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**The Impacts of Disturbance on Submerged Aquatic Macrophytes Populations of the
Jemez Mountains, New Mexico**

By

Virginia Frances Thompson

B.S., Biology, University of Washington, 2006

M.S., Biology, University of New Mexico, 2013

DISSERTATION

Submitted in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

Biology

The University of New Mexico, Albuquerque, New Mexico

July 2021

ACKNOWLEDGEMENTS

Thank you to the following people: Drs. Diane Marshall and Cliff Dahm for the opportunities to make this happen; Drs. Rebecca Bixby, David Hanson and Caroline Scruggs for their efforts on my committee, and Dr. Lynne Beene for never giving up on turning me into a writer. Thanks also go out to the many volunteers and members of the BioAnnex and Hydrogeoecology group who put in countless hours in the field and laboratory to help collect data.

I could not have made it through everything without the unwavering support of my mother, without whom none of this could have happened, and I have been kept alive and sane by the support of friends, family and dojomates who have been more valuable to me than they will ever know.

To Y.L. and D.C.—this is for you too. One out of three ain't bad.

Nevertheless, she persisted.

The Impacts of Disturbance on Submerged Aquatic Macrophytes Populations of the Jemez Mountains, New Mexico

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PhD, Biology, University of New Mexico, 2021

ABSTRACT

This dissertation investigates the effects of disturbance (a catastrophic forest fire and decadal-level multi-day flood) on populations of submerged aquatic macrophytes (SAMs) in the streams and rivers of the Jemez Mountains of northern New Mexico, USA. Research conducted and reported in this dissertation addresses the following research questions: 1.) What factors influence the presence or absence of SAMs in Jemez Mountain streams? 2.) How does disturbance (catastrophic wildfire and decadal-level flood) change the amount of aboveground SAM biomass? and 3.) How does that disturbance change the nutrient content (%C, %N, %P) and nutrient stoichiometry of SAMs? These disturbance events had significant effects on the biomass, nutrient content and nutrient stoichiometry of SAM tissues. The research illustrates the effects that environmental factors of various physical and temporal scales can have on the phenology and physiology of this key primary producer.

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INTRODUCTION

Submerged aquatic macrophytes (SAMs) are not ubiquitous components of stream and river ecosystems, but in ecosystems where they are present they commonly dominate primary producer biomass and can have tremendous impacts on ecosystem services ranging from support of food webs to water quality improvements. Given that SAMs are important but not universal components of aquatic ecosystems, this raised the question of what affects SAM distribution in stream and river ecosystems?

This dissertation investigated multiple aspects of SAM occurrence in the Jemez Mountains of northern New Mexico including the quantification of the effects of catastrophic forest fire on these plants. More specifically, my research investigated 1.) factors affecting the presence and absence of SAMs in prominent Jemez mountain streams and rivers, 2.) the effects of catastrophic forest fire on the biomass and growth of SAMs, and 3.) the effects of catastrophic wildfire on SAM tissue nutrient content (% carbon, nitrogen and phosphorus) and nutrient stoichiometry.

Personal observations of SAM presence and absence at different elevations on the same rivers in the Jemez Mountains motivated the first portion of my research. What factors control SAM presence and absence in the Jemez Mountains? Factors controlling the presence and absence of SAMs in lower elevation systems are well documented and generalizations from these studies create a narrative of the typical ecology of SAMs around the world. As documentation of SAMs in high elevation areas is limited, this led me to ask if the abiotic

factors controlling presence and absence of SAMs at low elevations have the same effects on SAMs at high elevations. We measured stream depth, width, velocity, and estimated discharge, canopy cover, stream gradient and elevation and used univariate and multivariate analyses to determine which combinations of factors were most associated with the presence of SAMs. I asked the following questions: 1.) Which of these physical factors were associated with SAM presence or absence in these high elevation sites in the Jemez Mountains? 2.) Do these drivers differ from factors influencing patterns in SAM presence/absence in lower elevation areas? 3.) What SAM species are present and in what proportions?

Next, I investigated the effects of major disturbances on SAMs. Disturbance regimes in stream and river ecosystems are well known to be a primary driving influence in the structure and function of lotic ecosystems (Resh et al. 1988, Minshall et al. 1989, Dwire and Kauffmann 2003). My particular focus was on the effects of a catastrophic wildfire on SAMs. Wildfires are growing in size, intensity, and frequency due to climate change, especially in the western US. Fires have been noted to have significant impacts on water quality such as increased turbidity, decreases in dissolved oxygen and increases in nutrients in stream ecosystems. These effects may result in changes in SAM growth and composition. The Las Conchas fire was a catastrophic forest fire that occurred in mid-2011 and burned 36% of the watershed of the East Fork Jemez River. Negative water quality effects were documented tens of kilometers downstream (Dahm et al. 2015) from the site, and substantial amounts of ash and charcoal were brought into the East Fork by seasonal monsoon flood events. The fire-affected flood events mobilized ash, charcoal, solutes and soils from burn-

scarred areas into overland flows that then were deposited or transported in the stream channel. I also assessed the impact of a major large multiday flood disturbance event on SAMs and how that that disturbance compared to the impacts from wildfire. as SAM biomass has been shown to be affected by altered flows. My driving questions for this study are: 1.) Will flood events reduce standing submerged macrophyte biomass through scour and elevated sediment loads? 2.) Will fire-related flood events increase the standing biomass faster than deposition from a non-fire related event due to the increased inorganic nutrient content of fire inputs?

Nitrogen and phosphorus are key nutrients for all organisms on Earth. Aquatic systems are commonly limited in one or both nutrients, and the transport of ash and soils into the East Fork Jemez River after the Las Conchas Fire prompted us to pose questions about the effects of fire and flood on SAM tissue nutrient content. I addressed the following questions: 1.) How did the percent nitrogen (%N) and percent phosphorus (%P) content in SAM tissues respond immediately after a catastrophic fire compared to the nutrient content of pre-fire SAM tissues? 2.) Did nutrient content of SAM tissues respond to a decadal large-scale multiday flood two years after the wildfire? 3.) Did the type of disturbance (catastrophic wildfire versus regional flood) alter nutrient content and stoichiometric ratios in SAM tissues compared to tissue nutrient content during baseflow conditions before the disturbances? I used subsamples of tissues that were collected for use in Chapter 2 in calculation of standing biomass and determined the percent concentration of carbon (%C), nitrogen (%N) and phosphorus (%P) and the stoichiometric ratios of these nutrients of these SAM tissues. I also compared our results to other available datasets that included continuous water quality data

for our site to see if any of these factors were correlated with changes in SAM tissue nutrient content or stoichiometry from catastrophic wildfire and regional flooding.

CHAPTER 1

FACTORS INFLUENCING THE DISTRIBUTION OF SUBMERGED AQUATIC MACROPHYTES IN JEMEZ MOUNTAIN STREAMS, NORTHERN NEW MEXICO, USA

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ABSTRACT

Submerged aquatic macrophytes (SAMs) have been extensively studied in lotic ecosystems at low elevations, but few studies have been conducted in high elevation systems and factors controlling SAM distribution at high elevation are not well understood. After anecdotal and published documentation of abundant SAMs in high elevation streams in the Jemez Mountains, northern New Mexico, USA, we wanted to determine what combination of physical factors are controlling the presence or absence of SAMs in the Jemez River watershed. We surveyed several sites on the three major river systems in the watershed along a gradient of elevation for physical factors, presence/absence and percent cover of each taxa.

Our results showed that SAMs were observed in 60% of surveyed sites that were associated with deeper, narrower, lower velocity streams with low gradients. This evidence suggests that SAMs at high elevations are subject to similar abiotic controls found for SAM presence at lower elevations.

INTRODUCTION

Submerged aquatic macrophytes (SAMs), aquatic plants that complete their life cycle completely underwater, can have extensive effects on ecosystem structure and function when present in abundance in aquatic ecosystems. Considered classic ecosystem engineers (Jones et al., 1994), SAMs can modify abiotic and biotic factors in the surrounding aquatic ecosystem in capacities ranging from geomorphological changes in rivers and streams (O’Briain et al., 2017) to moderating presence/absence of species in complex food webs (Diehl and Kornijow, 1998). Other influences of SAMs on physical factors in aquatic ecosystems include current velocities (Madsen and Warneke, 1983), flow patterns (Sand-Jensen and Petersen, 1999), channel morphology and hydraulics (O’Briain et al., 2017), and sediment accumulation/retention (Rovira et al., 2016). However, the relationship between macrophytes and physical factors is not unidirectional. As physical factors can be highly influential in riverine ecology (Gordon et al., 2004), factors like light availability (Bornette and Puijalón, 2011), velocity (Chambers et al., 1991; Riis and Biggs, 2003), and water depth (Riis and Biggs, 2003) are of particular interest as they have been documented to affect SAM distribution, presence, and success.

Most studies on submerged aquatic macrophytes (SAMs) in lotic ecosystems have focused on low elevation systems (defined here as < 500 m a.s.l.), low gradient (defined here as < 1% slope), low velocity (defined here as < 0.5 m/sec), open canopy systems (e.g., Baattrup-Pedersen et al., 2006; Franklin et al., 2008). However, SAMs are known to inhabit some higher elevation streams and have been anecdotally reported in many higher elevation

locations in New Mexico in gray literature as well as a study by Thompson et al. (2019) in the region. We are studying stream sites in the Jemez Mountains with seasonally abundant SAMs, but SAMs are rarely found at lower elevations in New Mexico. This led us to ask what factors are associated with SAM presence at higher elevations in streams of the Jemez Mountains of New Mexico.

It has been previously shown that SAMs have a notable seasonal presence in one higher elevation river in the Jemez Mountains (Thompson et al., 2019). To follow on this information, the objective of this study was to understand the wider SAM community and distributions in the Jemez River watershed. In order to elucidate which factors may be driving this initial SAM observation, we investigated what physical factors were associated with SAM presence or absence in these high elevation sites and whether these drivers differed from factors influencing patterns in SAM presence/absence in lower elevation areas.

We surveyed portions of the three major rivers of the Jemez Mountains of New Mexico, USA that appeared to have physical characteristics that are known to support SAM communities. We assessed physical parameters (e.g., elevation, canopy cover, depth, discharge, gradient, velocity, width) in all selected locations and measured key parameters (i.e., species present, percent cover of each species) of the SAM community at all sites in which they were present.

METHODS AND MATERIALS

Study Sites--We selected 15 study sites (Table 1) distributed over three river systems (Rio San Antonio, East Fork Jemez River and Rio Cebolla/Rio Guadalupe) in the Jemez Mountains in Sandoval County, north-central New Mexico, USA (elevation 2438 m – 3048 m a.s.l.). These river networks constitute most of the watershed area in the Jemez Mountains and form the Jemez River that ultimately flows into the Rio Grande just north of Bernalillo in central New Mexico.

The East Fork Jemez River and Rio San Antonio both originate in grassland meadows of the 1.25 Ma year-old Valles Caldera Natural Preserve (VALL) (Goff, 2009). These streams are surrounded mostly by mixed coniferous forests and are the two primary tributaries that drain the entire Valles Caldera. The Rio Cebolla/Rio Guadalupe watershed, originating in the northeastern Jemez Mountains, is completely outside of VALL boundaries. While outside the watershed of the caldera, mixed coniferous forests and surrounding grasslands are also the predominant land cover in the Rio Cebolla/Rio Guadalupe watershed. Half or more of the annual precipitation in the region comes from snowfall as the area is seasonally snow-covered (October-April) while the North American monsoon season from July to September can provide up to half of the approximately 475 mm mean annual precipitation as rainfall (Bowen, 1996). We evaluated multiple locations on these three river networks for presence and absence of SAMs as well as for key physical factors that could influence SAM presence using knowledge of conditions gained while conducting a prior study (Thompson et al., 2019).

Field methods--Using methods modified from Baattrup-Pedersen and Riis (1999) and Riis and Biggs (2003), we assessed 50 m reaches at 15 sites among the Rio San Antonio ($n = 4$ reaches), Jemez River ($n = 6$ reaches), and Rio Cebolla/Rio Guadalupe ($n = 5$ reaches). We placed transects every 5 m in each 50-meter reach for a total of 11 transects at each site (165 transects in total at all sites) and assessed each transect from the left bank to the right bank, moving from downstream to upstream. At each transect, we recorded GPS locations and measured water depth (m), stream width (m), and velocity (m/s) using 50-m tapes and a Flo-Mate 2000 flow meter (Marsh-McBirney, Inc., Frederick, MD) following USGS standard procedures (United States Geological Survey, 1982) to assess the transect geomorphology. Canopy cover (%) was estimated using a spherical crown densiometer (Forestry Suppliers, Inc., Jackson, MS) and the four-measurement method (Lemmon, 1956) in the center of each transect as determined by measured stream width.

A 25 cm x 25 cm quadrat was used to measure the percentage of SAM cover by each species at 5% interval scales every 50 cm along each transect. The number of quadrats assessed on each transect depended on stream width, ranging from 2 to 20 with an average of 5 quadrats. Taxa were identified in the field and verified using herbarium samples from the Museum of Southwestern Biology at the University of New Mexico.

Data Calculations-- Stream gradient percentages (m/km) were calculated by hand-tracing one km of river channel upstream from the survey site using digital orthography taken from Google Earth 7.0.2 (Google, Mountain View, CA). Estimated discharge (m^3/sec) was

calculated from geomorphological measurements (depth, width, velocity) taken along each transect.

Statistical Methods— For all analyses, means were calculated at the transect level for each factor (depth, width, velocity, estimated discharge and percent SAM cover) that had more than one measurement taken per transect to avoid pseudoreplication. Pearson's Correlations were first used to determine possible relationships between variables, and because many of the abiotic variables were correlated (Table 2) univariate and multivariate analyses were conducted to tease out potential relationships. Mean percent cover of SAM vegetation was arcsine square root transformed, grouped by sample site, and then compared among river systems and among species within and between each river system using a two-way analysis of variance (ANOVA) and post-hoc Tukey's HSD comparisons ($\alpha = 0.05$). Multivariate analyses were used to better understand the degree of influence of these variables. A Principal Component Analysis (PCA) was conducted to investigate possible combinations of abiotic variables that may differ among reaches with and without SAMs. Discriminant Function Analysis (DFA) was then used to test how accurately combinations of these factors could indicate presence or absence of SAMs. Statistical analyses were performed using SPSS 25 (IBM, Armonk, New York) and PC-ORD 6 (MjM Software, Gleneden Beach, Oregon.).

