

RESEARCH ARTICLE

Wood chip soil amendments in restored wetlands affect plant growth by reducing compaction and increasing dissolved phenolics

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Adding chipped wood to soil ameliorates compaction, allowing faster plant growth that is critical to successful wetland restorations. Following the filling and planting of an erosion gully in Halstead Meadow, Sequoia National Park, the tallest leaf height and maximum clone width of transplanted *Scirpus microcarpus* seedlings were negatively correlated with soil compaction. Plant height decreased by 9.8 cm and width decreased by 11.9 cm per MPa of soil compaction (range of 0.74–4.50 MPa). We experimentally amended mineral soil in a test trench and found that every 0.10 cm³/cm³ addition of wood chips (range of 0.00–0.75 cm³/cm³) reduced compaction by 0.174 MPa. Had the Halstead Meadow gully fill contained an equivalent volume of wood chips to the reference area soil organic matter content (0.64 cm³/cm³), we predict compaction would have been reduced by 1.11 MPa, increasing individual transplant width spread by 36%, approximately doubling the vegetated area after two growing seasons. In a greenhouse phytometer experiment, conifer bark leachate (phenolics 211 mg/L) significantly reduced plant growth and, in the presence of added nutrients, increased the production of the enzyme polyphenol oxidase (PPO). However, phenolics concentration in bark-free conifer wood leachate (12 mg/L), similar to field-sampled concentrations, did not affect plant growth or PPO production. Pure conifer bark is not recommended as a soil amendment, but the addition of low-bark-content wood chips to gully fill may be a feasible and effective means of reducing soil compaction, accelerating plant establishment, and lowering wetland restoration project costs.

Key words: meadow, phytometer, polyphenol oxidase, *Scirpus microcarpus*, Sierra Nevada, soil organic matter

Implications for Practice

- Substituting a portion of mineral soil with wood chips can speed plant growth and reduce transportation costs in gully fill wetland restoration projects.
- High conifer-bark-content chips or mulch may be inappropriate for use in wetland gully fill due to a high concentration of plant-inhibiting phenolics.

Introduction

About one-eighth of the remaining approximately 621,000 ha of freshwater non-lake wetlands in California are located in the Sierra Nevada (Viers et al. 2013; SFEI 2016). A significant proportion of these mountain wetlands, commonly referred to as meadows, need restoration (Odion et al. 1988; Kattelmann & Embury 1996). During the past 10,000 years, meadows in the Sierra Nevada formed by mineral sediment deposition and organic matter accumulation, without major fluvial channel processes (Wood 1975). However, high-intensity grazing between the 1860s and 1940s led to the removal of vegetation, disturbance of soil, and the formation of large erosion gullies in some sloping meadows (Sumner Jr. 1941; Armstrong 1942; Wolf & Cooper 2016).

Gullies capture and concentrate run-off, increasing erosion that enlarges the gullies in a feedback loop (Kirkby & Bracken

2009). The capture of both surface flow and groundwater by gullies lowers the surrounding meadow water table (Hammersmark et al. 2008), alters vegetation composition and cover (Loheide II & Gorelick 2007; Lowry et al. 2011), and accelerates soil organic matter decomposition (Chimner & Cooper 2003; Schimelpfenig et al. 2014). The formation of an erosion gully can shift a wetland ecosystem into an alternate upland state that requires management intervention to restore (Wolf et al. 2007).

Gully restoration commonly involves constructing a sequence of check dams using rock, wood, or soil with the goal of raising the water table to the meadow surface (Ramstead et al. 2012; Pollock et al. 2014). In high sediment-yield watersheds, impoundments can fill with sediment and become vegetated, rebuilding a level landscape during the multidecadal life span

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of check dams (Heede 1977; Polyakov et al. 2014). However, in a low sediment-yield watershed in the Sierra Nevada, 30 years of maintenance followed by 30 years of neglect resulted in the collapse of 39 of 41 wood check dams which had accumulated sediment to fill just 26% of the gully depth and failed to restore wetland conditions (Wolf & Cooper 2016). In gullied sites with low sediment input, completely filling gullies with imported material may be necessary for long-term stable restoration of wetland hydrology and vegetation.

Small peatland ditches, less than a meter deep and a few meters wide, have been restored effectively by complete filling (Armstrong et al. 2009; Grand-Clement et al. 2015; Chimner et al. 2017, 2019). Significant challenges complicate scaling up the complete gully fill technique to larger multimeter deep and tens-of-meters wide erosion features: (1) obtaining and transporting large volumes of heavy soil is expensive and (2) the massive vehicles required to place the fill in the gully cause soil compaction.

Mechanical soil compaction is a common problem in created wetlands (Nair et al. 2001; Campbell et al. 2002; Bruland & Richardson 2005; Sloey et al. 2015). Compaction negatively affects a broad range of plants, but most studies have investigated agricultural crops or upland species (Unger & Kaspar 1994; Passioura 2002; Nawaz et al. 2013). Compaction effects on plants often differ between soil types (Gomez et al. 2002) and moisture conditions (Amir et al. 1976), so wetland-specific studies are needed.

Soil compaction reduces pore volume and average pore size, which slows the diffusion of gasses (Xu et al. 1992) and limits water movement (Watabe et al. 2000). The constriction of soil pores may lead to hypoxia in the rooting zone, a hypothesized cause of stunted plant growth in compacted upland soil (Tardieu 1994). Wetland plants are adapted to hypoxic soil conditions and form aerenchyma to facilitate the flow of oxygen to their roots (Drew et al. 2000). This adaptation may confer some degree of resistance to the effects of soil compaction if hypoxia is a significant proximal cause of root growth inhibition.

Dense rhizomatous wetland vegetation forms a sod layer that is highly resistant to erosion (Micheli & Kirchner 2002) and is thought to have been essential in stabilizing sloping mountain meadows over their multi-millennial existence (Wood 1975; Ratliff 1985; Bartolome et al. 1990). Clonal plant cover provides significant soil stability while bare slopes are vulnerable to erosion by overland flow (Loch 2000). Wetland sedges transplanted into bare soil areas of Rocky Mountain wetlands took 4–5 years to clonally spread and reach reference-plot shoot density (Cooper et al. 2017). Maximizing plant growth by reducing potential limiting factors, such as soil compaction, minimizes the duration that bare soil is vulnerable to erosion.

