mycorrhizal vegetation in key reservoir microsites will be established by National Park Service employees during restoration to serve as seed, spore, and propagule sources for rapid reestablishment of native functioning ecosystems (Mussman et al. 2008).

Most arbuscular mycorrhizal plant species colonizing primary succession substrates are facultatively mycorrhizal (Allen 1991; Titus & del Moral 1998; del Moral et al. 2005), discretionarily forming mycorrhizae when beneficial. Thus, all planted perennial forb species and both seeded grasses were

expected to form mycorrhizas following inoculation in the seasonally dry and phosphorous-deficient sediment (Reeves et al. 1979; Titus & del Moral 1998; Eriksson 2001; Claassen & Marler 2004; Rowe et al. 2007). Low perennial forb colonization levels coupled with the complete lack of colonization in at least one replicate plot per treatment indicates that additional factors may be influencing mycorrhizal colonization. On the Mount St. Helens primary succession Pumice Plain substrate, Chapin (1995) found that *Anaphalis margaritacea* was completely nonmycorrhizal in contrast to abundant *A. margaritacea* mycorrhizae in a clear-cut forest 13 km northeast, evidencing the facultatively mycorrhizal nature of *A. margaritacea*. Similarly, Graham et al. (1991) found that plant species of low mycorrhizal dependency (i.e., facultatively mycorrhizal) have evolved mechanisms to regulate mycorrhizal colonization and, presumably, carbon expenditure on the fungus during periods of no mycorrhizal benefit. Since this study only measured colonization at a single point in time, it is possible that spring growth requirements limited mycorrhizal colonization based on high-priority allocation of carbon resources to biomass production during a period of little drought stress.

Treatment did not significantly affect individual plant growth. However, P + I + M treatment biomass tended to be greater than in P and P + I treatments, and vegetation cover in the P + I + M treatment was significantly greater than in all other treatments, particularly towards the end of the seasonal drought in September 2006. Typical plant growth responses to water deficiency includes reduced shoot growth coupled with increased root length, increasing root : shoot length ratios after periods of drought (Chaves et al. 2002). Since no significant treatment differences were found with respect to mycorrhizal colonization, increased soil moisture retention beneath the mulch sacks may explain greater biomass and vegetation cover coupled with lower root : shoot length ratios by reducing the effects of water stress within P + I + M plots.

Wood and Morris (1990) found that native seedling emergence and survival was promoted primarily by subsurface moisture during recolonization of Pumice Plains on Mount St. Helens. In our study, the significantly greater number of native volunteers established in the U treatment is likely due to lack of competition from planted species, but among planted treatments, the high number of native P + I + M volunteers may be due to improved establishment conditions associated with moisture retention from the mulch sacks. Again, the mulch treatment layer appeared primarily beneficial for this reason.

In two adjacent Olympic Peninsula watersheds, DeFerrari and Naiman (1994) found that exotic plant species accounted for 23% of species richness, while a germination study of the Lake Mills seed bank identified 18% of seedling species as known exotics (Brown & Chenoweth 2008). Thus, the ratio of exotic to native plant species in our U and P treatments was very similar to nearby watersheds and slightly higher than the reservoir seed bank. Wind dispersal and hydrochory, not sediment seed bank, is expected to dominate volunteer plant establishment in the reservoir, as the Brown and Chenoweth (2008) study found the sediment seed bank to be surprisingly limited. Therefore, native plant reintroduction

and establishment will be essential to limit exotics abundance. Exotic flora in P + I and P + I + M treatments accounted for only 9% of species richness, potentially due to immediate mycorrhizal colonization and competitive exclusion of exotics.

Extending the interpretation of mulch effects beyond the effects of inoculated plantings must be done with caution, as the experimental design was not fully factorial and the mulch effect cannot be teased out as an independent factor. However, the alder chip-filled mulch sacks were inoculated with a saprophytic fungus and layered onto mycorrhizal-inoculated plantings with the expectation that microbial decomposition would increase organic content in the reservoir sediment. While there was initial concern that microfauna activities within the mulch would consume and further reduce already low soil N levels, there was no evidence of decreased N or increased organic matter in P + I + M plots. Visual analysis of the mulch indicated little decomposition after 20 months, suggesting that the primary benefit of this treatment was increased moisture retention.