RESULTS

Macrophytes were present at nine of the 15 study reaches (60% of the reaches) in the three rivers, with the same three species, *Elodea canadensis* Michx., *Ranunculus aquatilis* L., and

Stuckenia pectinata (L.) Boerner found on each river system in varying proportions. All taxa are common species, native to the western United States (United States Department of Agriculture, <http://plants.usda.gov>). *Stuckenia pectinata* was a minor constituent, appearing only once on each river system ($n = 3$), while *E. canadensis* and *R. aquatilis* were much more prevalent ($n = 69$, $n = 22$ transects respectively).

Macrophyte Parameters— There were significant differences in total percent SAM cover among species pooled over all systems ($P < 0.0001$, two-way ANOVA). In contrast, the total SAM percent cover of all species was not significantly different among river systems ($P = 0.366$, two-way ANOVA); however, total mean SAM cover of all species pooled tended to be higher in the East Fork Jemez River; compared to the other two river systems (Figure 1). Additionally, there were statistically significant differences found among SAM cover of different taxa on the same river system (Figure 1, $P = 0.002$, two-way ANOVA).

Our results showed that *Elodea canadensis* was consistently the most abundant taxon across all river systems surveyed in the Jemez River watershed, present in approximately 40% of all transects in the surveyed reaches (69 of 165 transects). *Ranunculus aquatilis* was present in 13% of surveyed areas (22 of 165 transects). While consistently present in all three river systems, *Stuckenia pectinata* has little impact on community abundance and was found only in 0.3% of transects (5 of 165 transects), which prevented analysis regarding influence of abiotic factors on their distribution in the Jemez.

On the Rio San Antonio, the mean percent cover of *E. canadensis* was significantly higher than both *R. aquatilis* and *S. pectinata* (Figure 1). On the Cebolla/Guadalupe, the mean percent cover of *E. canadensis* was also significantly higher than the percent cover of both *R. aquatilis* and *S. pectinata*; however, there was no difference between the mean cover values of *R. aquatilis* and *S. pectinata* (Figure 1). In the East Fork Jemez River, the percent coverage results between *E. canadensis* and *R. aquatilis* were not statistically significant but both species had significantly higher cover compared to the cover of *S. pectinata* in this river.

Effects of Abiotic Factors— No single abiotic factor stood out as the major influence on presence or absence of SAMs in Jemez Mountains river systems (Table 2); rather our results showed that there were significant differences in multiple variables that acted as drivers of macrophyte presence (Figure 2). Mean values of all abiotic variables measured differed significantly among stream reaches with and without SAMs present (Figure 2). Every physical factor was significantly different ($P \leq 0.01$) among the sites with and without *E. canadensis* (Table 3). However, only mean values of stream gradient and site elevation differed significantly among sites with and without *R. aquatilis* (Figure 3, Table 3).

To examine the abiotic variables simultaneously, a PCA indicated notable differences in physical parameters between sites with and without macrophytes. The first two principal components combined accounted for 72.6% of the variance in abiotic factors (47.1% for PC1 and 27.5% for PC2, respectively) (Figure 4). Principal Component 1 factors that supported the presence of SAMs were higher elevation, lower estimated discharge, and narrower stream

widths, while Principal Component 2 factors associated with SAM presence included deeper stream depths and lower stream gradients.

Discriminant Function Analysis showed that differences in physical factors shown in the PCA ordination were a good predictor of the presence or absence of SAMs ($P < 0.0001$, $df_{(1,163)}$), predicting overall occurrence of SAMs with 94% accuracy. Streams described as open canopy, low gradient, lower velocity, with a deep and narrow stream channel and located at higher elevation were most likely to have species of SAM present in the stream (Figure 2). The influence of physical factors on the presence or absence of *E. canadensis* was also significant ($P < 0.0001$, $df_{(1,163)}$), showing preference for the same combination of factors (Figure 3, Table 3). Presence/absence of *R. aquatilis* was also found to be significantly influenced by multiple factors ($P < 0.0001$, $df_{(1,163)}$) indicating that shallower, narrower, higher velocity, lower gradient streams at higher elevations were favored. Predictions for presence and absence of both *E. canadensis* and *R. aquatilis* were made with over 87% accuracy, given these physical factors.

DISCUSSION

We found that multiple physical factors affected the presence or absence of SAMs in high elevation rivers of the Jemez Mountains in northern New Mexico. Narrower, deeper stream reaches with lower velocities, lower estimated discharges, and lower stream gradients that are located at higher elevations and lacking canopy cover were the most likely to support communities of SAMs (Figures 2, 3 and 4).

However, the best combinations of these factors and their overall degree of influence on presence varied among the SAM species in question. *Elodea canadensis* and *R. aquatilis* both showed a similar prediction accuracy of 87% based on a combination of deeper, narrower streams with slower velocities and lower estimated discharges, but we were not able to accurately predict influencing factors for *Stuckenia pectinata* due to small sample size. While local conditions may drive patchiness and particular species composition on smaller scales, coarser scale measures show a cosmopolitan distribution of these taxa in rivers of the Jemez Mountains.

Stream velocity can have a variety of effects on submerged macrophytes, including inducing changes in morphological structure and causing physical damage that can scour SAMs from a location (Janauer et al., 2010), but these effects varied by taxon. Reaches with *E. canadensis* present had an average velocity of 0.18 m/s (Figure 3), while reaches with *R. aquatilis* averaged faster velocities at 0.26 m/s. These values fall well within the preferred velocity range of *E. canadensis* (Haslam, 1978; Riis and Biggs, 2003), but were slower than the velocity preferences of *Ranunculus trichophyllus* (a taxon closely related and morphologically similar to *R. aquatilis*) at 0.4 – 0.6 m/s (Haslam, 1978; Chambers et al., 1991; Riis and Biggs, 2003). None of our velocity measurements in any reach, including reaches where SAMs were absent, exceeded 0.71 m/s, well below the tolerance limit for SAM presence of 1.0 m/s (Chambers et al., 1989). Thus, velocity was not an exclusionary factor for SAMs in Jemez Mountain river systems.

Slower, deeper streams were more likely to host both the mixed species SAM communities in the assessed reaches (Figure 2) as well as the dominant taxon in our study, *E. canadensis* (Figure 3). Of the measured abiotic variables in our study, depth and velocity have been repeatedly found to influence SAM success (Bornette and Puijalon, 2011) and abundance (Riis and Biggs, 2003) in other systems. Depth has a notable influence on SAMs as changes to depth change relative velocities when discharge rates stay the same; therefore, shallower areas will have higher water velocities compared to deeper reaches. These changes in velocity affect SAMs differently depending on taxa and growth habit (Schoelynck et al., 2013). Species with an upright growth habit and less stable anchoring mechanisms, such as *E. canadensis*, are subject to more stress forces from higher stream velocity and subsequent damage and breakage along multiple points along the stem simply by their position in the water column. Species that lay prostrate against the benthos with more anchor points, like *R. aquatilis*, can withstand higher velocities and lower water levels with less damage (Sand-Jensen, 2003), which can offer a competitive advantage in some situations.

Stream gradient varied throughout the study sites; additionally, low or high gradient systems were not exclusive to lower or higher elevation areas, but sites without SAMs averaged a stream gradient over 7x steeper than the average gradient of the sites with SAMs present (Figure 2). Stream gradient, the elevational rise over a given distance, affects multiple variables including water velocity and turbulence (Asaeda and Rashid, 2017) that could ultimately affect SAM presence/absence in a reach. However, the effects of gradient and velocity are hard to disentangle as changes in gradient can increase or decrease the velocity of a stream system.

We also found that riparian canopy cover was significantly different between sites that had SAMs and those that did not. Riparian canopy cover can also affect the growth of SAMs given that it can intercept and reduce the amount of light/photosynthetically active radiation that reaches the river surface, thereby reducing available light resources for SAMs. Canfield and Hoyer (1988) also found riparian shading to be a controlling factor on presence and abundance of aquatic macrophytes in low elevation sites. However, there were multiple sites at which SAMs were absent that had no canopy cover, implying that other physical factors were more influential in controlling SAM presence/absence in those locations. We hypothesize that presence/absence in these locations was likely more influenced by velocity and stream gradient than canopy cover as mean velocities and gradients at those sites were all above both the mean velocities and gradients for sites with SAMs present.

We were particularly interested in the role of elevation in SAM presence, given the geographic location, anecdotal observations in the field, and the far greater number of published studies on SAMs that have been conducted in low elevation areas (< 500 m a. s. l.) (e.g., Baattrup-Pedersen et al., 2006; Franklin et al., 2008) than high elevation areas. Our study locations ranged from 1724 m a. s. l. to 2665 m a. s. l., thus our sites should be considered to be high elevation. Supplemental analysis with elevation excluded from the abiotic factors list for all three datasets (all SAMs, *E. canadensis* and *R. aquatilis*) showed little change in classification accuracy (< 4% change in any classification accuracy—94%, 84%, and 87%, respectively) and no changes in statistical significance. Instead, the multiple environmental factors that correlated with elevation were the major determinants of the

presence of SAMs. This result is of interest as high elevation areas often differ substantially in many abiotic parameters compared to low elevation sites, including diel and seasonal temperature extremes that can limit physiological functions of SAMs. However, in the Jemez Mountains, physical conditions at high elevation reaches are a close match to the conditions often observed and documented in low to moderate elevation forested ecosystems during the majority of the growing season.

In these low elevation studies mentioned above, specific physical parameters including velocity, depth and gradient affected the presence of SAMs; our findings illustrate similar effects on SAM presence/absence in high elevations areas as well. While not always a ubiquitous aquatic ecosystem component, SAMs can create notable effects on the biotic components of stream and river ecosystems simply by their presence (Champion and Tanner, 2000). These effects occur through creating a multitude of physical and chemical changes ranging from decreasing stream velocities to increasing dissolved oxygen levels. These changes have substantial effects on biota of higher trophic levels such as macroinvertebrates (Wolters et al., 2018) and fish (Lusardi et al., 2018), creating a much more biotically diverse and complex aquatic ecosystem. This complexity, in turn, creates more robust aquatic ecosystems (Thomaz and Cunha, 2010) with benefits to both the health and function of the ecosystem at large as well as ecosystem services of interest to humans such as improvements in water quality and nutrient cycling. Aquatic ecosystems are predicted to see significant changes to abiotic conditions from climate change (citation). In addition, our works showed that complex combinations of abiotic factors influence the presence and absence of SAMs. Therefore, a greater understanding of how changes to these abiotic factors may affect SAM

presence and absence can help predict potential changes to water quality and ecological function of montane headwater ecosystems of importance for source waters to downstream areas.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge members of the Department of Biology (University of New Mexico) and the UNM Hydrogeoecology group for assistance in both the field and laboratory. The National Science Foundation provided support for this project through the New Mexico Established Program to Stimulate Competitive Research (EPSCoR) RII Track I Project (award 0814449). V.F. Thompson was also supported by a New Mexico Water Resources Research Institute (WRRI) Student Research Grant and the University of New Mexico Department of Biology.

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TABLES

TABLE 1-- List of site names, river system names, and latitude/longitude (decimal degrees) for the 15 stream reaches surveyed, Jemez River watershed, northern New Mexico.

Site Name	River System	Latitude (N)	Longitude (W)	Elevation (m a. s. l.)
Upper Cebolla	Cebolla/Guadalupe	35.876175	106.741411	2323
Middle Cebolla	Cebolla/Guadalupe	35.861	106.757506	2286
Lower Cebolla	Cebolla/Guadalupe	35.844422	106.781514	2255
Gilman Tunnels	Cebolla/Guadalupe	35.737908	106.764714	1887
367 Bridge	Cebolla/Guadalupe	35.820764	106.788217	2198
Upper East Fork	Jemez	35.971444	106.517697	2600
Middle East Fork	Jemez	35.854878	106.478811	2591
Lower East Fork	Jemez	35.841519	106.501125	2586
Guadalupe/Jemez Confluence	Jemez	35.668967	106.743375	1724
Redondo Creek	Jemez	35.862811	106.613028	2430
La Jara Creek	Jemez	35.866053	106.517036	2665
Indios Creek	San Antonio	35.968303	106.483911	2625
Upper San Antonio	San Antonio	35.962994	106.490614	2611
Middle San Antonio	San Antonio	35.971444	106.517697	2590
Lower San Antonio	San Antonio	35.973633	106.596942	2553

TABLE 2-- Pearson correlations (r^2) between physical factors measured at each transect, Jemez River watershed, northern New Mexico.

	Estimated			Canopy	Stream	
	Discharge	Depth	Width	Cover	Gradient	Elevation
Velocity (m/s)	0.539**	-0.346**	0.026	0.296**	0.213**	-0.235**
Estimated Discharge						
(m³/sec)	---	-0.0107	0.673**	0.517**	-0.052	-0.783**
Depth (m)	---	---	-0.217**	-0.181**	-0.502**	0.148
Width (m)	---	---	---	0.133	-0.111	-0.788**
Canopy Cover (%)	---	---	---	---	0.139	-0.411**
Stream Gradient (%)	---	---	---	---	---	0.103

** = significant at the $P < 0.01$ level

TABLE 3--Results of Discriminant Function Analysis as P-values describing significant differences in physical variables between stream reaches with and without *Elodea* or *Ranunculus* present. Reaches with *Elodea canadensis* present $n = 69$, absent $n = 96$; reaches with *Ranunculus aquatilis* present $n = 22$, absent $n = 143$. Discriminant Function Analysis was able to correctly predict presence or absence of *E. canadensis* or *R. aquatilis* with 87% accuracy.