Adding organic matter to soil can decrease compaction by increasing aggregate strength and elasticity (Soane & Estate 1990). The wood and bark of native conifer trees is a readily available source of organic matter in most mountainous regions including the Sierra Nevada of California. A potential drawback of amending gully fill with woody organic matter is that wood and bark contain phenolic compounds that can inhibit plant growth (Siqueira et al. 1991; Taylor et al. 1996; Garnett et al.

2004). Inhibition may involve direct toxicity to plants, complexing of phenolics with nutrient-bearing proteins, or suppression of soil microbiota that play a key role in plant nutrient acquisition (Kuiters 1990; Hättenschwiler & Vitousek 2000). Plants, as well as other organisms, produce the enzyme polyphenol oxidase (PPO) in the presence of phenolics and when exposed to stresses such as herbivore damage (Appel 1993). Presumably, the enzyme confers a protective effect on plants, although the specific functions and mechanisms are not completely known (Mayer 2006; Constabel & Barbehenn 2008). However, it is clear that PPO activity is oxygen limited and that its ability to transform phenolic compounds facilitates the activity of other enzymes that are important to the decomposition of soil organic matter and plant acquisition of nutrients (Freeman et al. 2001).

We investigated how chipped conifer wood and bark affect wetland plant growth via their effects on soil compaction and the concentration of leached phenolics. Our hypotheses were (1) wetland plant growth will be negatively correlated to soil compaction, (2) the addition of chipped conifer trees (a mixture of wood and bark) will reduce soil compaction, and (3) phenolic compounds leached from chipped wood and bark (tested separately) will inhibit wetland plant growth and stimulate PPO production.

Methods

Soil Compaction and Plant Growth at Halstead Meadow

At Halstead Meadow in Sequoia National Park during September 2007 a large erosion gully 330 m long, up to 6 m deep, and 30 m wide was filled with 6,100 m³ of off-site stockpiled local mineral soil with no organic matter amendment. Heavy machinery transported, placed, and contoured the soil, recreating the pre-gully level-in-cross-section meadow surface and restoring sheet flow hydrology (Wolf & Cooper 2011).

In June 2008, the gully fill soil was planted at a density of four plants per square meter with 37,300 three-month-old seedlings of a native rhizomatous bulrush, *Scirpus microcarpus* J. Presl & C. Presl (panicked bulrush). In September 2009, after two growing seasons, we measured soil compaction and plant size in a spatially stratified random sample of 110 plants within the planted fill. At each measurement location plant height, plant width, and soil compaction were measured. Plant height was measured as the vertical distance from the ground surface to the top of the tallest leaf. Plant width was the maximum clone diameter, measured as the longest horizontal distance at ground level between ramets of each seedling. Soil compaction was measured using a soil penetrometer (FieldScout SC900; Spectrum Technologies; Aurora, IL, U.S.A.). Compaction readings were averaged between three measurement points within the growth radius of each plant, and within each single point through the top 20 cm of soil depth penetrated. Soil compaction is expressed as the average resistance to penetration pressure, in megapascals (MPa), within this sampled volume. Hereafter, all instances of “soil compaction” refer to this measure of resistance to penetration pressure.

Similar measurements were made at 14 random *Scirpus microcarpus*-dominated natural wetland reference locations of Halstead Meadow that had not been drained by the erosion gully and were not filled, compacted, or planted as part of the restoration. Width measurements of *S. microcarpus* plants in the reference locations were not possible because genets had merged and individuals could not be distinguished.

Soil Compaction and Wood Chip Amendments in a Test Trench

We tested the effect of wood chip amendments on soil compaction in a grid of 24 soil cells, each 1.2 m by 1.2 m and 0.9 m deep (1.3 m³ in volume), within a trench dug 0.9 m deep, 4 m wide, and 21 m long. Wood with bark was chipped on-site in Sequoia National Park from a mixture of conifer tree species including *Abies concolor*, *Pinus lambertiana*, *Calocedrus decurrens*, *Pinus jeffreyi*, *Abies magnifica*, and *Pinus contorta*. Approximately half of the volume was composed of chips 1–6 cm in length, and the other half were particles less than 1 cm long.

The trench was divided into four replicates of six cells each along the long axis. Wood chips were added to native sandy-silt mineral soil at six levels: 0.00, 0.05, 0.15, 0.30, 0.50, and 0.75 cm³/cm³. The treatments were applied to randomly selected cells in each of the four replicated sections of trench. Prior to filling with soil, the bottom and sides of the trench were lined with a water-impermeable pond barrier to maintain saturated soil conditions in the trench. The volume of chips for each treatment cell was measured using graduated buckets. Cells were filled using 1.2 m × 1.2 m × 0.3 m plywood forms with mineral soil placed in them by a backhoe and the wood chips added and mixed using hand tools. A 0.3-m wide buffer of unamended mineral soil was placed around each cell. The buffer provided space to walk and prevented direct hydrologic and compression interaction between treatments. The soil within all treatment cells and buffers was wetted and compacted evenly using a jumping jack plate-rammer (Wacker Neuson DS 72Y, Munich, Germany). The test cells within the trench were irrigated regularly to maintain saturated soil conditions. Two months after construction soil compaction in the top 20 cm was measured and averaged at five points within each test cell using the soil penetrometer.

Phenolics, Plant Growth, and PPO Production in a Greenhouse Experiment

A 16-day greenhouse phytometer experiment was conducted to measure the effect of phenolics on plant growth. We use the term “phenolics” to include total soluble phenolics, not including insoluble compounds such as lignin (Waterman & Mole 1994). We grew 72 *Scirpus microcarpus* seedlings to serve as phytometers (Clements & Goldsmith 1924; Dietrich et al. 2013). Seeds collected in Halstead Meadow were germinated and hydroponically grown for 4 weeks in a 1% Hoagland nutrient solution (Hoagland & Arnon 1950). The 4-week-old plants were weighed live at the start of the experiment, and a size-stratified random sample of 12 plants was removed for

destructive measurement of initial aboveground and belowground dry biomass. The remaining 60 size-stratified plants served as the phytometers and were each placed in a sponge stopper with their roots suspended in an opaque Erlenmeyer flask. Each phytometer was randomly assigned to one of six treatments, 10 plants per treatment: (1) deionized (DI) water, (2) 10% Hoagland nutrient solution, (3) wood leachate, (4) wood leachate with 10% Hoagland nutrient solution, (5) bark leachate, and (6) bark leachate with 10% Hoagland nutrient solution.