Compared to original reservoir sediment, all dewatered treatments significantly improved soil aggregate stability, as indicated by a >50% reduction in dispersion curve parameter a . Since application of ultrasonic energy occurs in the laboratory following oven-dried sieving, it cannot quantify physical macro-aggregation due to hyphal binding described by Tisdall (1991). However, the primary contribution of AMF to soil aggregate stability appears to be through the production of glomalin, which acts as a particle-binding glycoprotein to form water-stable aggregates (Wright & Upadhyaya 1996, 1998). Because P plots became mycorrhizal without inoculation, we can assume U plots also became mycorrhizal, retaining the possibility that AMF were directly responsible for improved soil aggregate stability. Alternatively, or additionally, polysaccharides associated with roots or other microbes

in the rhizosphere may bind water-stable aggregates (Tisdall & Oades 1982). Regardless of the binding mechanism, all treatments produced more stable and persistent soil aggregates than original (C) reservoir sediment.

Typical agricultural soils west of the Cascades contain about 0.10–0.15% total N, with only 1–4% available to plants; furthermore, <20 ppm plant-available phosphorus (Bray-P test for acidic soils) is considered low, with 20–40 ppm desirable (Marx et al. 1999). In our study, TKN levels in treatment soils were somewhat low, but Bray-P levels were very low (4.6–6 ppm) and potentially limiting to plant growth, creating an ideal scenario for active formation of mycorrhizas. Thus, it was surprising that perennial forb species appeared to be only facultatively mycorrhizal with low colonization levels under such nutrient-limited soil conditions. However, Rowe et al. (2007) also reported little effect of similar soil phosphorus levels on AMF growth response for native plant species. When costs of supporting mycorrhizas outweigh benefits, the plant-AMF relationship can become less mutualistic and more parasitic (Johnson et al. 1997; Klironomos 2003; Jones & Smith 2004). Hence, additional environmental factors (e.g., seasonal timing) are likely dictating lower mycorrhizal colonization of plant roots in this study.

In a region-by-region assessment, Moldenhauer et al. (1983) found that, in the Pacific Northwest, vegetation effectively reduced erosion following establishment. In our study, even U plots developed a vegetation cover >20%, resulting in minimal erosion under every treatment. Loch (2000) recorded similarly low sediment runoff concentrations for simulated rainfall on vegetation cover $\geq 47\%$, consistent with P, P + I, and P + I + M treatments. Vegetation cover reduces runoff and erosion by diminishing kinetic energy delivered to the soil through raindrops, reducing soil-water repellence and surface scaling, increasing stable macropores, and preventing crust

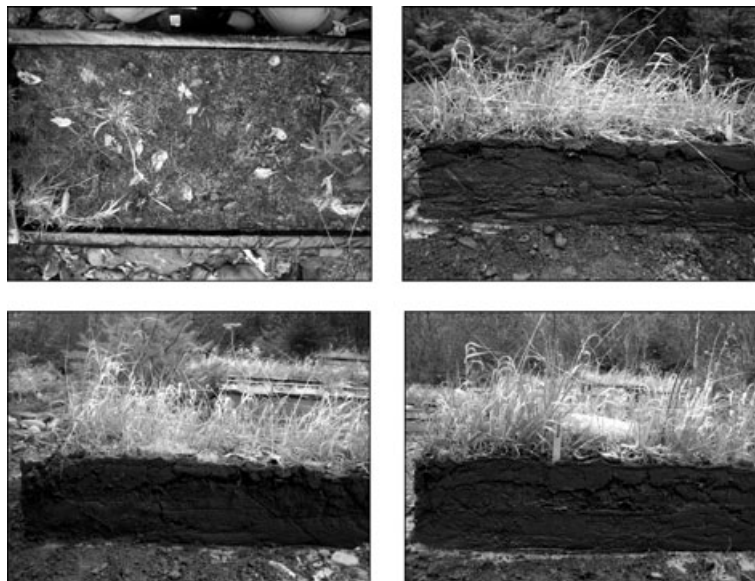


Figure 4. Plan view and soil profiles of representative plots for each treatment. Clockwise, from upper left: U, unplanted and uninoculated; P + I, plants with inoculum; P + I + M, plants with inoculum and mulch; and P, planted but uninoculated. Boulder Creek Delta, Elwha River, Washington, May 2007.