	<i>Elodea</i>	<i>Ranunculus</i>
Velocity (m/sec)	0.002*	0.24
Estimated Discharge (m³/sec)	0.009*	0.32
Depth (m)	< 0.0001*	0.56
Width (m)	< 0.0001*	0.08
Canopy Cover (%)	< 0.0001*	0.10
Stream Gradient (%)	< 0.0001*	0.013*
Elevation (m a.s.l.)	0.013*	0.006*

* denotes statistical ($P < 0.05$) significance

FIGURES

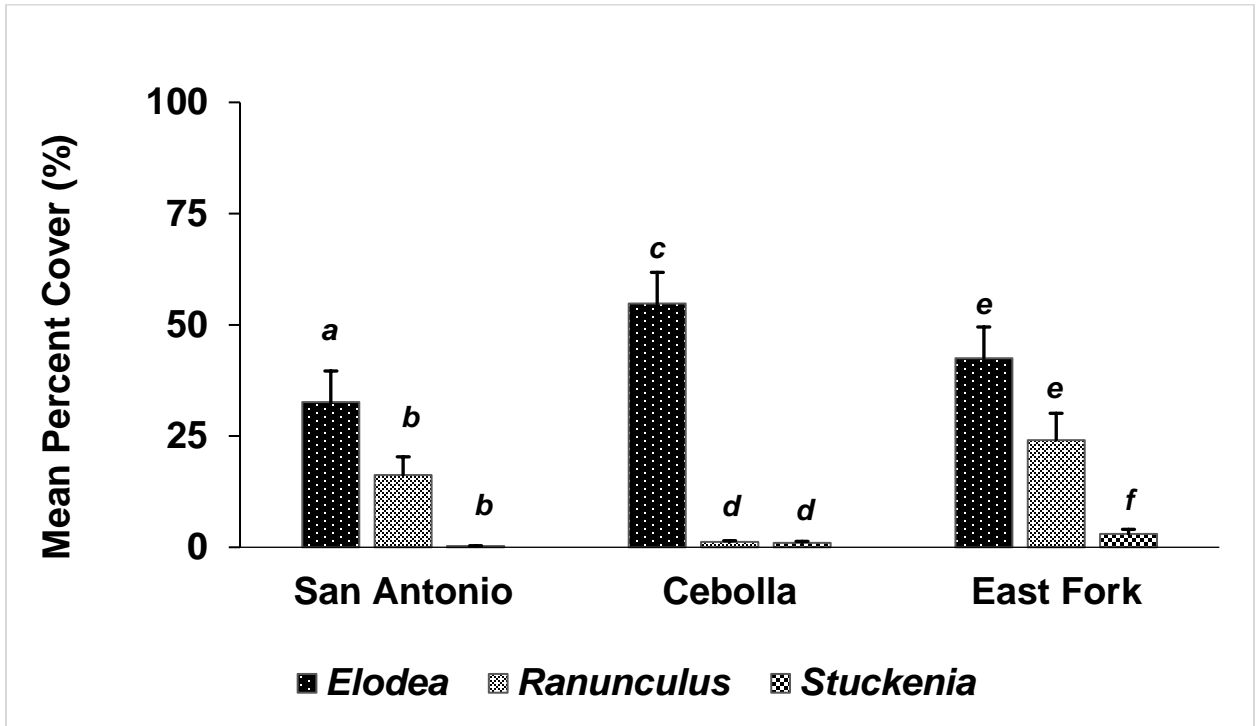


FIGURE 1--Mean percent cover (\pm standard error) of each submerged aquatic macrophyte species, with individual reaches pooled into their respective river systems. Letters denote significant differences between mean percent cover by species within each river system (two-way ANOVA, Tukey's HSD).

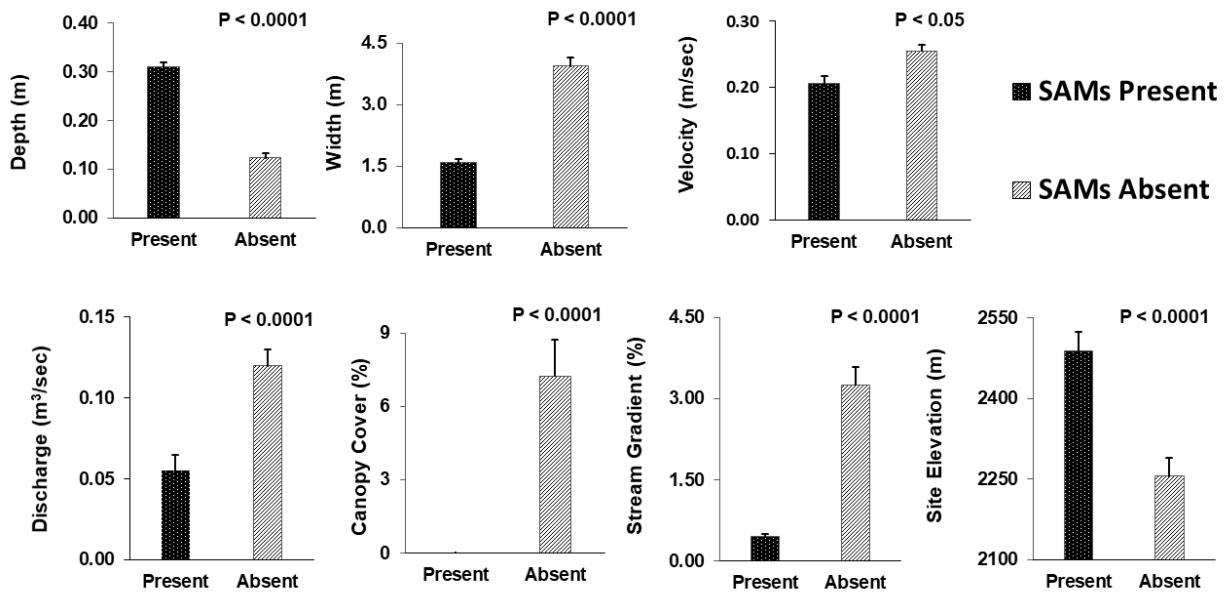


FIGURE 2--Mean (\pm standard error) values of each factor for stream reaches with and without submerged aquatic macrophytes (SAMs) present. P values indicate significance differences in abiotic factors in reaches with and without macrophytes, All transects in reaches with any SAM species present were pooled for calculation (present $n = 99$, absent $n = 66$)

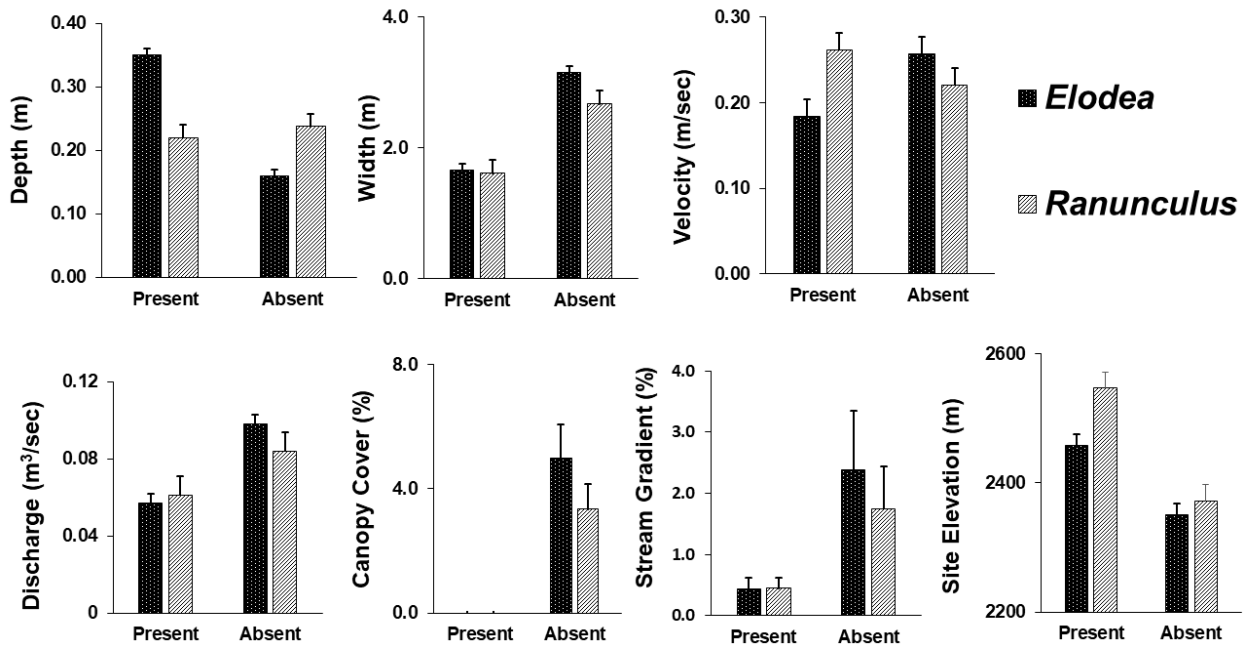


FIGURE 3--Mean (\pm standard error) values of each factor in stream reaches with and without *Elodea* or *Ranunculus* present. All factors were significantly different for *Elodea*, but only elevation and stream gradient were significant for *Ranunculus* (see Table 3). Transects with each taxa present were pooled for calculation. Reaches with *Elodea canadensis* present $n = 69$, absent $n = 96$; reaches with *Ranunculus aquatilis* present $n = 22$, absent $n = 143$.

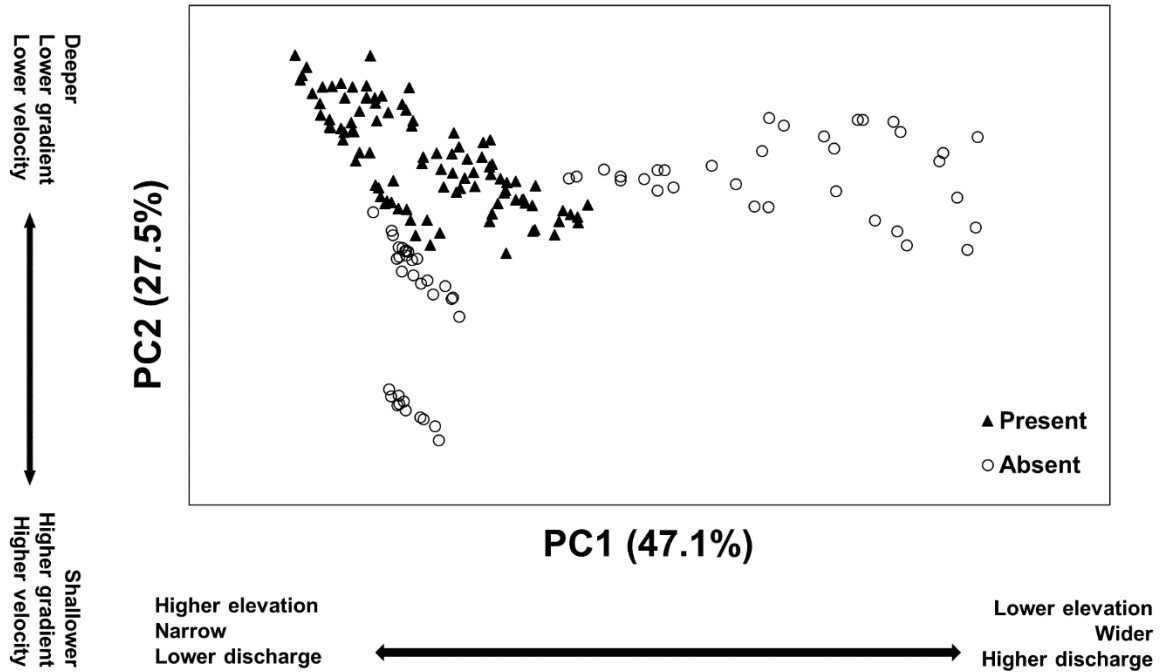


FIGURE 4--Principal Component Analysis ordination of transects with all abiotic factors included. Sites are coded by the presence or absence of macrophytes at transects ($n = 165$). Principal Component 1 (PC1) is most strongly associated with elevation, discharge, and width while Principal Component 2 (PC2) is most strongly associated with depth, stream gradient, and velocity.

CHAPTER 2

THE EFFECTS OF A CATASTROPHIC FOREST FIRE ON THE BIOMASS OF SUBMERGED STREAM MACROPHYTES

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KEYWORDS: SUBMERGED AQUATIC MACROPHYTES; DISTURBANCE; WILDFIRE; BIOMASS;
HYDROLOGY; WATER QUALITY

ABSTRACT

Primary production during the growing season in the low-gradient meadow streams of the Valles Caldera in northern New Mexico (USA) is dominated by submerged aquatic macrophytes. A catastrophic wildfire beginning on June 28, 2011, the Las Conchas fire, burned 36% of the East Fork Jemez River catchment above an intensively instrumented stream reach where water quality, hydrology, and aquatic ecology are being studied.

Submerged macrophyte biomass in the late summer of 2011 was reduced about 20% after a series of high turbidity spates (> 1200 NTU) in late July through early September. Stable flows and deposition of fire-related nutrient-rich sediments in the fall of 2011 led to maximum mean macrophyte biomass during the three-year period of study of 234 g ash free dry-mass (AFDM) m^{-2} in October of 2011. Peak mean biomass in 2012 was 228 g AFDM m^{-2} in September during a growing season with only minor hydrologic and water quality disruptions. A major regional storm over multiple days in mid-September of 2013 produced the highest discharge during the three years of study with turbidities reaching ~ 400 NTU.

Peak mean biomass in 2013 did not reach levels measured in 2011 and 2012. *Elodea canadensis* was more sensitive to biomass removal during these high flow conditions while *Ranunculus aquatilis* added biomass following higher flow conditions in 2011 and 2013.

Disturbance impacts on submerged macrophytes from major wildfires can be both negative and positive depending upon species types, stream hydrology, catchment geomorphology and water quality.

1. INTRODUCTION

Disturbance alters the structure and function of stream ecosystems, and stream ecosystem responses to disturbance depend on the frequency, magnitude, and duration of the various types of disturbances that impact streams (Lake, 2000). Physical and chemical changes wrought by these disturbances can have notable effects on biological groups within streams. For instance, short-term pulse disturbances, such as flash floods, have potential long-term effects on stream biota. Floods have been shown to be a key influence on submerged aquatic macrophytes in perennial rivers (Riis and Biggs, 2003), and altered flows due to such disturbances can affect macrophytes in both positive and negative ways. Macrophytes can both affect and be affected by flow conditions to varying degrees depending on both the composition of the macrophyte community and the velocity of the stream water during floods (Wang et al., 2015). Floods and accompanying scour can reduce standing submerged plant biomass in an initial pulse, but populations have been shown to recover rapidly from remaining plant tissues (Henry et al., 1996; Townsend et al., 2017).

Another pulse disturbance of potentially large magnitude that can affect hydrophytes is flooding after catastrophic wildfire. Riparian plants have been shown to both be impacted by fire as well as to alter active fire behavior (Bixby et al., 2015), and wildfires can have both positive and negative effects on wetland plant communities (Osborne et al., 2013). Unlike riparian plants and emergent macrophytes, submerged macrophytes are not directly affected by fire during the event. Instead, they are affected indirectly, well after the active fire danger has passed. This reaction occurs primarily via fire-influenced alterations in physical and chemical stream parameters. These impacts include changes in light regime, increases in

water temperature due to destruction of riparian canopy cover, and altered water quality such as increases in turbidity and inorganic nutrients and sags in dissolved oxygen (DO) and pH (Earl and Blinn, 2003; Smith et al., 2011; Stephan et al., 2012; Verkaik et al., 2013). These impacts generally occur when precipitation events mobilize ash, charcoal, soil, and solutes (Gresswell, 1999; Verkaik et al., 2013) and transport these materials into stream ecosystems with traceable effects far downstream from the footprint of the fire (Dahm et al., 2015; Reale et al., 2015).