Each phytometer flask was filled to the same mark daily with DI water to prevent desiccation and concentration of leachate or nutrients. Flasks were shaken for 30 seconds daily to prevent root hypoxia. The phytometer experiment lasted 16 days following initiation of the treatments, after which the plants were separated into above- and belowground parts, dried, and weighed.

Separate batches of wood-only chips and bark-only chips of the same Sierra Nevada mixed conifer tree species used in the experimental trench (see above) were soaked in water to create wood and bark leachates. The wood and bark were oven dried and 1.75 kg each were separately submerged in 14 L DI water for 6 days at 20°C. The leachate liquids were poured through a 0.152-mm screen to remove solids prior to use as phytometer treatments.

A small area of the Halstead Meadow restoration was repaired in late fall of 2009 with fill that contained 0.30 cm³/cm³ mixed wood and bark chips. The following year four interstitial soil water samples were collected from this repaired area at 20 cm depth to quantify phenolics concentration from wood and bark amended fill in a field setting. Note that most of the restored area of Halstead Meadow, where transplant height and width were compared to soil compaction, contained no wood/bark chips in the fill.

The phenolics concentrations of the wood and bark lab leachates and Halstead field samples were determined using the Folin–Ciocalteu method (Singleton & Rossi 1965; Yu & Dahlgren 2000) with *p*-coumaric acid standards. Phenolics concentrations are expressed as *p*-coumaric acid equivalent mass per volume (mg/L).

The PPO activity of each phytometer was determined from two approximately 2-cm long clippings (with intact side roots and hairs) from the middle of two separate randomly selected roots. The root pieces were collected from the plants at the end of the 16-day treatment, rinsed with DI, and placed into 20 mL of 10 mM L-DOPA substrate solution with 25 mM MES buffer and shaken for 15 minutes. The liquid was spectrophotometrically analyzed for absorbance at 475 nm in a 4-cm path-length cell. Using the Beer–Lambert law and an empirically derived value for the molar attenuation coefficient (3,600 * M⁻¹ * cm⁻¹; Muñoz et al. 2006), we converted measured absorbance values to molar concentrations of dopachrome, the PPO-catalyzed oxidation product of L-DOPA. After analysis of PPO activity, the root sections were scanned for total root length, including all side roots and hairs (WinRHIZO, Regent Instruments, Quebec, CA, U.S.A.). PPO activity is expressed as the molar

concentration of dopachrome produced per minute per cm total root length ($\mu\text{M dopachrome} \cdot \text{min}^{-1} \cdot \text{cm}^{-1}$).

Statistical Analyses

The correlations between Halstead Meadow soil compaction and transplant width and height and between wood chip volume added in the test trench and soil compaction were analyzed using linear regression.

Phytometer treatment effects on plant growth and PPO activity were evaluated by multiple linear regression. Using multi-model selection (library “glmulti,” Calcagno 2013) in R 3.4.0 (R Core Team 2017) we exhaustively evaluated all possible permutations of models with the explanatory variables of (1) phenolics treatment concentration (three levels), (2) nutrient addition treatment (two levels), (3) initial fresh plant mass, and (4) the ratio of above- to belowground dry plant biomass. We also included the six possible two-way interactions of these four variables, for a total of 10 model terms and an intercept. The four primary variables were evaluated for multicollinearity by calculating their variance inflation factors (VIF, library “usdm” in R, Naimi 2015), and all were found to have VIF less than 2 and were appropriate to use together in the models. Homogeneity of variance across levels of tested variables was confirmed by examining plots of model residuals. All variances were well within a four-factor similarity and were considered homogeneous (Zuur et al. 2010). Plots of each parameter were visually examined for outliers, but none were found. Models were ranked by Akaike information criterion corrected (AICc) and single model terms were deleted to find the simplest AICc-equivalent (within 2 AICc of the minimum) best model. Using leave-one-out cross validation (library “boot” in R, Canty & Ripley 2017), we estimated the prediction error for the best model. Partial-residual plots (library “visreg” in R, Breheny & Burchett 2017) were constructed to isolate and visualize important and interacting effects of the best models. Effects of modeled explanatory variables not shown in partial residual plots are already accounted for, removing their influence on the patterns in the plotted data. All confidence intervals (CI) for modeled parameters are reported at the 95% level.

Results

Soil Compaction and Plant Growth at Halstead Meadow

Soil compaction within the top 20 cm of the fill at *Scirpus microcarpus* plantings ranged from 0.74 to 4.50 MPa, with a mean of 2.36 MPa ($n = 110$). Compaction in the intact natural wetland reference areas ranged from 0.13 to 0.64 MPa, with a mean of 0.39 MPa ($n = 14$). All compaction measurements in the fill exceeded all measures in the reference areas. Height and width of the transplants were each significantly ($p \ll 0.0001$) negatively correlated with soil compaction, with linear regression intercepts of 62.0 and 65.1, slopes of -9.77 and -11.90 , and adjusted- r^2 of 0.353 and 0.366, respectively (Fig. 1). After two growing seasons the tallest transplant in the fill (90 cm) was 1 cm shorter than the shortest measured plant in the unfilled reference area (91 cm).

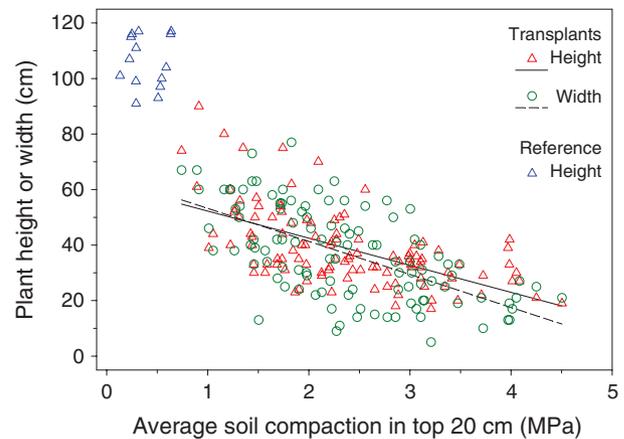


Figure 1. Soil compaction in Halstead Meadow was significantly correlated with the height (red triangles, solid trend line) and width (green circles, dashed trend line) of 110 *Scirpus microcarpus* transplants. The soil compaction and maximum height (blue triangles) for 14 plants within nonfilled and noncompacted natural reference areas are shown but not included in the regression analysis.