formation (Loch 2000), as seen in the soil profiles of Figure 4. However, the most significant improvement came from the mulch effects of P + I + M, which reduced runoff and erosion by an order of magnitude over the U treatment. Field data from our study were corroborated by a separate laboratory study assessing sediment erosion and stabilization treatments on the same reservoir sediment under similar slopes and rainfall intensities (Mussman et al. 2008). Mussman et al. (2008) found that un-bagged mulch wood chips reduced erosion by 98% over no treatment on a 15° slope under high-intensity rainfall of 19 cm/hr and recommended a combination of mulch with plants as the most effective method of erosion reduction during reservoir restoration. Thus, the 10-fold reduction in runoff and erosion in this experiment may again result from water retention capabilities associated with mulch sacks. No significant differences in soil moisture content were detected prior to overland flow application on account of recent rainfall events (data not shown).

Conclusion

The ubiquity of mycorrhizal spores within the surrounding ecosystem was sufficient to colonize most planted species on the plot scale after 20 months regardless of treatment, effectively eliminating plot differences specifically associated with AMF activity. All treatments resulted in pH and nutrient level changes as sediment shifted from anaerobic to aerobic. There was significant improvement in soil aggregate stability in all treatment sediments compared to original reservoir sediment. The addition of mulch sacks to inoculated planted plots resulted in significantly greater vegetation cover, significantly more native volunteer species than other planted plots, and a significant 10-fold decrease in plot runoff and erosion compared to unplanted plots. Mulch sacks appeared beneficial primarily due to increased moisture retention. Therefore, commercial inoculum, whether mycorrhizal or saprophytic, appears unnecessary for ensuring successful restoration of reservoir sediment on the plot scale. Reservoir-scale restoration, however, will likely require active establishment of mycorrhizal vegetation in key reservoir microsites to provide native seed and spore sources to rapidly regain critical ecosystem functioning and reduce initial establishment of exotic flora.

Implications for Practice

- Natural mycorrhizal inoculation through wind or animal spore dispersal from neighboring ecosystem source areas can sufficiently colonize native plant species over time without requiring commercial inoculum at the plot scale.
- Reservoir-scale restoration may greatly benefit from active establishment of key plant and fungus source areas to achieve rapid native ecosystem restoration.
- Increasing soil moisture retention through placement of mulch sacks may significantly improve establishment and growth of native vegetation.
- Rhizosphere activity, including mycorrhizal colonization, will reestablish following reservoir dewatering, significantly improving soil aggregate stability over time.

- Revegetation coupled with mulch sacks will reduce runoff and erosion 10-fold compared to plots with no planting or mulch sacks.

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Appendix A. Presence or absence and anticipated mycorrhizal status (based on literature review) of native and exotic volunteer plant species in experimental plots after 20 months. Species identified as both mycorrhizal and nonmycorrhizal are considered facultatively mycorrhizal. (U, unplanted and uninoculated; P, planted but uninoculated; PI, plants with inoculum; PIM, plants with inoculum and mulch; AM, arbuscular mycorrhizal; EM, ectomycorrhizal; N, nonmycorrhizal).