The frequency, intensity, duration, and extent of forest fires are increasing with climate change worldwide (Luo et al., 2013; Westerling, 2016). Large, intense forest fires have direct and indirect effects on stream and river ecosystems, including increased flooding, erosion, and altered hydrologic regimes. Monsoon-affected regions like the southwestern United States get high-intensity, short-duration rainfall from thunderstorms in the summer months that can rapidly boost peak stream flows; and peak flow pulses from burned catchments are strongly accentuated immediately after wildfire (Reale et al., 2015). In addition, high-intensity precipitation events greatly increase post-fire sediment yields in burned catchments compared to unburned catchments (Smith et al., 2011). Transported sediment increases the likelihood of damaging disturbance events to biotic communities in streams during these events. Fire also creates physical changes in the soil that allow for greater transport of both fire debris and burned soils through overland flows during precipitation events. Ultimately, burn-scar material is delivered into the stream channel and water column (Dahm et al., 2015). Fire ash often contains elevated levels of particulate carbon and nutrients that are bound to fine particles (Smith et al., 2011). These particles are redistributed in the stream channel and

can create available nutrients for primary production as fires transform organic nutrients to more biologically accessible forms (Certini, 2005).

Beginning in late June and extending into early August of 2011, the Las Conchas fire burned ~63,370 ha of forested uplands and meadow lowlands in the Jemez Mountains in north-central New Mexico, USA (USDA, Forest Service, 2011). This was the largest fire in New Mexico recorded history and included about 36% of the watershed of the East Fork Jemez River (East Fork) where a major stream and groundwater research project was ongoing. Fire impacts, including carbon-rich blackwater flow events, were observed over hundreds of kilometers of the Rio Grande downstream of the fire scar and throughout many tributaries of the Jemez River (Dahm et al., 2015; Reale et al., 2015). These blackwater and other high turbidity events that originated from burn scars from the Las Conchas fire were widespread; water quality impacts were documented with data from before, during, and after the wildfire at the East Fork study site (Sherson et al., 2015). The spring of 2011 was also the start of our study on the biomass of the submerged aquatic plant community at the site. The Las Conchas fire impacted much of the catchment during the summer of 2011 and presented opportunities to study the role of wildfire on submerged macrophyte biomass and to examine the effects of disturbance on the macrophyte community as the burn scars recovered.

This event created a fortuitous combination of catastrophic wildfire, monsoon flood events, a large rainfall event from dissipating tropical storms with available data collected before, during, and after the fire. After the major wildfire, we hypothesized that flood events would

reduce standing submerged macrophyte biomass through elevated turbidity and sediment loads from burn-scarred areas. We also hypothesized that, after the fire-related flood events, deposition of nutrient-rich ash and sediment in the stream channel would create a fertilization effect that would increase the biomass of submerged macrophytes that would accrue after disturbance events.

2. MATERIALS AND METHODS

2.1 Study Site

The East Fork Jemez River originates in the Valle Grande, a large grassland meadow located at approximately 2600 m elevation in the largest of the valleys within the approximately 21 km wide circular depression known as the Valles Caldera. This caldera has formed about 1.25 Ma years ago and is now part of the Valle Caldera National Preserve in the Jemez Mountains of northern New Mexico, USA (Goff et al., 2006). The Valle Grande is surrounded by multiple types of coniferous forests (Muldavin and Tonne, 2003) that reach up to 3,400 m in elevation. The area is seasonally (October-March) snow-covered during wet winters, and snowfall generally provides about half of the approximately 475 mm mean annual precipitation. The other half of the area's precipitation usually arrives as thunderstorms with the North American monsoon that typically extends from July to early September (Bowen, 1996). The East Fork is a high-elevation, low-gradient, high-light intensity, low dissolved nutrient, perennial headwater stream ecosystem where submerged macrophytes proliferate between April and October. The study site extends over approximately 300 m of a meandering, third-order stream that lies inside a cattle and native ungulate grazing enclosure established in 2004 (Sherson et al., 2015).

The East Fork was affected in 2011 by the Las Conchas fire, which started on 26 June 2011 and was officially 100% contained on 3 August 2011. This wildfire burned over 63,000 ha of mixed coniferous forests, high elevation grasslands, and montane meadows. Using severity categories as defined by Parsons et al. (2010), the U.S. Forest Service's Burned Area Emergency Response (BAER) team for the Las Conchas fire reported fire severity proportions of 20% high, 26% moderate, 39% low, and 15% unburned areas (USDA, Forest Service, 2011). Thirty-six percent of the East Fork catchment upstream of the study reach burned, an area encompassing approximately 9700 ha near and within the Valles Caldera National Preserve (Reale et al., 2015). Orem and Pelletier (2015) documented the elevated overland flow, rill formation, erosion and deposition, channel incision and avulsion, infilling of incised channels, and debris flows within the Valles Caldera catchments after the Las Conchas wildfire.

In September 2013, a very large precipitation event occurred within the East Fork catchment and caused a large disturbance event. Two dissipating tropical storms—one from the Pacific Ocean and one from the Gulf of Mexico—were drawn northward through New Mexico and into Colorado producing widespread flooding (Trenberth et al., 2015). The precipitation gage closest to the study site within the East Fork's catchment captured 8.6 cm of rainfall on 12-13 September 2013, nearly half (3.9 cm) falling in the first 24 hours (WRCC 2018). This unusually strong regional storm from dissipating tropical storms resulted in a long-duration flood with a peak discharge of $\sim 3.6 \text{ m}^3 \text{ s}^{-1}$, up to two orders of magnitude higher than the average baseline streamflow found in the East Fork.

2.2 Macrophyte Identification and Assessment

In 2011 and 2013, we identified and verified the taxa in the study reach using vegetative and flowering parts from the herbarium collections at the Museum of Southwestern Biology at the University of New Mexico, Albuquerque, NM, USA. Observations of initial emergence, growth, and senescence were taken at approximately six-week intervals starting in June 2011 and extending through the course of the 2011, 2012, and 2013 growing seasons (April-October) to evaluate the basic phenology of the species present in the East Fork. General observations were taken at each of six sampling locations along the 300 m study reach for emergence, flowering, and senescence of each of the four species present.

2.3 Biomass

To quantify the biomass for each species, we estimated the aboveground biomass using a standard ash free dry-mass (AFDM) procedure (Raschke and Rusanowski, 1984). Plant biomass estimates included six sampling locations with three transects across the width of the stream at each location. Three samples were taken from each transect across the stream: one from the center and two from approximately 30 cm inward from each bank. A total of 54 samples were taken on each sampling date. Samples were collected approximately every six weeks during each growing season to reduce possible cumulative impacts from sampling. We constructed a sampling device for collecting all aboveground plant tissues in a known surface area in shallow flowing waters that consisted of a circular metal tube 80 cm in height, 7 cm

in diameter with a sampling area of 40 cm² and multiple ~1 cm drainage holes along the tube. The tube was pressed flat against the benthos, and a sharpened metal cutting device was used to cut all aboveground biomass within the tube at the stream bed. The cutting device covered the bottom of the tube while the detached sample was raised to the surface. Samples were preserved on ice and transported to the BioAnnex Analytical Laboratories at the University of New Mexico, Albuquerque for analysis.

In the lab, plant tissues were cleaned and manually separated by taxon. Each separated sample was then sonicated in an ultrasonic bath with deionized water for at least 10 minutes to remove epiphytic organisms. After sonication, samples were dried at 60°C for 48 hours and weighed. Samples were then incinerated at 500°C for two hours and weighed again to determine ash content and AFDM. The biomass estimates for the four species along with the total biomass on each of the 12 sampling dates were used to determine the proportion of biomass for each taxa.

2.4 Continuous Hydrology and Water Quality Measurements

Stream discharge (Q) estimates for the East Fork were obtained from a streamflow station located < 1 km downstream from the sampling reach. The station consisted of a pressure transducer (HOBO 30-Foot Depth Water Level Data Logger; Onset Computer Corporation, Bourne, MA, USA) in the bottom of a stilling well that collected data at 10- to 30-minute intervals to determine water levels; these levels were then corrected for barometric pressure and temperature and used to estimate Q. Dissolved oxygen (DO), pH, turbidity, specific

conductivity, and temperature measurements were collected at 15-minute intervals within the enclosure using a Yellow Springs Instruments (YSI) 6920 multi-parameter sonde (YSI Inc., Yellow Springs, OH, USA). Discharge, DO, turbidity, and temperature data were compiled and validated using Aquarius Workstation 3.3 (Aquatic Informatics, Vancouver, British Columbia, Canada). Further details on the methods used to collect continuous discharge and water quality data at the study site are found in Sherson et al. (2015) and Reale et al. (2015). The DO data were used to calculate the daily DO amplitude (mg L^{-1}). Minimum DO concentrations before sunrise were subtracted from maximum DO concentrations in the late afternoon to give a daily amplitude of DO during the growing season.

2.5 Statistical Methods

Statistical tests were run in R (RStudio, 2015) and SAS (version 9.4, SAS Institute, Cary, NC). Generalized Linear Models (GLMs) were constructed to investigate the influence of various factors, including disturbance type and turbidity, on aboveground biomass values collected on each sampling date. While descriptive statistics are presented in tables and figures as untransformed biomass (measured in g AFDM m^{-2}) for ease of interpretation, this variable was log transformed prior to analysis to improve normality. Log transformed biomass was used as the dependent variable in linear models whereas peak flow and turbidity (see definitions below) were used as continuous independent variables; disturbance type (defined below), season (early or late), habitat (riffle or pool), and species were used as fixed, categorical variables. Where possible without overspecifying the model, two-way interaction terms between independent variables were added to the model (see Table 2 for details).

Peak flow was defined as the peak streamflow measured in the time between the last and current biomass collection date. Turbidity was defined as the number of hours between the last and current biomass collection where turbidity values exceeded 500 NTUs. Habitats were defined as either pools or riffle/runs based on field observations. Seasons were defined as early (April-July) and late (August-October) to approximate a halfway point in a typical growing season in the area. Disturbance type was a categorical variable that differentiated between phases where the system was unaffected by disturbances, directly affected by the disturbances, and in initial recovery from the preceding disturbance event (e.g. Undisturbed, Disturbed, and Recovering). These groupings were then sub-categorized into the lower stream discharge disturbance events in 2011 that mobilized fire ash into the East Fork and the larger magnitude discharge regional storm associated event in 2013 (Figure 1). These sub-categories were Fire Disturbance, Post-Fire Recovery, Storm Disturbance and Post-Storm Recovery. The sampling dates classified as Undisturbed were June and July 2011, all sampling dates in 2012, and April and June of 2013. Fire Disturbance is the sampling date in September 2011, while the associated sampling date for Post-Fire Recovery was in October 2011. Storm Disturbance associated sampling was August 2013, and Post-Storm Recovery is October 2013.

3. RESULTS

3.1 Identification and Phenology

Submerged macrophyte taxa present were *Elodea canadensis* (Michx.), *Ranunculus aquatilis* (L.), *Potamogeton richardsonii* (Benn.) Rydb., and *Stuckenia pectinata* (L.) Boerner. All

species are native to the United States; furthermore, the USDA PLANTS database lists all but *R. aquatilis* as native to New Mexico (USDA, 2016). *Elodea canadensis* and *R. aquatilis* were the dominant species present, while *P. richardsonii* and *S. pectinata* were minor constituents. *Elodea* was the overall dominant species of the biomass gathered over 12 sampling dates. Aboveground biomass was observed to increase in April/May, while senescence generally occurred in September/October.

The study site's elevation (~2600 m) created climatic conditions that resemble higher latitude temperate regions with cold winters and warm summers, and all species present showed a typical seasonally-driven phenology like phenologies observed in temperate regions. Phenology, therefore, was consistent with the phenology of *E. canadensis* that has been described at more northerly latitudes (Nichols and Shaw, 1986; Spicer and Catling, 1988). Initial new growth and emergence began in April/May for all species followed by rapid growth with plant density increasing steadily through late summer. Clear species dominance was observed by July of each year with *E. canadensis* or *R. aquatilis* the dominant species in any given sampling location. Visible senescence started in late September/early October for all species. Peak biomass for all species occurred in August/September in 2012 and 2013 and in October in 2011. Flowering was observed only once in *E. canadensis* in July 2012, while flowering was observed in *R. aquatilis* in July 2011 and June 2013. Flowering was never observed in *P. richardsonii* or *S. pectinata* during the study. Reduced amounts of biomass of *E. canadensis* were observed to overwinter, but aboveground overwintering tissue was not noted for any other taxa.

3.2 Biomass

Total mean biomass estimates ranged from 42.4 g AFDM m⁻² to 234.1 g AFDM m⁻² (Table 1). *Elodea canadensis* accounted for an average of 54% of the total biomass collected over all sampling dates, and *R. aquatilis* accounted for 28%. Peak mean biomass over the three years of sampling measured in October 2011 reached 234.1 g AFDM m⁻² (Table 1). The species with upright growth forms (*E. canadensis*, *S. pectinata*, and *P. richardsonii*) lost more biomass than *R. aquatilis* during the high-turbidity spates in late July to early September of 2011. While the magnitude of gain varied, all four species had large biomass gains between September and October of 2011 averaging 205%.

We were interested in variation in mean biomass among the disturbance categories to test the hypotheses. However, to evaluate effects of disturbance effectively, we also considered other major drivers of biomass including species, season, and habitat type (Table 2). Differences in biomass were substantial, as indicated above, and these differences were statistically significant (Table 2). Mean biomass was marginally higher in pool (46.4 ± 5.6 g AFDM m⁻², means \pm SE) than in riffle/run habitats (17.9 ± 2.2 g AFDM m⁻²; Table 2, $p = 0.096$), driven by differences in species preferences. Significantly more *Elodea* biomass was found in pools (178.0 ± 16.9 g AFDM m⁻²) than riffles/runs (10.5 ± 2.8 g AFDM m⁻²). This outcome is in contrast to the other three taxa where means were much higher in riffles/runs (45.8 ± 7.5 , 5.3 ± 1.4 , and 9.9 ± 2.0 g AFDM m⁻²) versus pools (4.1 ± 3.0 , 0.23 ± 0.17 , and 1.0 ± 0.76 g AFDM m⁻²) for *Ranunculus*, *Potamogeton* and *Stuckenia*, respectively. The species by habitat interaction effect on mean biomass was highly significant ($p < 0.0001$, Table 2).

Mean biomass was slightly higher in the late season (40.6 ± 5.2 g AFDM m^{-2}) than early season (23.7 ± 3.3 g AFDM m^{-2} ; Table 2, $p = .056$).