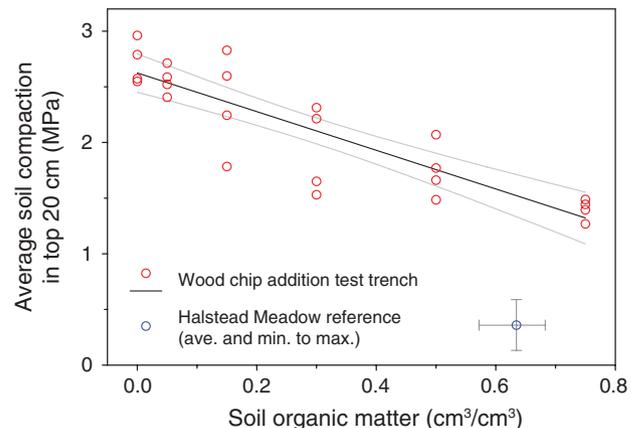


Figure 2. Soil compaction at different treatment levels (four replicates each of six levels) of chipped wood with bark additions in a test trench (red circles), compared to the average and range of compaction and soil organic content of the nonfilled and noncompacted natural reference areas in Halstead Meadow (blue circle with bars). Black line shows the linear regression of the test trench data, with 95% confidence intervals.

Soil Compaction and Wood Chip Amendments in a Test Trench

We found a significant negative correlation between the proportional volume of added wood chips and soil compaction in the test trench ($p \ll 0.0001$). The estimated linear regression parameters were: y-intercept of 2.624 MPa and a slope of -0.174 MPa per $0.1 \text{ cm}^3/\text{cm}^3$ addition of wood chips, with an adjusted- r^2 of 0.743 (Fig. 2). At the highest concentration of wood chips tested, $0.75 \text{ cm}^3/\text{cm}^3$, the average soil compaction in the trench (1.40 MPa) was more than three times higher than the average Halstead Meadow reference site (0.391 MPa), which was never mechanically compacted and where the average volumetric organic matter content was $0.64 \text{ cm}^3/\text{cm}^3$.

Table 1. Parameters and statistics for the best phytometer proportional-growth and PPO-activity models.

Proportional growth			PPO activity		
Best-model terms	Parameter estimate	p value	Best-model terms	Parameter estimate	p value
Intercept	0.664900	0.000000	Intercept	0.046080	0.000000
Phenolics	-0.004828	0.000001	Nutrients	-0.047190	0.004190
Phenolics: initial mass	0.000074	0.035340	Nutrients: initial mass	0.001720	0.003390
Phenolics: nutrients	0.002055	0.005250	Phenolics: nutrients	0.000187	0.020520
			Phenolics: shoot-root ratio	0.000101	0.000009
			Phenolics: initial mass	-0.000013	0.003470
	Full-model p value	0.000001		Full-model p value	0.000000
	Adjusted r^2	0.396800		Adjusted r^2	0.493400
	Cross-validated prediction error	0.116200		Cross-validated prediction error	0.001389

Phenolics, Plant Growth, and PPO Production in a Greenhouse Experiment

The concentration of phenolics leached from wood-only chips in the lab was similar to field samples, while lab bark-only leachate contained much higher phenolics levels. The phenolics concentration in soaked wood chip leachate was 11.6 mg/L and the concentration in bark leachate was 210.6 mg/L. These are the two leachates that were applied as phenolics treatments in the phytometer experiment. The four Halstead Meadow field samples of interstitial water from soil with 0.30 cm³/cm³ mixed wood and bark chips yielded phenolics concentrations ranging from 0.8 to 6.5 mg/L (mean: 3.5 mg/L).

Both the phenolics and nutrient treatments significantly affected phytometer growth. The phytometer proportional growth model with the lowest AICc contained three terms: phenolics concentration, interaction of phenolics with initial plant mass, and interaction of phenolics with nutrient addition treatment (Table 1). No other AICc-equivalent models contained fewer terms, so we selected this as the best model. The phenolics effect on proportional plant growth was contingent on both the initial plant mass and the nutrient addition treatment.

At the lowest two phenolics treatment levels (0 and 12 mg/L), initial plant mass did not significantly change proportional growth (Fig. 3). At the highest level (211 mg/L), however, plants that were initially smaller grew proportionally less. The estimated linear regression parameters for the partial residuals of the high-phenol treatment were: y-intercept of -0.3518 proportional growth and a slope of 0.0165 proportional growth per gram of initial live plant mass. For every additional gram of initial plant mass, proportional growth was 1.65% greater. The predicted proportional growth was negative for plants grown in the high phenol treatment with an initial mass less than 21.4 g. Initial plant mass ranged from 3.4 to 45.5 g, with an average of 18.2 g.

At the lowest two phenolics levels, the presence or absence of nutrients did not significantly affect modeled proportional growth, which ranged from 62 to 66% (CI range: 52–77%) of initial mass (Fig. 4). However, at the highest phenolics level (211 mg/L) with no nutrients added, plants lost 10% of their initial mass (CI: -31–11%), while

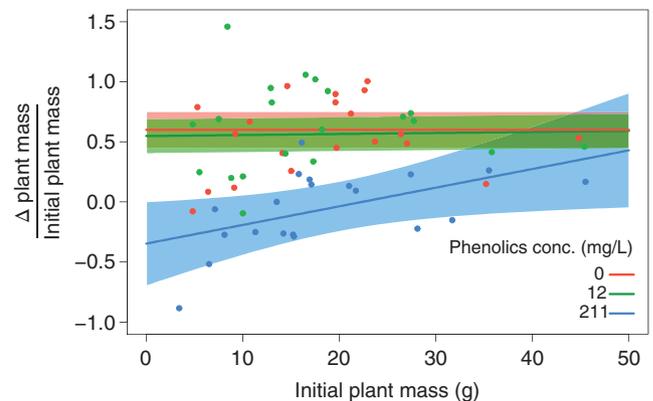


Figure 3. Partial-residual plot of the best model for proportional plant growth. The different effects of the three levels of phenolics (red, green, blue) on the relationship between initial plant mass (x-axis) and proportional growth (y-axis) are shown. Solid colored lines depict linear regression model and shaded 95% confidence intervals with corresponding-color partial residual points.

plants with added nutrients gained 33% of their initial mass (CI: 13–54%).