Native species	Common name	Family	Treatment				Mycorrhizal Status
			U	P	PI	PIM	
Trees							
<i>Acer macrophyllum</i>	bigleaf maple	<i>Sapindaceae</i>				x	AM ¹¹
<i>Alnus rubra</i>	red alder	<i>Betulaceae</i>	x			x	AM ⁹ –EM ¹⁴
<i>Pseudotsuga menziesii</i>	Douglas fir	<i>Pinaceae</i>	x		x	x	AM ¹³ –EM ¹⁴
<i>Thuja plicata</i>	western redcedar	<i>Cupressaceae</i>	x				AM ^{12,13}
Forbs							
<i>Anaphalis margaritacea</i>	pearly everlasting	<i>Asteraceae</i>	x				AM ^{3,8} –N ^{3,8}
<i>Cardamine</i> sp.	bitter-cress	<i>Brassicaceae</i>	x				AM ^{*4} –N ^{*2}
<i>Epilobium angustifolium</i>	fireweed	<i>Onagraceae</i>	x				AM ^{3,7,8} –N ^{3,7,8}
<i>Galium triflorum</i>	sweet-scent bedstraw	<i>Rubiaceae</i>				x	N ^{*2}
<i>Heracleum lanatum</i>	cow-parsnip	<i>Apiaceae</i>	x			x	AM ¹⁰ –N ¹⁰
<i>Moehringia macrophylla</i>	big-leaved sandwort	<i>Caryophyllaceae</i>	x				N ^{*2}
<i>Saxifraga</i> sp.	saxifrage	<i>Saxifragaceae</i>	x			x	
<i>Stellaria calycantha</i>	northern starwort	<i>Caryophyllaceae</i>		x	x	x	N ^{*2,4}
<i>Stellaria crispa</i>	crisp sandwort	<i>Caryophyllaceae</i>	x			x	N ^{*2,4}
<i>Stellaria</i> sp.	starwort	<i>Caryophyllaceae</i>	x				N ^{*2,4}
Graminoids							
<i>Agrostis</i> sp.	bentgrass	<i>Poaceae</i>	x				AM ^{*2,6}
<i>Bromus</i> sp.	brome	<i>Poaceae</i>	x	x	x		AM ^{*2}
<i>Carex deweyana</i>	Dewey's sedge	<i>Cyperaceae</i>	x				N ^{*4,6}
<i>Deschampsia elongata</i>	slender hairgrass	<i>Poaceae</i>	x		x	x	AM ^{*2}
<i>Elymus glaucus</i>	blue wildrye	<i>Poaceae</i>	x				AM ^{*2}
<i>Juncus balticus</i>	Baltic rush	<i>Juncaceae</i>	x			x	N ^{*4}
<i>Juncus effusus</i>	common rush	<i>Juncaceae</i>	x				N ^{*4}
<i>Juncus ensifolius</i>	dagger-leaved rush	<i>Juncaceae</i>	x				N ^{*4}
<i>Glyceria elata</i>	tall mannagrass	<i>Poaceae</i>	x	x			AM ^{*2}
Bryophytes							
<i>Bryum</i> sp.	moss	<i>Bryaceae</i>	x	x	x	x	
Exotic species							
Forbs							
<i>Geranium robertianum</i>	herb-Robert	<i>Geraniaceae</i>		x			AM ⁵
<i>Hypochaeris radicata</i>	hairy cat's-ear	<i>Asteraceae</i>	x				AM ³ –N ³
<i>Hypochaeris glabra</i>	smooth cat's-ear	<i>Asteraceae</i>	x	x	x		AM ^{*2,4}
<i>Mycelis muralis</i>	wall lettuce	<i>Asteraceae</i>	x	x	x	x	AM ^{*2,4}
<i>Leucanthemum vulgare</i>	oxeye daisy	<i>Asteraceae</i>	x	x	x	x	AM ^{*2,4}
<i>Trifolium repens</i>	white clover	<i>Fabaceae</i>	x				AM ¹ –N ¹
Graminoids							
<i>Digitaria ischaemum</i>	smooth crabgrass	<i>Poaceae</i>	x				AM ²

*Status determined by family, not species.

¹Wright et al. (1998)

⁴Väre et al. (1997)

⁷Allen et al. (1987)

¹⁰Laursen et al. (1997)

¹³Smith et al. (1998)

²Pendleton and Smith (1983)

⁵Harris and Boerner (1990)

⁸Chapin (1995)

¹¹Minore and Zasada (1990)

¹⁴Miller et al. (1992)

³Titus and del Moral (1998)

⁶Titus and Tsuyuzaki (2002)

⁹Allen et al. (2005)

¹²Kough et al. (1985)