Mean biomass increased for the four macrophyte taxa in the initial recovery period after the multiple fire-associated flood events in late July to early September of 2011 that brought fire-associated ash into the river and produced very high turbidity (Figure 1). Biomass recovery was different among taxa after the large storm-associated flood event in 2013; only *Ranunculus* increased biomass over its pre-disturbance level after this event, while the other three taxa did not (Figure 1). Both the main effect of disturbance type and the species by disturbance type effects on biomass were statistically significant (Table 2). Despite the differing effects of disturbance types on biomass (Figure 1), no pairwise comparisons among disturbance type groupings (e.g., Undisturbed vs Flood Disturbance, Post-Fire Recovery vs Post-Flood Recovery, etc.) using Tukey's Studentized Range tests showed statistically significant effects on biomass (P-values all > 0.05). The lack of significant pairwise effects of disturbance type on biomass is likely due to the strong interaction effect of disturbance type and species.

3.3 Hydrology and Water Quality Parameters

During the study period, median and mean discharge were 0.07 and 0.11 m^3s^{-1} , respectively. The hydrograph exhibited stable baseflow conditions during most of the study period. The periods of stability were interrupted by occasional increased flows from surface/near-surface runoff from monsoonal thunderstorm events within the catchment or from larger regional storm systems (Figure 2A). When precipitation from monsoonal thunderstorms fell within

the East Fork catchment, increased discharge was measured in late July through early September of 2011 and in August of 2013 (Figure 2A). These spates mobilized ash, charcoal, and sediment within the burn scar areas as seen in the high turbidity values. Discharge measured for the East Fork during the 2012 growing season showed generally stable flows that were weakly influenced by monsoonal events except for one event in July of 2012, unlike the multiple distinct monsoonal flow peaks in 2011 and 2013 (Figure 2A). The largest magnitude discharge peak with an extended period of high flow during the study period was observed in September of 2013. Two dissipating tropical storms—one from the Pacific Ocean and one from the Gulf of Mexico—were drawn northward through New Mexico and into Colorado producing widespread flooding (Trenberth et al., 2015) and a large extended flow event in the East Fork that peaked at an estimated $3.6 \text{ m}^3\text{s}^{-1}$ on 13 September 2013.

Turbidity values ranged from 0 to over 1200 NTU during the study. A reported value of 1200 NTU is the maximum detectable value for the instrument, and values of 1200 NTU are conservative estimates of actual turbidity. Turbidities above 1200 NTU were caused by ash, charcoal, and sediment transport from burn-scar areas to the East Fork (Dahm et al. 2015; Reale et al. 2015; Reale 2018). There were three > 1200 NTU turbidity events in late August and early September of 2011, one event in late July of 2012, and one event in late July of 2013. Events with turbidities ranging from ~ 100 to ~ 400 NTU also occurred multiple times in 2011 and 2013, commonly co-occurring with major ($> 3 \text{ m}^3\text{s}^{-1}$) and smaller ($> 0.5 \text{ m}^3\text{s}^{-1}$ and $< 1.0 \text{ m}^3\text{s}^{-1}$) flood events. The longer-term, much higher discharge magnitude flood event in September of 2013 produced turbidities up to ~ 400 NTU.

DO during the growing season at the East Fork showed strong diurnal fluctuations and large daily amplitudes (Figures 2C and 2D). Strong DO diurnal variability, driven by daily solar cycles combined with a productive biotic community, was observed in DO concentrations both pre- and post-fire during baseflow conditions (Reale et al., 2015). Daily DO amplitudes were as high as 16.2 mg L^{-1} during the growing season from 2011-2013 (Figure 2D). DO sags and decreased daily amplitudes occurred when burn-scar materials from the Las Conchas wildfire were routed through the study site. These sags were generally linked to monsoonal thunderstorms with daily DO amplitudes often $< 3 \text{ mg L}^{-1}$. This DO signal dampening ranged in duration from a single day to several weeks during the high flow event of September 2013 (Figure 2D).

Water temperatures also showed strong diurnal fluctuations throughout the growing season due to strong day to night changes in air temperature. Water temperatures consistently were above 10°C beginning in early to mid-May. Nighttime water temperatures consistently dipped below 10°C in early to mid-October, and daytime temperatures stayed above 10°C until late October, covering most of the growing season (Figure 2E). Ice and snow covered the East Fork from approximately November/December to March/April, paralleling the phenological patterns of the aquatic macrophytes.

4. DISCUSSION

Catastrophic wildfire is increasing in intensity, frequency, duration, and extent (Westerling 2016), and the impacts of these wildfires on aquatic resources is of much interest. Recent review articles on the effects of wildfires on streams and rivers have discussed how wildfire affects sediment transport, nutrient dynamics, riparian zones, aquatic invertebrate communities, and fish communities (Smith et al., 2011; Verkaik et al., 2013; Bixby et al., 2015). Primary producer composition and biomass are other components of stream ecosystems that have not been as well studied with regards to disturbance from wildfires. This study examines the submerged aquatic macrophyte community in a meadow stream impacted by a large and intense wildfire in 2011. Research began on the macrophyte community in the spring before the catastrophic wildfire and continued for three summers after this major disturbance.

4.1 Initial Macrophyte Responses to Wildfire (2011)

Macrophyte sampling began in early June of 2011 before the onset of the Las Conchas fire in late June and included a second sample in mid-July of 2011 during the fire but before the onset of monsoonal precipitation that affected streamflow in the East Fork. The monsoons began in late July of 2011 with multiple flow events from late July through early September (Figure 2A). The loss of plant biomass stemming from these spates in late July through early September reduced total and mean biomass in September 2011 (Table 1), supporting the hypothesis that fire-linked flood events would cause a notable reduction in macrophyte biomass (Figure 1). Mean biomass in September 2011 was lower than in June 2011, resetting biomass present to early season levels and making the rapid recovery of biomass in October

2011 even more notable (Table 1, Figure 1). Post-fire flood events also resulted in significantly larger stream discharge responses in the East Fork than pre-fire responses (Reale et al., 2015; Sherson et al., 2015), and these pulses carried sediment, ash, and charcoal from the burn scars that repeatedly increased turbidity to the maximum measurement capability of our turbidity sensor (Figure 2B). These pulses also decreased DO concentrations (Figure 1C) and DO daily amplitudes (Figure 1D). Sherson et al. (2015) also measured increases in turbidity, specific conductance, nitrogen (as N-NO_3^-), and phosphorus (as P-PO_4^{3-}) and dips in pH and DO in the East Fork during post-fire monsoon events when compared to pre-fire flow events. The response of the aquatic macrophyte community was lost biomass from these spates associated with the summer monsoon in 2011 after the Las Conchas wildfire.

After the cessation of the summer monsoons in early September of 2011 and a period of low flows and low turbidity, notable increases in biomass for all macrophyte taxa were found in mid-October of 2011 (Table 1; Figure 1). Macrophytes can increase the rate of accumulation of fine sediments that can then be used as a nutrient source (Lacoul and Freedman, 2006). Erosion of fire-altered soils containing enriched ammonium (N-NH_4^+), nitrate (N-NO_3^-), and orthophosphate P-PO_4^{3-} (Certini, 2005) increases stream water concentrations of these nutrients (Earl and Blinn, 2003; Stephan et al., 2012; Verkaik et al., 2013). As a byproduct of the Las Conchas fire, large amounts of nutrient-rich sediments and ash were deposited into the East Fork (Orem and Pelletier, 2015), a normally low dissolved nutrient system (Van Horn et al., 2012; Sherson et al., 2015). We observed post-fire sediment depositions in many of the pools along the study reach. Nutrient-rich ash and soil particles from the Las Conchas burn scars were detected in episodic high turbidity measurements (Figure 2B) and likely

deposited into the pools, becoming a nutrient source for rooted submerged macrophytes as they retrieve much of their nutrients from the sediment (Carignan and Kalff, 1980) and sediment composition potentially affects plant growth (Franklin et al., 2008). This nutrient-rich material settled around the plants, creating a fertilization effect that yielded increased macrophyte biomass (Figure 1), including the highest biomass measures recorded during the study period.

4.2 Macrophyte Responses in Years Two and Three after Wildfire (2012 and 2013)

Macrophyte biomass in June of 2012 was less than in June of 2011 for all four taxa and for total biomass (Table 1). Lower biomass persisted in late July, and low flow persisted throughout the growing season (Figure 2A). One small flow event in late July was accompanied by very high turbidity (> 1200 NTU), but the growing season was characterized by a weak monsoon and baseflow conditions. We suggest that the large amount of sediment that was deposited in the study reach and filled in most of the pools acted to reduce early season growth of the submerged aquatic macrophyte community and increased growth in the late summer months. Peak mean biomass was measured in September 2012 and was close to the overall peak biomass measured in October 2011 (227.6 g AFDM m^{-2} versus 234.1 g AFDM m^{-2} ; Table 1). This result suggests a fertilization effect from the deposited sediment, especially when contrasted to the 2013 peak mean biomass that was the lowest peak biomass of the three seasons (Table 1). Sampling in October of 2012 showed a decrease in total biomass and in all four taxa from September as macrophyte senescence was apparent.

The hydrology of 2013 in the East Fork included an active monsoon season and the major flood event in mid-September (Figure 2A). While other flood events during the study period

lasted only one to two days and receded quickly, elevated discharge persisted for approximately two weeks in September of 2013 during a major regional storm event (Trenberth et al., 2015). After the 2013 storm-related flood event, all taxa except *Ranunculus* notably decreased in total and mean biomass, including some to the point of temporary extirpation (Table 1, Figure 1). Drag and stress forces can have drastically different effects on aquatic organisms depending on the plant's placement in the water column and relative distance to the benthos (Koehl, 1984). Because *E. canadensis*, *S. pectinata*, and *P. richardsonii* grow upright and are higher in the water column, these populations are more likely to break and be damaged from increases in discharge, discharge-associated increases in velocity, and higher concentrations of particulate matter that moved through the system. In contrast, the more prostrate *R. aquatilis* stays firmly attached to the benthos at multiple points along the stem, reducing possible mechanical damage during the post-fire spates and large flood events. The extended September 2013 flood event also affected functional components of the stream for about three weeks as indicated by DO concentrations and daily DO amplitudes (Figures 2C and 2D). Diurnal DO amplitudes were reduced, suggesting lower in-stream primary production (Figure 2C). In addition, DO amplitudes did not recover post-flood in the way diurnal DO concentrations did after shorter duration spates (Figure 1D), again suggesting reduced rates of instream primary production. Modeling of instream gross primary production (GPP) using measured DO values in the East Fork from 2008-2016 (Reale 2018) suggested that nutrient enrichment from fire-linked deposits ceased after the 2013 growing season in the East Fork as daily GPP rates moved back to typical pre-fire rates after higher values in the growing seasons of 2012 and 2013.

4.3 Conclusions

This study was originally intended to assess the composition, phenology, and standing biomass of submerged macrophytes in a high elevation caldera meadow stream where aquatic plants were thought to be a major driver of aquatic primary production. Shortly after beginning the study in 2011, a large catastrophic wildfire burned 36% of the stream catchment, presenting an opportunity to investigate the effects of fire on submerged macrophytes. We hypothesized that this high-intensity wildfire would reduce aquatic plant biomass when summer monsoonal thunderstorms would deliver both burn-scar materials and higher instream flows. Biomass reduction was measured in early fall of 2011 immediately after the wildfire and a series of spates produced by summer thunderstorms. However, biomass strongly rebounded in mid-October of 2011 after the deposition of burn scar materials in the study reach, and macrophyte biomass reached the highest levels measured during the three years of this study. We hypothesized that this strong late season growth response was a fertilization response to nutrient-rich ash and sediment delivery to the stream ecosystem the first few months after the fire. The largest storm during the three years of study occurred in September of 2013, and the high flows reduced macrophyte biomass; post-flood measurements, however, did not show substantial short-term biomass accrual, unlike in October 2011. This study shows that wildfires can impact submerged macrophyte biomass both positively and negatively well after the wildfire is over, and responses depend on the interactions of multiple factors including aquatic plant biomass and taxa, stream hydrology, catchment geomorphology, and water quality.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge Robert Parmenter, Scott Compton, and Kate Condon of the Valles Caldera National Preserve and current and former members of the HydroGeoEcology group at the University of New Mexico including Betsy Summers, Lauren Sherson, Tyler Van Riper, Laura Crossey, Becky Bixby, David Van Horn, Jim Thibault, Alex Clark, Eddie O'Brien, Chelsea Reale and John Craig. Our deepest appreciation goes to L.D. Beene, who was invaluable in the development and execution of this manuscript. The National Science Foundation provided support for this project to the Catalina-Jemez Critical Zone Observatory (grant numbers EAR-0724958 and EAR-1331408), the New Mexico Experimental Program to Stimulate Competitive Research (EPSCoR) RII Track I Project (award 0814449), and the Sevilleta Long Term Ecological Research (LTER) Program (award DEB 0620482). V.F. Thompson was also supported by the New Mexico Water Resources Research Institute (WRRI) Student Research Grant and the University of New Mexico College of Arts and Sciences Dissertation Completion Award.

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TABLES

Table 1. Mean biomass in grams ash-free dry mass per meter squared (g AFDM m⁻²) and standard error for each species found at the East Fork study site during the 2011-2013 growing seasons (n = 648).

	2 Jun	15 Jul	5 Sep	13 Oct	11 Jun	25 Jul	9 Sep	11 Oct	14 Apr	27 Jun	6 Aug	20 Oct
	2011	2011	2011	2011	2012	2012	2012	2012	2013	2013	2013	2013
<i>Elodea</i>	85.9 ±	128.5 ±	67.1 ±	156.7 ±	39.2 ±	31 ±	136 ±	133.7±	50.3 ±	109.3 ±	144.1 ±	62.5 ±
<i>canadensis</i>	38.0	38.9	24.8	58.6	14.0	10.1	38.9	50.7	18.1	28.5	46.7	20.4
<i>Ranunculus</i>	36.9 ±	12.3 ±	14.5 ±	62.9 ±	1.5 ±	4.7 ±	70.7 ±	37.4 ±	5.4 ± 3.3	22.6 ±	7.4 ±	11.9 ±
<i>aquatilis</i>	15.8	9.3	8.2	23.4	1.2	2.7	30.0	18.7		8.9	3.4	8.0
<i>Potamogeton</i>	3.6 ±	2.9 ±	5.0 ±	5.4 ±	1.0 ±	1.7 ±	7.1 ± 5.3	2.7 ±	0	3.6 ±	0.04 ±	0
<i>richardsonii</i>	2.4	2.0	3.0	4.8	0.5	1.4		1.7		1.9	0.04	
<i>Stuckenia</i>	7.3 ±	11.9 ±	2.1 ±	9.1 ±	0.7 ±	5.9 ±	13.8 ±	7.6 ±	0	0.4 ±	6.4 ±	0
<i>pectinata</i>	4.6	8.0	1.4	5.3	0.5	3.2	5.6	2.6		0.4	2.9	
Total	133.7 ±	155.6 ±	88.7 ±	234.1 ±	42.4 ±	43.3 ±	227.6 ±	181.4 ±	55.7 ±	135.9 ±	158 ±	74.4 ±
	30.2	33.9	19.6	44.4	14.5	8.4	43.2	55.6	20.4	25.5	33.4	19.5

Table 2. Generalized linear model to explain variation in biomass of aquatic macrophytes among species, seasons, habitats and disturbances types. For the overall model, $N = 835$, $F_{31,835} = 23.31$, $P < 0.001$ and $R^2 = 0.46$. Results in the table are based on Type III sums of squares.