As in the growth model, the phenolics and nutrient treatments both significantly affected PPO production. The PPO model with the lowest AICc contained five terms: nutrient addition treatment, and the following four interactions: Nutrients with initial mass, nutrients with phenolics, phenolics with above-ground/belowground mass ratio, and phenolics with initial mass (Table 1). All other AICc-equivalent models contained more terms, so we selected this as the best model. The phenolics treatment effect on PPO production was contingent on the presence or absence of nutrients (Fig. 5). At the 211 mg/L phenolics level, PPO activity was significantly lower in the no nutrients treatment (0.064, CI: 0.038–0.089) compared with the nutrients-added treatment (0.010, CI: 0.079–0.120). Conversely, the two lower phenolics levels (0 and 12 mg/L) had significantly higher PPO activity in the no-nutrients treatment (0 mg/L = 0.049, CI: 0.034–0.064; 12 mg/L = 0.050, CI: 0.036–0.064) compared with the nutrients-added treatment (0 mg/L = 0.028, CI: 0.012–0.043; 12 mg/L = 0.032, CI: 0.017–0.046).

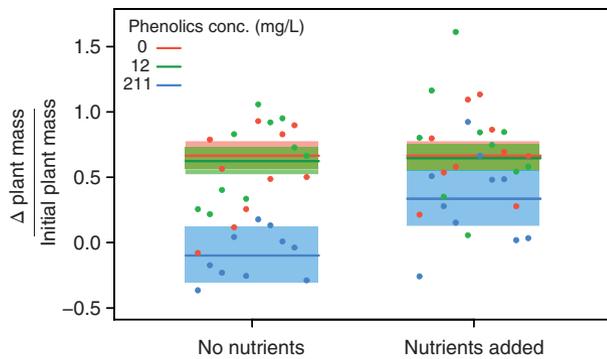


Figure 4. Partial-residual plot showing the interacting effect of phenolics concentration level (red, green, blue) and nutrient addition (x-axis) on proportional plant growth (y-axis). There is no growth difference at the two lower phenolics levels (red and green), but at the highest level (blue, 211 mg/L), plants growing with no nutrients lost mass, while those growing in a nutrient solution maintained significantly higher positive growth. Solid colored lines show modeled values, with shaded color 95% confidence intervals. Note: The horizontal spread of data points within each nutrient category is solely for visual clarity and conveys no information.

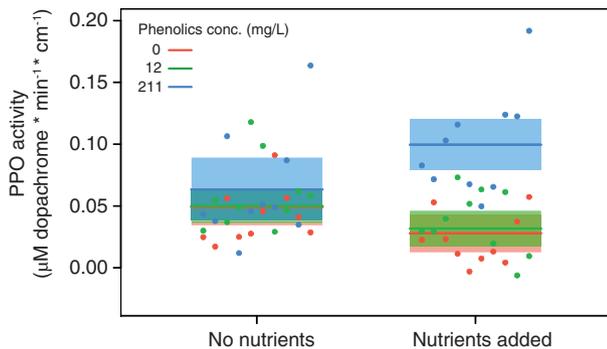


Figure 5. Partial-residual plot showing the interacting effect of phenolics concentration level (red, green, blue) and nutrient addition (x-axis) on polyphenol oxidase activity (y-axis). With no nutrients all levels of phenolics have similar PPO activity. In the nutrients-added treatment the highest phenolics level (211 mg/L) has significantly higher PPO activity, and the two lowest phenolics levels have significantly lower PPO activity. Solid colored lines show modeled values, with shaded color 95% confidence intervals. Note: The horizontal spread of data points within each nutrient category is solely for visual clarity and conveys no information.

Discussion

Despite the restoration of wetland sheet-flow hydrology and soil saturation at Halstead Meadow (Wolf & Cooper 2011), plant width expansion by belowground rhizomatous spread and aboveground growth in leaf height of the wetland sedge *Scirpus microcarpus* were reduced by soil compaction. Because this species thrives in anoxic soil conditions in the reference area and throughout its range, it is unlikely that a compaction-related reduction in soil aeration negatively affected growth. Rather, it is probable that the compaction produced a physical impediment to root and rhizome spread (Kirby & Bengough 2002; Hamza & Anderson 2005). This study showed that *S. microcarpus*

seedlings were stunted by 1.0–4.5 MPa of soil compaction produced by heavy equipment in wetland gully fill restoration.

Rapidly establishing dense wetland plant cover on bare sloping soil is essential for preventing reformation of erosion gullies. We demonstrated that plants grew faster in less compact soil and our test trench illustrated that mineral soil amended with wood chips was less compacted than unamended soil. If the inorganic fill used in Halstead Meadow had been amended with a volume of wood chips matching the organic matter content of the reference area ($0.64 \text{ cm}^3/\text{cm}^3$), we project the average compaction would have been reduced by 1.11 MPa, based on the test trench regression slope. This reduced compaction would be predicted to increase individual plant width by 13.2 cm after two growing seasons, based on the linear regression of Halstead Meadow transplant data. The average width of 2-year-old *S. microcarpus* plantings in Halstead Meadow was 37.0 cm. A 13.2 cm increase in average plant width would have approximately doubled the area vegetated by *S. microcarpus*, from 1,075 to 1,980 cm^2 per plant, increasing total areal cover from 43 to 79%.

Rhizomatous sedges, such as the planted *S. microcarpus*, grow dense belowground root and rhizome networks (Manning et al. 1989; Kauffman et al. 2004) that are critical for stabilizing soil in sloping sites like Halstead Meadow that receive overland flow (Simon & Collison 2002; Quistberg & Stringham 2010). In addition to the soil-binding properties of belowground plant parts, sedges with long leaves and stems trap more sediment than short individuals (Clary et al. 1996). Both plant root and shoot density are positively correlated with soil shear strength and erosion resistance (Dunaway et al. 1994; Micheli & Kirchner 2002; Yildiz et al. 2018). The addition of wood chips reduces soil compaction, which should shorten the time to establishment of a dense sedge community and lessen the risk of gully formation and project failure.