Independent variable	df	Type III sums of squares	f-value	P value
Species	3	2153.1	25.63	<0.0001
Season	1	844.9	30.17	<0.0001
Habitat	1	77.7	2.77	0.096
Disturbance Type	4	872.6	7.79	<0.0001
Species*Season	3	212.6	2.53	0.056
Species*Habitat	3	10286.9	122.43	<0.0001
Species*Disturbance Type	12	670.3	1.99	0.022
Habitat*Disturbance Type	4	230.8	2.06	0.084

FIGURES

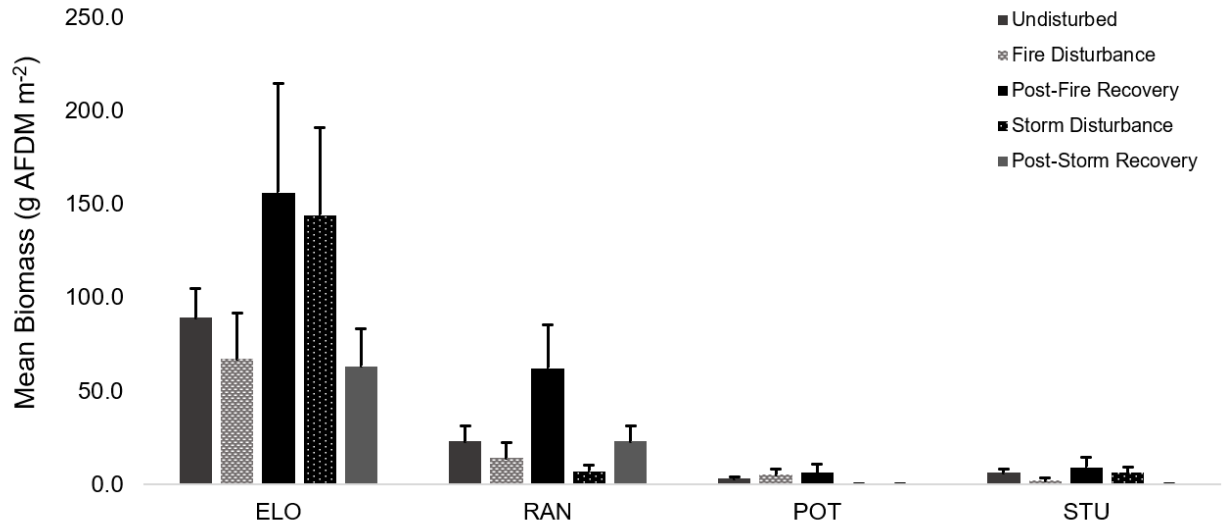


Figure 1: Calculated means of biomass data in g AFDM m⁻² for *Elodea canadensis* (ELO), *Ranunculus aquatilis* (RAN), *Potamogeton richardsonii* (POT), and *Stuckenia pectinata* (STU). Variables are designated based on the timing and type of disturbance that occurred and are broken into three major time periods: undisturbed, affected by the disturbance, and immediate recovery.

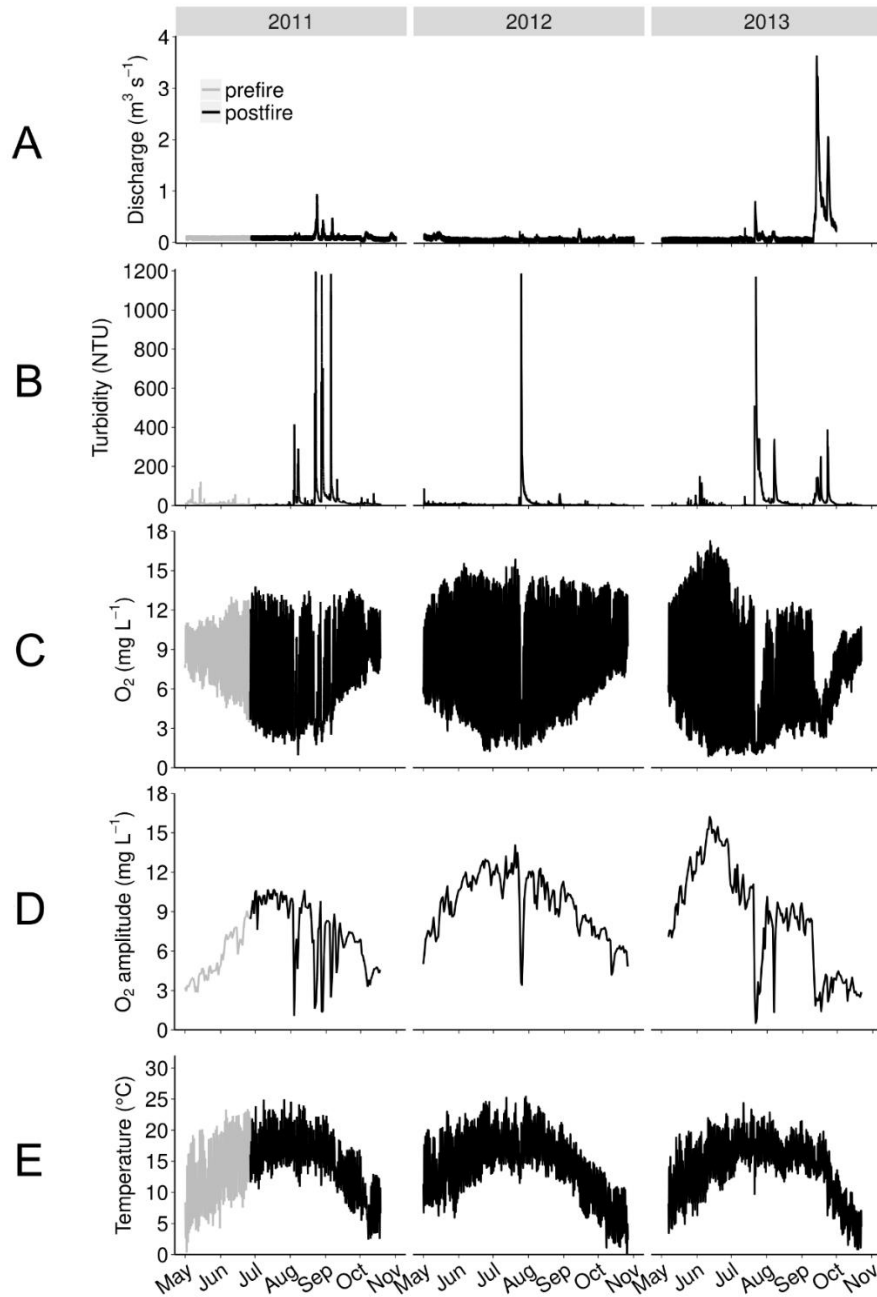


Figure 2: (A) Stream discharge ($\text{m}^3 \text{s}^{-1}$), (B) turbidity (NTU) (C) dissolved oxygen (mg L^{-1}), (D) daily amplitude of dissolved oxygen (mg L^{-1}) and (E) stream temperature ($^{\circ}\text{C}$) measured in 15-minute increments during much of the growing season (May to November) at the East Fork for 2011-2013.

CHAPTER 3

DISTURBANCE, FIRE, AND SUBMERGED AQUATIC MACROPHYTES: ARE CHANGES TO KEY NUTRIENTS LURKING BELOW THE SURFACE?

Virginia F. Thompson, Diane L. Marshall, Rebecca J. Bixby, and Clifford N. Dahm

ABSTRACT

Disturbance events in lotic ecosystems can stem from overland flows that transport soils into aquatic ecosystems and temporarily boost nutrient availability. Wildfires are disturbance events that increase stocks of nutrients, including nitrogen and phosphorus in soils and stream and river networks. Submerged aquatic macrophytes (SAMs) are aquatic primary producers that uptake nitrogen and phosphorus and convert these nutrients to biomass. Our objectives were to determine if temporary increases of key nutrients following catastrophic wildfire would be absorbed by these aquatic plants and reflected in their tissues. We collected SAM tissues from a high elevation stream site in northern New Mexico, USA in 2011, 2012 and 2013 growing seasons before and immediately after a catastrophic forest fire and analyzed the tissue content of %C, %N, and %P to determine whether these disturbance events alter tissue nutrient content of key nutrients. We also collected tissues before and after a decadal flood two years after the catastrophic forest fire at the same site to see if there was

a similar alteration in plant nutrient content and calculated stoichiometric ratios from these samples. %P tissue content significantly increased in post-fire macrophyte tissues while %N had a measurable but not significant increase. C:P and N:P ratios decreased after both disturbance events. %N, %P, C:P and N:P returned to baseline levels the next growing season after the wildfire. We also found that mean macrophyte tissue %N and %P contents increased and C:P and N:P decreased after a large flood that mobilized soils into the stream channel, but to a lesser extent than directly after the wildfire.

INTRODUCTION

Nitrogen (N) and phosphorus (P) are essential nutrients for all living organisms on Earth, including primary producers such as vascular plants. However, the majority of the world's terrestrial and aquatic ecosystems are often deficient in one or both of those essential nutrients. Numerous studies have shown that both N and P can be limiting in freshwater systems (Elser et al., 2007), which can cause growth limitations for organisms such as primary producers and decomposers. However, it has also been shown that macrophytes can accumulate these nutrients during times of abundance (Demars and Edwards 2007).

Nutrient stoichiometry, a field originated by Redfield in 1934, examines the relative abundances of key nutrients in organisms and the proportions required in the environment for

success of the organism. Ecological stoichiometry uses the measures and ratios of key nutrients (most commonly carbon (C), nitrogen (N) and phosphorus (P)) to assess the interweaving of energy movement through both organisms and their environment, allowing for comparison across different biomes and organism types (Elser et al. 2000). Imbalances or limitations in key elements in organisms can cause physiological changes that can alter function in an individual but also can also have a broader effect on populations and communities in a given system (Moe et. al. 2005). Stoichiometry is variable based on the organism, but aquatic primary producers are much more nutrient constrained than terrestrial primary producers (Elser et al. 2000). These concentrations and their proportions in primary producers impact many physiological processes, including the allocation of resources to build key structures (Abbas et al. 2013) metabolic pathways, including those of secondary compounds, changing their palatability to consumers (Dorenbosch and Bakker, 2011). Nutrient content and stoichiometry in macrophytes can also change based on environmental factors such as carbon availability (Velthuis et al. 2017) and water depth (Li et al. 2013).

Lotic ecosystems transport important nutrients downstream (Cole et al., 2007), both dissolved in the water and suspended in organic matter in the water column. Organic matter and nutrients are introduced into the system from outside the ecosystem (allochthonous) and inside the ecosystem (autochthonous) (Raymond and Bauer, 2001) with overland flows being an important source of allochthonous input. Downstream transport of organic matter and nutrients can be facilitated by the movement of the water itself, sediment absorption and adsorption, and capture of these nutrients in stream by primary producers. Primary producers convert nutrients such as nitrogen and phosphorus into organic forms that are incorporated

into food webs through direct and indirect consumption, but these nutrients can also be transported downstream in lotic systems through a combination of streamflow and breakage derived from mechanical disturbance (streamflow or biologically mediated) and/or seasonal senescence.

Submerged aquatic macrophytes (SAMs) are primary producers that spend their complete life cycle underwater. Where present, they can have a greater impact on aquatic ecosystems than other classes of macrophytes because of their extensive interaction with the water column. While not a universal component of aquatic ecosystems, they can be an ecosystem engineer where prominent (Jones 1994), having extensive effects on ecosystem structure and function through physical alteration of hydrologic and geomorphologic conditions when present in abundance in aquatic ecosystems. These macrophytes may also improve water quality, provide food and refugia, and both retain and facilitate nutrient cycling in these systems. SAMs can modify abiotic and biotic factors in the surrounding aquatic ecosystem in capacities ranging from geomorphological changes in rivers and streams (O'Briain et al., 2017) to mediating the presence or absence of species in complex food webs (Diehl and Kornijow, 1998). SAMs also have the ability, unlike emergent macrophytes and terrestrial plants, to source some or all vital nutrients (e.g., carbon, nitrogen, phosphorus) directly from the water column through their leaves and shoots. Depending on the species and conditions, SAMs can utilize water column bicarbonate (HCO_3^-) as an inorganic carbon source (Allen and Spence 1981; Cavalli et al. 2012) and both ammonium (NH_4^+) and nitrate (NO_3^-) as nitrogen sources (Madsen and Cedergreen, 2002). Although debate still remains on specific proportions of nitrogen and phosphorus sourced from either the sediments or water column

(Carignan and Kalff 1980; Chambers et al. 1989), most researchers accept that SAMs are able to acquire nutrients from the water column.

Disturbance regimes in aquatic ecosystems are driving influences on their structure and function (Resh et al. 1988, Minshall et al. 1989, Dwire and Kauffmann 2003). For example, forest fires often create a variety of disturbances to the ecosystems within the burned watersheds. Forest fires have been documented to have negative impacts on surface water systems, especially on sediment inputs and water quality (Hauer and Spencer 1998, Earl and Blinn 2003, Smith et al. 2011, Stephan et al. 2012). Fire-induced changes in water quality, such as increased turbidity, decreased dissolved oxygen, increased organic contaminants, increased trace metals, and increased nutrients, can have significant and far-reaching effects on both the stream reaches that were burned and areas many kilometers downstream from the fire. This can include urban areas far from the forested watershed (Dahm et al. 2015, Reale et al. 2015). These effects from wildfires on stream ecosystems occur when precipitation events mobilize ash, charcoal, soil, and solutes (Gresswell 1999; Verkaik et al. 2013), transporting these materials into stream ecosystems.