This study demonstrated that the leachate of Sierra Nevada mixed conifer bark contains approximately 20 times higher phenolics concentration than similarly prepared wood-only leachate. High levels of phenolics (211 mg/L) inhibited *S. microcarpus* growth; this growth inhibition was more pronounced in nutrient-limited conditions and in smaller individuals. However, such a high concentration of phenolics is atypical of field conditions. The highest concentration phenolics treatment (211 mg/L) was about 60 times greater than field-measured values (ave. 3.5 mg/L) in Halstead Meadow and about 7 times higher than a leachate pond (30 mg/L) at an aspen logging operation in Canada (Taylor et al. 1996). The lower concentration of phenolics (12 mg/L) typical of field conditions did not significantly affect plant growth in our experiments. But site-specific topography and hydrology could result in areas of stagnant water with elevated phenolics concentrations, especially if significant amounts of conifer bark are present.

Our greenhouse phytometer study illustrated that plants in nutrient-rich conditions modulated their PPO production according to phenolics concentration, whereas plants grown without nutrients produce a similar level of PPO regardless of phenolics concentration. The nutrient-limited ability to adjust PPO production corresponds to different growth rates at high phenolics concentrations between nutrient treatments. The

nutrient status of wetlands will be an important determinant in how plants respond to increased concentrations of phenolics. The majority of meadows in the Sierra Nevada have very low dissolved ion and nutrient concentrations due to the dominance of silica-rich low-metal-content granodiorite bedrock (Wolf & Cooper 2015). Low nutrient status can lead to higher in-situ production of phenolics by wetland plants (Rejmánková 2016). Additionally, the presence of phenolics deactivates hydrolytic enzymes that break down soil organic matter (Ximenes et al. 2011), an important source of plant nutrients. High levels of dissolved phenolics can limit access to plant-available nutrients.

Our results indicate that avoiding pure bark soil amendments and minimizing the bark content of mixed wood/bark chips can reduce the risk of phenolics inhibiting plant growth. An additional safeguard against plant growth inhibition is to transplant large individuals, which we show are less prone to stunting, into areas that may contain high levels of phenolics.

Other important considerations when deciding whether to amend fill soil with wood chips are their rate of decomposition and their buoyancy. Perennially saturated soil conditions, such as those in Halstead Meadow, create soil hypoxia and slow rates of wood chip decomposition. A fluctuating water table that leads to unsaturated soil and the presence of oxygen results in more rapid decomposition of soil organic matter (Chimner & Cooper 2003; Schimelpfenig et al. 2014). Significant decomposition of wood chips could lead to a loss of soil volume and settling of the fill. This could create a topographic low point that concentrates water, potentially leading to reformation of an erosion gully. Because wood floats, chips should not be placed directly on the surface but should be buried under a shallow layer of mineral fill and/or erosion blanket.

In addition to reducing compaction, soil organic matter increases water holding (Hudson 1994; Saxton & Rawls 2006; Ankenbauer & Loheide II 2017) and nutrient exchange capacity (van Erp et al. 2001). Therefore, amending mineral soil to match the organic matter content of local native wetland soil should have ecological benefits beyond reduced compaction. Incorporating wood chips into gully fill is also likely to have financial benefits. The transportation of large quantities of heavy mineral soil is expensive, accounting for roughly one-quarter of the total \$480K Halstead project cost. Many areas in the Sierra Nevada and other mountain regions of the world are subject to forest thinning to reduce fire risk and severity (Safford et al. 2012). Using chipped waste wood to improve meadow restoration outcomes could prove economical where fuels treatments or hazard tree removal areas are close to gullied meadows.

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LITERATURE CITED

- Amir I, Raghavan GSV, Mckyes E, Broughton RS (1976) Soil compaction as a function of contact pressure and soil moisture content. *Canadian Agricultural Engineering* 18:54–57
- Ankenbauer KJ, Loheide SP II (2017) The effects of soil organic matter on soil water retention and plant water use in a meadow of the Sierra Nevada, CA. *Hydrological Processes* 31:891–901
- Appel HM (1993) Phenolics in ecological interactions: the importance of oxidation. *Journal of Chemical Ecology* 19:1521–1552
- Armstrong JE (1942) Study of grazing conditions in the Roaring River District, Kings Canyon National Park. Sequoia and Kings Canyon National Parks, Three Rivers, California
- Armstrong A, Holden J, Kay P, Foulger M, Gledhill S, McDonald AT, Walker A (2009) Drain-blocking techniques on blanket peat: a framework for best practice. *Journal of Environmental Management* 90:3512–3519
- Bartolome JW, Erman DC, Schwarz CF (1990) Stability and change in minerotrophic peatlands, Sierra Nevada of California and Nevada. U.S. Dept. of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California
- Breheny P, Burchett W (2017) visreg: visualization of regression models. R package version 2.4-0. R Foundation for Statistical Computing, Vienna, Austria
- Brunland GL, Richardson CJ (2005) Spatial variability of soil properties in created, restored, and paired natural wetlands. *Soil Science Society of America Journal* 69:273–284
- Calcagno V (2013) Glmulti: model selection and multimodel inference made easy. R package version 1.0.7. R Foundation for Statistical Computing, Vienna, Austria
- Campbell DA, Cole CA, Brooks RP (2002) A comparison of created and natural wetlands in Pennsylvania, USA. *Wetlands Ecology and Management* 10:41–49
- Canty A, Ripley B (2017) boot: Bootstrap R (S-Plus) Functions. R package version 1.3-19. R Foundation for Statistical Computing, Vienna, Austria
- Chimner RA, Cooper DJ (2003) Carbon dynamics of pristine and hydrologically modified fens in the southern rocky mountains. *Canadian Journal of Botany* 81:477–491
- Chimner RA, Cooper DJ, Wurster FC, Rochefort L (2017) An overview of peatland restoration in North America: where are we after 25 years? *Restoration Ecology* 25:283–292
- Chimner RA, Cooper DJ, Bidwell MD, Culpepper A, Zillich K, Nydick K (2019) A new method for restoring ditches in peatlands: ditch filling with fiber bales. *Restoration Ecology* 27:63–69
- Clary WP, Thornton CI, Abt SR (1996) Riparian stubble height and recovery of degraded streambanks. *Rangelands* 18:137–140
- Clements FE, Goldsmith GW (1924) The phytometer method in ecology, the plant and community as instruments. The Carnegie Institution of Washington, Publication no. 356, Washington D.C.
- Constabel P, Barbehenn R (2008) Defensive role of polyphenol oxidase in plants. Pages 253–269. In: Schaller A (ed) *Induced plant resistance to herbivory*. Springer, Amsterdam, Netherlands
- Cooper DJ, Kaczynski KM, Sueltenfuss J, Gaucherand S, Hazen C (2017) Mountain wetland restoration: the role of hydrologic regime and plant introductions after 15 years in the Colorado Rocky Mountains, U.S.A. *Ecological Engineering* 101:46–59
- Dietrich AL, Nilsson C, Jansson R (2013) Phytometers are underutilised for evaluating ecological restoration. *Basic and Applied Ecology* 14:369–377
- Drew MC, He CJ, Morgan PW (2000) Programmed cell death and aerenchyma formation in roots. *Trends in Plant Science* 5:123–127

- Dunaway D, Swanson SR, Wendel J, Clary W (1994) The effect of herbaceous plant communities and soil textures on particle erosion of alluvial stream-banks. *Geomorphology* 9:47–56
- van Erp PJ, Houba VJG, van Beusichem ML (2001) Actual cation exchange capacity of agricultural soils and its relationship with pH and content of organic carbon and clay. *Communications in Soil Science and Plant Analysis* 32:19–31
- Freeman C, Ostle N, Kang H (2001) An enzymic ‘latch’ on a global carbon store. *Nature* 409:149
- Garnett E, Jonsson LM, Dighton J, Murnen K (2004) Control of pitch pine seed germination and initial growth exerted by leaf litters and polyphenolic compounds. *Biology and Fertility of Soils* 40:421–426
- Gomez A, Powers RF, Singer MJ, Horwath WR (2002) Soil compaction effects on growth of young ponderosa pine following litter removal in California’s Sierra Nevada. *Soil Science Society of America Journal* 66:1334
- Grand-Clement E, Anderson K, Smith D, Angus M, Luscombe DJ, Gatis N, Bray LS, Brazier RE (2015) New approaches to the restoration of shallow marginal peatlands. *Journal of Environmental Management* 161:417–430
- Hammersmark CT, Rains MC, Mount JF (2008) Quantifying the hydrological effects of stream restoration in a montane meadow, northern California, USA. *River Research and Applications* 24:735–753
- Hamza MA, Anderson WK (2005) Soil compaction in cropping systems: a review of the nature, causes and possible solutions. *Soil and Tillage Research* 82:121–145
- Hättenschwiler S, Vitousek PM (2000) The role of polyphenols in terrestrial ecosystems nutrient cycling. *Trends in Ecology & Evolution* 15:238–243
- Heede BH (1977) Case study of a watershed rehabilitation project: Alkali Creek, CO. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado
- Hoagland DR, Arnon DI (1950) The water-culture method for growing plants without soil. *California Agricultural Experiment Station* 347:1–32
- Hudson BD (1994) Soil organic matter and available water capacity. *Journal of Soil and Water Conservation* 49:189–194
- Kattelmann R, Embury M (1996) Riparian areas and wetlands. In: Erman DC (ed) *Sierra Nevada Ecosystem Project: Final report to Congress. Assessments and scientific basis for management options. Vol III.* University of California, Davis, Centers for Water and Wildland Resources, Davis, California
- Kauffman JB, Thorpe AS, Brookshire ENJ (2004) Livestock exclusion and belowground ecosystem responses in riparian meadows of eastern Oregon. *Ecological Applications* 14:1671–1679
- Kirby JM, Bengough AG (2002) Influence of soil strength on root growth: experiments and analysis using a critical-state model. *European Journal of Soil Science* 53:119–127
- Kirkby MJ, Bracken LJ (2009) Gully processes and gully dynamics. *Earth Surface Processes and Landforms* 34:1841–1851
- Kuiters AT (1990) Role of phenolic substances from decomposing forest litter in plant-soil interactions. *Acta Botanica Neerlandica* 39:329–348
- Loch RJ (2000) Effects of vegetation cover on runoff and erosion under simulated rain and overland flow on a rehabilitated site on the Meandu Mine, Tarong, Queensland. *Soil Research* 38:299
- Loheide SP II, Gorelick SM (2007) Riparian hydroecology: a coupled model of the observed interactions between groundwater flow and meadow vegetation patterning. *Water Resources Research* 43:1–16
- Lowry CS, Loheide SP II, Moore CE, Lundquist JD (2011) Groundwater controls on vegetation composition and patterning in mountain meadows. *Water Resources Research* 47:16
- Manning ME, Swanson SR, Svejcar T, Trent J (1989) Rooting characteristics of four intermountain meadow community types. *Journal of Range Management* 42:309–312
- Mayer AM (2006) Polyphenol oxidases in plants and fungi: going places? A review. *Phytochemistry* 67:2318–2331
- Micheli ER, Kirchner JW (2002) Effects of wet meadow riparian vegetation on streambank erosion. 2. Measurements of vegetated bank strength and consequences for failure mechanics. *Earth Surface Processes and Landforms* 27:687–697
- Muñoz JL, García-Molina F, Varón R, Rodríguez-Lopez JN, García-Cánovas F, Tudela J (2006) Calculating molar absorptivities for quinones: application to the measurement of tyrosinase activity. *Analytical Biochemistry* 351:128–138
- Naimi B (2015) *usdm: uncertainty analysis for species distribution models.* R package version 1.1-15. R Foundation for Statistical Computing, Vienna, Austria
- Nair VD, Graetz DA, Reddy KR, Olila OG (2001) Soil development in phosphate-mined created wetlands of Florida, USA. *Wetlands* 21:232–239
- Nawaz MF, Bourrié G, Trolard F (2013) Soil compaction impact and modelling. A review. *Agronomy for Sustainable Development* 33:291–309
- Odion DC, Dudley TI, D’Antonio CM (1988) Cattle grazing in southeastern Sierran meadows: Ecosystem change and prospects for recovery. Pages 277–292. In: *The Mary DeDecker symposium: plant biology of eastern California.* White Mountain Research Station, University of California, Los Angeles, California
- Passioura JB (2002) Soil conditions and plant growth. *Plant, Cell and Environment* 25:311–318
- Pollock MM, Beechie TJ, Wheaton JM, Jordan CE, Bouwes N, Weber N, Volk C (2014) Using beaver dams to restore incised stream ecosystems. *Bioscience* 64:279–290
- Polyakov VO, Nichols MH, McClaran MP, Nearing MA (2014) Effect of check dams on runoff, sediment yield, and retention on small semiarid watersheds. *Journal of Soil and Water Conservation* 69:414–421
- Quistberg SE, Stringham TK (2010) Sedge transplant survival in a reconstructed channel: influences of planting location, erosion, and invasive species. *Restoration Ecology* 18:401–408
- R Core Team (2017) *R: a language and environment for statistical computing.* 3.4.1. R Foundation for Statistical Computing, Vienna, Austria
- Ramstead KM, Allen JA, Springer AE (2012) Have wet meadow restoration projects in the southwestern U.S. been effective in restoring geomorphology, hydrology, soils, and plant species composition? *Environmental Evidence* 1:11
- Ratliff RD (1985) *Meadows in the Sierra Nevada of California: state of knowledge.* Pacific Southwest Forest and Range Experiment Station, Berkeley, California
- Rejmánková E (2016) Phenolic content and growth of wetland macrophytes: is the allocation to secondary compounds driven by nutrient availability? *Folia Geobotanica* 51:239–250
- Safford HD, Stevens JT, Merriam K, Meyer MD, Latimer AM (2012) Fuel treatment effectiveness in California yellow pine and mixed conifer forests. *Forest Ecology and Management* 274:17–28
- Saxton KE, Rawls WJ (2006) Soil water characteristic estimates by texture and organic matter for hydrologic solutions. *Soil Science Society of America Journal* 70:1569
- Schimelpfenig DW, Cooper DJ, Chimner RA (2014) Effectiveness of ditch blockage for restoring hydrologic and soil processes in mountain peatlands. *Restoration Ecology* 22:257–265
- SFEI (2016) *California Aquatic Resource Inventory (CARI) version 0.2 GIS Data.* San Francisco Estuary Institute (SFEI), Richmond, California
- Simon A, Collison AJC (2002) Quantifying the mechanical and hydrologic effects of riparian vegetation on streambank stability. *Earth Surface Processes and Landforms* 27:527–546
- Singleton VL, Rossi JA (1965) Colorimetry of total phenolics with phosphotungstic acid reagents. *American Journal of Enology and Viticulture* 16:2349–2351
- Siqueira JO, Nair MG, Hammerschmidt R, Safrir GR, Putnam AR (1991) Significance of phenolic compounds in plant-soil-microbial systems. *Critical Reviews in Plant Sciences* 10:63–121
- Sloey TM, Willis JM, Hester MW (2015) Hydrologic and edaphic constraints on *Schoenoplectus acutus*, *Schoenoplectus californicus*, and *Typha latifolia* in tidal marsh restoration. *Restoration Ecology* 23:430–438
- Soane BD, Estate B (1990) The role of organic matter in soil compactibility: a review of some practical aspects. *Soil and Tillage Research* 16:179–201