Disturbances from catastrophic wildfires have increased in frequency and intensity, especially in the western United States (Westerling et al. 2006, Vose et al. 2012, Luo et al. 2013). These disturbances have greatly increased both direct and indirect effects on stream ecosystems including increased flooding, erosion, and altered hydrologic regimes (Vose et al. 2012). Erosive processes are a common source of nutrient introduction in lotic ecosystems,

especially in areas prone to high intensity storms that mobilize large amounts of sediment into stream and river channels. Monsoon-prone regions like the southwestern US tend to get high-intensity, short duration rainfall during the summer (Neary et al. 2003, Verkaik et al. 2013) that can boost peak flows up to 400x from severely burned catchments in the southwest (Neary et al. 2003). Fires have been found to dramatically increase the availability of ammonium (NH_4^+) and nitrate (NO_3^-) in soils (Certini 2005) and burning also converts organic P into PO_4^{3-} in soils (Certini 2005). Erosion of these fire-transformed soils into aquatic ecosystems increases the stream water concentration of these nutrients (Earl and Blinn 2003, Stephan et al. 2012, Verkaik et al. 2013).

Short-term pulse disturbances such as fire inputs and flooding from precipitation events have potential long-term effects on both stream ecosystems and their biota. SAM populations have been shown to be altered by flow conditions depending on stream velocity and taxa during floods (Wang et al. 2015). Floods and accompanying scour can reduce standing biomass of SAMs in an initial pulse (Henry et al. 1996; Townsend et al. 2017). However, after the return of normal flow conditions following a flood, SAMs often quickly reestablish to post-flood biomass levels (Sousa et al. 2010). Fire effects have been documented for both wetland (Osborne et al. 2013) and riparian plant communities (Bixby et al. 2015), but little is known about the effects of catastrophic wildfire on SAMs. Thompson et al. (2019) found that SAMs increased in biomass a few months after a catastrophic wildfire in the catchment. A hypothesized mechanism for this response was that this increase in biomass was due to the temporary increase of available nutrients that were introduced after ash-related materials were deposited into the river by overland flows driven by seasonal monsoon precipitation

events (Sherson et al. 2015). Our objective is to investigate changes to key nutrients in SAM tissues after major disturbances (fire and flood) by posing the following questions:

Question 1: How was the percent nitrogen (%N) and percent phosphorus (%P) content in SAM tissues different immediately after a catastrophic fire compared to the nutrient content of pre-fire SAM tissues?

Question 2: Did nutrient content of SAM tissues respond to a decadal large-scale multi-day flood two years after the wildfire?

Question 3: Did the type of disturbance (fire versus flood) alter nutrient content and stoichiometric ratios in SAM tissues compared to tissue nutrient content during baseflow conditions?

METHODS AND MATERIALS

Study Site and Disturbance Events

The East Fork Jemez River (East Fork) originates in the Valle Grande, a large grassland meadow located at approximately 2600 m elevation in the largest of the valleys within the 1.25 Ma year-old Valles Caldera in the Jemez Mountains of northern New Mexico, USA (Goff et al. 2006). The Valle Grande is mostly surrounded by mixed conifer forests (Muldavin and Tonne, 2003) that reach up to 3,400 m in elevation. The area is seasonally (October-April) snow-covered, and the annual mean precipitation is 475 mm, approximately half of which comes from precipitation inputs from the North American monsoon that fall

from July to early September while the other half comes from winter snows (Bowen, 1996). The East Fork is a high elevation, low gradient, high-light intensity, low nutrient, perennial headwater river ecosystem where SAMs proliferate between May and October. Samples were collected from an approximately 300 m stretch of meandering stream inside an ungulate grazing exclosure established in 2004 (Van Horn et al. 2012, Sherson et al., 2015). The East Fork lies in a large grassland valley of the caldera (Valle Grande), providing a combination of lower elevation stream habitat elements within a higher elevation environment.

In 2011, the largest recorded wildfire in New Mexico up until that time, the Las Conchas fire, burned for nearly six weeks (26 June 2011 to 3 August 2011) and involved over 63,000 hectares of coniferous forests and high elevation grasslands in northern New Mexico. Nearly 36% of the East Fork's catchment was burned during the Las Conchas fire (Dahm et al., 2015). Almost 50% of the land burned in the Las Conchas fire was burned either moderately or severely, including 100% vegetation mortality in the severely burned areas.

Approximately 9700 hectares near and within the Valles Caldera's boundaries and 36% of the East Fork's headwater catchment were burned (Reale et al., 2015). Burn scars produce fire-transformed soils that often find their way into streams and rivers. Pelletier and Orem (2014) documented post-fire elevated overland flow, rill formation, erosion and deposition, channel incision and avulsion, infilling of incised channels, and debris flows in the Valles Caldera's watersheds after the Las Conchas fire.

Multiple fire-associated flood events occurred in late July to early September of 2011 that deposited fire-associated ash and debris into the East Fork that both increased and decreased

SAM biomass and in September 2013, a large precipitation event occurred within the East Fork watershed (Thompson et al. 2019). Two dissipating tropical storms—one from the Pacific Ocean and one from the Gulf of Mexico—were drawn northward through New Mexico and into Colorado producing widespread flooding (Trenberth et al., 2015). A precipitation gage close to the East Fork’s study site captured 8.6 cm of rainfall on 12-13 September 2013, nearly half (3.9 cm) of which fell in the first 24 hours (WRCC 2018). This large regional system from multiple dissipating tropical storms resulted in a long-duration flood with a peak discharge of $\sim 3.6 \text{ m}^3/\text{sec}$, up to two orders of magnitude higher than the average baseline streamflow found in the East Fork (Thompson et al. 2019) that included overland flows.

Tissue sampling, percent carbon (%C), nitrogen (%N) and phosphorus (%P) measurements

Thompson et al. (2019) sampled six locations along the East Fork with three transects across the width of the stream at each location. Sampling occurred during the 2011-2013 growing seasons. Samples were collected approximately every six weeks during each growing season (April-October) to reduce possible cumulative impacts from sampling. Three samples were taken from each transect across the stream, one from the center and the other two taken approximately 30 cm inward from each bank for a total of 54 samples taken on each sampling date. Not all sampling locations had macrophytes present. A sampling device for collecting all aboveground plant tissues in a known surface area was constructed for shallow flowing water use based on the design of Marshall and Lee (1994). The sampling device consisted of a circular metal tube 80 cm in height and 7 cm in diameter with a sampling area

of 40 cm² and multiple one cm drainage holes along the tube. The tube was pressed flat against the benthos and a sharpened metal cutting device was used to cut all aboveground biomass within the tube at the stream bed with the cutting device covering the bottom of the tube while the sample was raised to the surface. Samples were preserved on ice and transported to the BioAnnex Analytical Laboratories at the University of New Mexico, Albuquerque, NM, USA, for analysis. In the lab, the plant tissue materials for each sample were manually separated by SAM taxon. Each separated sample was then sonicated in an ultrasonic water bath filled with deionized water for at least 10 minutes to remove epiphytic organisms.

Subsamples were placed in a drying oven at 60°C for 48 hours and stored in sealed 1 dram glass vials. Samples were then placed in a 49mL sapphire mortar and approximately 5-10mL of liquid nitrogen was applied to the sample and allowed to boil off. Samples were hand-ground into a fine powder using a sapphire pestle and returned to the 1-dram vials for storage. The finely ground samples (20-25 mg) were packed in aluminum foil for high temperature combustion and gas chromatography using a ThermoQuest Carlo Erba Instrument NC2100 Elemental Analyzer (CARLO ERBA, Cornaredo, Italy) to determine percent carbon (%C) and percent nitrogen (%N) of the given sample of plant tissues by weight. Percent phosphorous (%P) content by weight of plant tissues was determined by combustion of samples and acid dissolution following methods of Stelzer and Lamberti (2001). Dissolved phosphate content analysis was conducted using a Technicon AutoAnalyzer II (Technicon Corporation, Oakland, California). Molar mass of each element (C, N, P) in the given sample was then calculated using the calculated percent content of the

analyzed sample, mass of the sample and atomic mass of the element in g/mol for stoichiometric analysis.

Water Quality Measurements

Water quality measurements were collected continuously from May to October in 2011, 2012 and 2013. Dissolved oxygen (DO) (mg/L), pH, temperature (°C), specific conductance ($\mu\text{s}/\text{cm}$) and turbidity (NTU) were collected at 15-minute intervals within the enclosure using a YSI 6920 multi-parameter sonde (YSI Inc., Yellow Springs, OH, USA). Estimated stream discharge (m^3/sec) for the East Fork was calculated from a streamflow station located < 1 km downstream from the sampling area. The station consisted of a pressure transducer (HOBO 30-foot depth water level data logger; Onset Computer Corporation, Bourne, MA, USA) that collected data at 10- to 30-minute increments in the bottom of a stilling well to determine water levels; these levels were corrected for barometric pressure and temperature. Water column nitrogen (as $\text{NO}_3\text{-N}$) was measured using a Satlantic V1 submersible ultraviolet nitrate analyzer (SUNA) (Satlantic, Cesena, Italy). Measurements were taken at 30-min intervals. Water column phosphorus (as $\text{PO}_4\text{-P}$) was measured using a WETLabs Cycle- PO_4 dissolved phosphate analyzer at 1-hour intervals (WETLabs, Surrey, UK). Additionally, data used for estimates of gross primary production (GPP) in the East Fork were collected from 2008 to 2016 as described in Reale et al. (2018).

Supplemental Data

As the other datasets were collected on different temporal scales than the macrophyte data, harmonizing datasets was a necessary analytical step. Biological collections were snapshots

in time representing measures limited to a single day on twelve different sampling days. Water quality parameters were collected at a higher frequency (ranging from dozens to hundreds of measurements per day), but varied based on the instrumentation used to collect the data. Water quality data were collected from May to October, 2011-2013 (Sherson et al. 2015 and Dahm et al. 2015). Suspect water quality data were flagged and possible cause was noted (i.e., instrument fouling, exposure to air, burial, probe and/or wiper malfunction, low voltage, reagent deterioration). Data were corrected for fouling drift and calibration drift, and data that could not be corrected were removed from the record. In order to harmonize data sets to the greatest extent, repeated measurements of supplemental data were reduced to a daily mean value. GPP estimates from Reale et al. (2018) were converted to a mean value per day. SAM biomass data from Thompson et al. (2019) did not require adjustment. For datasets with mean daily values, data were taken from the 7 days preceding the date of sampling, the day that biological samples were taken, and the 7 days following the date of sampling for a total of up to 15 daily means associated with each biological sampling date.

Data were then grouped into disturbance groups (pre- and post-fire and pre- and post-flood) based on dates sampled by Thompson et al. (2019). Data were grouped based on flood events that exceeded baseline flows in the East Fork in mid-August 2011 (post-fire) and mid-September 2013 (post-flood), respectively. Pre-fire measurements were grouped from June and July 2011, while post-fire measurements were grouped from August and September of 2011. Pre-flood measures were designated as all data points from beginning of the 2012 growing season through all collections through the 2013 flood event. Post-flood samples were collected in late September and mid-October 2013.

Statistical Methods

To test for differences in mean nutrient percentages (%C, %N, and %P) and stoichiometric ratios (C:N, C:P, N:P) in the SAM tissues pre-fire, post-fire, pre-flood and post-flood, all data were first arcsine square root transformed and then tested with General Linear Models (GLMs) and post-hoc Tukey's HSD comparisons ($P < 0.05$) using SPSS 25 (IBM 2017). All stoichiometric ratios were calculated using the molar mass of each element in the sample and then tested with GLMs. Nutrient percentages (%C, %N and %P) were arcsine square root transformed and then compared among disturbance groups and among species within and between disturbance groups using a two-way analysis of variance (ANOVA) and post-hoc Tukey's HSD comparisons ($\alpha = 0.05$). C:N, C:P and N:P ratios were also compared among groups using a two-way ANOVA as described previously. Pearson's Correlations were used to examine relationships between the SAM tissue data (%C, %N, %P, C:N, C:P and N:P) and other available datasets (temperature, specific conductance, pH, turbidity, estimated discharge, dissolved oxygen, $\text{NO}_3\text{-N}$, $\text{PO}_4\text{-P}$, GPP estimates, and SAM biomass) and were calculated in SPSS 25 (IBM 2017).

To investigate combinations of abiotic factors and biological factors that were related to environmental conditions at different times in the season, we used our data and other available data (see Supplemental Data) to conduct Principal Component Analyses (PCA) using PC-ORD (McCune and Mefford, 2011). Biological factors that were analyzed in one PCA included mean % carbon, nitrogen and phosphorus (mean % C, N and P) and ratios of these nutrients (C:N, C:P, N:P). Abiotic factors that had sufficient data available were analyzed in a second PCA that included temperature, specific conductance, pH, turbidity,

estimated discharge, and dissolved oxygen contents. GLMs were run on the first two axes from each PCA to determine if there were significant differences between each disturbance group within these new variables.

RESULTS

Submerged macrophyte taxa collected and processed for nutrient composition testing were *Elodea canadensis* (Michx.), *Ranunculus aquatilis* (L.), *Potamogeton richardsonii* (Benn.) Rydb., and *Stuckenia pectinata* (L.) Boerner. *Elodea canadensis* and *R. aquatilis* were the dominant species present, while *P. richardsonii* and *S. pectinata* were minor constituents. *Elodea* was the overall dominant species of the biomass gathered over the sampling dates, and 90% of the samples processed were either *E. canadensis* or *R. aquatilis*.

Mean SAM tissue %C content declined from 41.5% to 39.3% post-fire but increased from 40.0% to 42.3% post-flood (Figure 1). Overall, mean %C values only varied by 3% among all pre-/post- event groups at any time, and these differences were not significantly different (Table 1). In comparison, mean tissue %N content increased from 2.2 % pre-fire to 2.7 % post-fire, and from 2.0 % pre-flood to 2.2% post-flood (Figure 1). These changes represented a net increase of 11% in mean tissue %N content between pre- and post-fire contents, as well as a net 4% increase in percent nitrogen content between pre- and post-flood conditions. However, these differences only approached significance (Table 1). Finally, SAM tissue % P content increased from 0.22% pre-fire to 0.33% post-fire, and from 0.22% pre-flood to 0.24% post-flood (Figure 1, Table 2). The overall differences in mean %P were statistically

significant among disturbance periods (Table 1). Mean tissue % P content had a net increase of 22% between pre- and post-fire measures and 4% between pre- and post-flood measures (Figure 1).