- Sumner Jr. EL (1941) Special report on range management and wildlife protection in Kings Canyon National Park. Sequoia and Kings Canyon National Parks, Three Rivers, California
- Tardieu F (1994) Growth and functioning of roots and of root systems subjected to soil compaction. Towards a system with multiple signalling? *Soil and Tillage Research* 30:217–243
- Taylor BR, Goudey JS, Carmichael NB (1996) Toxicity of aspen wood leachate to aquatic life: laboratory studies. *Environmental Toxicology and Chemistry* 15:150–159
- Unger PW, Kaspar TC (1994) Soil compaction and root growth: a review. *Agronomy Journal* 86:759–766
- Viers JH, Purdy SE, Peek RA, Fryjoff-Hung A, Santos NR, Katz JVE, Emmons JD, Dolan DV, Yarnell SM (2013) Montane meadows in the Sierra Nevada: Changing hydroclimatic conditions and concepts for vulnerability assessment. Center for Watershed Sciences Technical Report CWS-2013-0:63, Davis, California
- Watabe Y, Leroueil S, Le Bihan J-P (2000) Influence of compaction conditions on pore-size distribution and saturated hydraulic conductivity of a glacial till. *Canadian Geotechnical Journal* 37:1184–1194
- Waterman PG, Mole VH (1994) Analysis of phenolic plant metabolites. Wiley-Blackwell, Oxford, United Kingdom
- Wolf E, Cooper D (2011) Restoration of geomorphic structure, hydrologic regime, and vegetation in Upper Halstead meadow. Sequoia and Kings Canyon National Parks, Three Rivers, California
- Wolf EC, Cooper DJ (2015) Fens of the Sierra Nevada, California, USA : patterns of distribution and vegetation. *Mires and Peat* 15:1–22
- Wolf EC, Cooper DJ (2016) Assessment of soil and moisture conservation crew meadow restoration. Sequoia and Kings Canyon National Parks, Three Rivers, California
- Wolf EC, Cooper DJ, Hobbs NT (2007) Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecological Applications* 17:1572–1587
- Wood SH (1975) Holocene stratigraphy and chronology of mountain meadows, Sierra Nevada, California. PhD dissertation. California Institute of Technology, Pasadena, California
- Ximenes E, Kim Y, Mosier N, Dien B, Ladisch M (2011) Deactivation of cellulases by phenols. *Enzyme and Microbial Technology* 48:54–60
- Xu X, Nieber JL, Gupta SC (1992) Compaction effect on the gas diffusion coefficient in soils. *Soil Science Society of America Journal* 56:1743–1750
- Yildiz A, Graf F, Rickli C, Springman SM (2018) Determination of the shearing behaviour of root-permeated soils with a large-scale direct shear apparatus. *Catena* 166:98–113
- Yu Z, Dahlgren RA (2000) Evaluation of methods for measuring polyphenols in conifer foliage. *Journal of Chemical Ecology* 26:2119–2140
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14

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