N:P stoichiometry decreased before and after disturbance events (Table 2). N:P ratios decreased after disturbance, moving from 14 pre-fire to 11 post-fire and 15 pre-flood to 9 post-flood (Table 2), with an overall significant difference ($P < 0.0001$). Post-hoc comparisons (Tukey's HSD) only showed significant differences between and Pre-and Post-Flood ($P < 0.0001$) while Pre- vs Post-Fire only approached significance ($P = 0.09$).

To investigate whether nutrient content and nutrient stoichiometry responded differently to disturbance among species, we compared responses in the two most common species *E. canadensis* and *R. aquatilis*. % P in *E. canadensis* tissue tended to increase after both fire and flood and there were accompanying decreases in C:P and N:P (Table 3). In contrast, %P in *R. aquatilis* tissue tended to decrease after the *fire* and increase after the flood (Table 4). Two-way ANOVA analyses of percent nutrient content and stoichiometric ratios comparing response to disturbance by species had differing results. All content measures (%C, %N, %P) were statistically significant while none of the stoichiometric ratios were significant when species and disturbance were both considered (Table 5).

Elodea only had statistically significant differences in %P ($P < 0.0001$) and N:P ($P = 0.04$), when evaluated by GLM. Pre-/post- disturbance event post-hoc comparisons for %P in *Elodea* were statistically significant; pre-fire vs post-fire ($P < 0.0001$) and pre-flood vs post-flood ($P = 0.03$). However, no pairwise comparisons in N:P ratios when evaluated by Tukey's HSD yielded a statistically significant difference and only pre-flood vs post-flood even approached significance ($P = 0.07$). There was an overall significant difference in the mean N:P ratio of *Ranunculus* ($P = 0.02$), however, only pre-flood vs post-flood means showed a significant difference in post-hoc analysis ($P = 0.03$).

Pearson's correlations indicated multiple statistically significant positive and negative correlations between nutrient and supplemental datasets (Table 6). Tissue %N and %P were positively correlated while C:P and N:P ratios were strongly negatively correlated with increases in tissue %P as expected. Increases in tissue %C, %N and %P were all positively correlated with estimated discharge. Increases in water column $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ were strongly positively correlated with turbidity indicating overland flow as sources of N and P entering the stream. Increases in biomass were strongly correlated with increases in tissue %P and increases in water column $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ contents (Table 6).

Because the biotic variables correlated with each other and the abiotic variables are also intercorrelated, a multivariate analysis was used to give a clearer picture of patterns before and after disturbances. A PCA examining patterns of association with abiotic variables (including only those variables that had robust enough data for the periods when plants were

sampled) based on disturbance timeframes showed clustering of pre-(fire/flood) data as well as clustering of post-(fire/flood) data. Principal Components 1 and 2 accounted for 77.2% of the variance in the data with Principal Component 1 associated with dissolved oxygen, pH, specific conductance, and turbidity while Principal Component 2 was associated with temperature and estimated discharge, (Figure 2). Additionally, a PCA of the biotic variables which in total explained 76.4% of the variance in data showed a distinct shift in post-fire and flood data, driven strongly by increases in tissue % P in Principal Component 1 and tissue % N in Principal Component 2, (Figure 3). However, the pattern in the biotic data was not as clear as in the abiotic data. The overall differences in means across disturbance types for each of the principal components were significant for both the abiotic and biotic variables (Table 7). Post-hoc analysis (Tukey's HSD) showed significant differences ($P < 0.001$) before and after each disturbance event (fire/flood) for Principal Component 1 for both the abiotic (Figure 2) and biotic (Figure 3) PCAs.

DISCUSSION

We asked if the nutrient (%N and %P) content of SAM tissues increased in tandem with the macrophyte biomass after disturbance events as we previously found a steep increase in SAM biomass after fire-related flood events in July and August of 2011 (Thompson et al. 2019). We hypothesized that this increase was due either to the input of nutrient-rich ash and soils into the stream channel or the dissolution of nutrients from the ash as water was transported to the channel. We found changes in the mean SAM tissue concentration of P and

N post-fire with the largest changes in mean tissue nutrient concentrations in mean %P. In fact, there were significant differences in %P content found in SAM tissues after both types of disturbances in the East Fork— fire and flood. While there was a notable increase in mean %N in tissues, these increases approached significance but did not reach significance. Meanwhile, mean percentage of P in post-fire SAM tissues had a net increase of 22% post-fire compared to pre-fire concentrations (Figure 1). We also found a net 11% increase in mean %N in these post-fire tissues, but this change in concentration was not statistically significant but did approach significance (Table 1).

We also found statistically significant changes in phosphorous concentrations in SAM tissues after a major disturbance caused by a large multi-day flood. The post-flood net increase in mean %N was 4%, from 2.0% to 2.2%, a notable but not statistically significant change (Figure 1). Changes to % P in these post-flood tissues were a net gain of 4%. This was a statistically significant difference. Both the increased and baseline levels of %N and %P that we measured are within the range of measured %N and %P content of freshwater angiosperms as reported by Duarte (1992).

N:P stoichiometric ratios can be used as a tool to understand nutrient limitation in macrophytes and other organisms, which can, in turn change everything from physiological functions to reproductive ability (Frost et al. 2005) N:P ratios > 16 in plants are evidence of P limitations, while an N:P of < 14 is indicative of N limitation; N and P are co- or alternately limiting at an N:P between 14 and 16 (Koerselman and Meuleman 1996). Pre-fire

and pre-flood values were 14 and 15, respectively, solidly in the range where both N and P can be co-limiting nutrients. The East Fork is a low nutrient system during base flows (Van Horn et al. 2012), which could create a limitation of N or P for SAMs during these conditions. However, we found decreases in the N:P ratio after both the fire and large flood events (Table 2) that were well below the threshold of 14, indicating a shift to nitrogen limitation in SAM tissues after these events. Van Horn et al. (2012) found that nutrient inputs from soils were not a significant contributor to nutrient content in the East Fork except during monsoons and snowmelt. Therefore, we hypothesize that the overland flows that occurred after the fire and during the flood event acted as nutrient sources to stream biota in a system that is normally limiting in one or both of these key nutrients. These inputs are reflected in changes in both reduction of the N:P ratio and increase in the %P found in SAM tissues after these events. C:P ratios also followed a similar pattern of reduction after these disturbance events (Table 2), further supporting an input of P that temporarily increased P content in SAM tissues and made P not the limiting nutrient at that time. These ratios can greatly vary by taxa (Demars and Edwards 2007) but %P was found to be fairly conserved between all taxa (Gusewell and Koerselman 2002).

Nutrient content and stoichiometry differed by taxon, as is widely accepted as a fundamental part of ecological stoichiometry (Moe et al. 2005). Two taxa found at the site, *Potamogeton richardsonii* and *Stuckenia pectinata*, did not have samples from each time period (pre-/post-fire or flood) and could not be analyzed. The two dominant species, *Elodea canadensis* and *Ranunculus aquatilis* had a sufficient number of samples during each time period to allow for analysis. *Elodea* showed increased %P content after disturbance events (Table 3), while

Ranunculus showed a slight decrease in %P after fire and an increase after the flood (Table 4). %N was more variable in both taxa, increasing in *Elodea* after the fire (Table 3) and holding steady in *Ranunculus* (Table 4), however, both showed decreased N content after the flood. Stoichiometry varied between both taxa, with *Elodea* staying fairly stable in mean C:N (Table 3) while *Ranunculus* was highest before the fire and after the flood (Table 4). Both taxa showed reductions in C:P and N:P of a similar magnitude after the flood and the fire as compared to pre-disturbance stoichiometric measures (Tables 3 and 4). Two-way ANOVAs showed significant differences only in percent content and not by taxa when considering species and disturbance together (Table 5), which mirrors significant differences in these values when GLMs were applied to the data. Not surprisingly, the patterns for individual species had less statistical support than the patterns in the lumped data due to small sample sizes and high variability in the samples throughout both the nutrient content and stoichiometry measures.

These increases in tissue nutrient concentration and reduction in N:P and C:P stoichiometric ratios when all taxa are pooled parallel the spike in SAM biomass observed by Thompson et al. (2019) over the same period. Increases in mean turbidity, mean estimated discharge, decreases in mean dissolved oxygen and increases in water column $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ were also found in the post-fire period, indicating input of fire-associated solutes and sediments into the stream channel that have been reported (Sherson et al. 2015, Dahm et al. 2015).

Given that we used subsamples of the SAM tissues that Thompson et al (2019) processed for biomass measures, it is likely that enrichment was driven by this addition of available nutrients to the East Fork. These nutrients were available in an inorganic form that the SAMs

could readily access and convert quickly into biomass before the end of the growing season. The fire debris transported into the system by rainfall events provided essential and limiting nutrients, particularly P, as noted by the significant increase in mean tissue %P and changes to the N:P stoichiometry in the post-fire tissues. It is generally accepted that streams in the southwestern US are nitrogen limited for algae (Grimm and Fisher 1986); however, this limitation is not a critical issue for SAMs as they source nutrients from the benthos via root systems as well as the water column (Carignan and Kalff 1980; Chambers et al. 1989). This increase in available nutrients allowed for rapid regrowth despite scouring, as described in Thompson et al. (2019). Scouring initially decreased the amount of standing biomass in the East Fork after the fire-associated precipitation events. Once flows returned to baseline this post-fire increase in biomass and an increase in %N and %P was likely from fire-related dissolved inputs to the stream after the summer monsoon and an enhanced growing season in late summer and early fall.

Besides chemical changes to organic matter from combustion (Cerrato et al. 2016, Rahman et al. 2018) fire also physically transforms soils and allows for increased movement of both fire debris and burned soils through overland flows. During precipitation events, burn-scar material moves into stream channels and the water column (Dahm et al. 2015). Although ash from these flows varies in composition, particulate carbon and nutrients that are bound to fine particles are often found within these ash flows (Smith et al 2011). Marked increases in nitrate and phosphate also were found in the water column after the Las Conchas fire at the study site (Sherson et al. 2015). Fire-associated impacts on SAMs develop through physical and chemical changes to the stream ecosystem that occur after soils and other fire-associated

debris enter the stream channel and water column. These impacts include reduced light availability, increases in water temperature, and changes to water quality (e.g., increases in turbidity and inorganic nutrients and decreases in dissolved oxygen and pH) (Earl and Blinn 2003; Smith et al. 2011, Stephan et al. 2012; Verkaik et al. 2013).

Increases in available nitrogen and phosphorous can cause increases in growth and biomass of plants. SAMs are no exception. SAMs are by their nature ecosystem engineers (Jones, 1994); they grow in ways that create dense, monotypic stands of vegetation that can modify the geomorphology and flow of lotic ecosystems by reducing current velocities (Madsen and Warneke, 1983), concentrating flows into the open portion of a channel (Sand-Jensen and Petersen, 1999), and increasing water residence time leading to more fine sediment settlement (Gregg and Rose, 1982). The macrophyte stands present in the East Fork act as ecosystem engineers and retain some of the sediments deposited in each high flow event, essentially creating a new sediment layer in the stream channel that we have observed during sampling dates after the 2011 post-fire period through the end of the 2012 growing season (personal obs.). This sediment layer likely provided additional stocks of fire-transformed nutrients that were previously unavailable for plant use. However, this effect was only temporary as the plants depleted the ‘bonus’ supply of nutrients and returned to similar baseline mean tissue concentration as pre-fire tissues for the duration of the pre-flood growth period, which included both early and late season samples. While sediment accumulation was observed through the 2012 growing season and increased biomass was observed (Thompson et al. 2019), increased nitrogen and phosphorous were not observed in tissues in samples collected pre-flood (2012 and first half of 2013 growing seasons; Figure 1). This suggests

that much of the immediately available nitrogen and phosphorous introduced into the water column during the post-fire event was used in the immediate growth period in late 2011 that produced a dramatic increase in biomass and was not retained in the system for the following growing season (Thompson et al. 2019).

While overland flows in areas that have not been transformed by fire can bring a new source of nutrients for primary producers into the river via soils, the concentrations of nutrients and metals are typically not as high in unaltered soils as they are in ash and fire-transformed soils (Certini 2005, Cerrato et al. 2016, Rahman et al. 2018). Thus, overland flows that brought in this second burst of soil inputs from the flood in 2013 created another fertilization event in the stream with a combination of fire-transformed and untransformed soils. However, the longer duration flood's timing and size inhibited regrowth as shown by the modest increase in post-flood SAM biomass as compared to post-fire SAM biomass observed by Thompson et al. (2019). SAM-dominated lakes and rivers at lower elevations have been shown to remove more P from the water column and new sediment inputs than wetland areas with only emergent macrophyte vegetation (Knight et al., 2003), implying that SAMs may be more efficient at assimilating dissolved P compared to other macrophyte growth forms. Velthuis et al. (2017) also found that increasing available nutrients caused an increase in the N and P uptake/tissue content and consequent decrease in the C:N and C:P ratio of a species of *Elodea nuttallii* in a manner similar to increases in N and P and decreases in the C:N and C:P ratios we observed in post-fire and post-flood tissue samples.

Both nutrient input events we sampled occurred in the mid-late portion of the growing season. Due to the timing of the North American monsoon in the region, the changes in %P and N:P stoichiometry that we observed might have been due to seasonal effects rather than disturbance effects. We calculated GLMs (IBM 2017) comparing mean tissue % P content and N:P stoichiometry late in the season versus early in the growing season to ensure that a seasonal effect in the physiology of the plants was not skewing results. These growing season data included a year between the two events when no major disturbances occurred. No significant difference was found between the tissue % P content ($P = 0.462$) and the N:P stoichiometry ($P = 0.956$) in early and later season tissues when accounting for these data. Therefore, it is reasonable to conclude that the effects we observed were due to disturbance and punctuated overland flow inputs of dissolved nutrient solutes and nutrient-rich sediments.

We also compared SAM tissue nutrient content and stoichiometry with other datasets examining conditions in this watershed to ask whether there were any correlations with nutrient content and stoichiometry. While these present interesting opportunities for interpretation of our results, not all supplemental datasets matched our sampling regime closely enough to be included in our primary analyses. Decreases in C:P and N:P ratio and increases in %P content were strongly correlated with increases of SAM biomass as measured by Thompson et al. (2019), indicating that increases in P content was likely a contributing factor in this increased biomass. Increases in SAM tissue %N and %P concentrations were weakly positively correlated with increases in NO_3 and PO_4 detected in the water column and strongly negatively correlated with C:P and N:P stoichiometry (Table

6). However, increases in water column NO_3 and PO_4 were strongly positively correlated with increases in turbidity and decreases in dissolved oxygen, further illustrating the role of ash and soil deposition into the stream by overland flows as documented by Reale et al. (2015). Estimates of GPP by Reale et al. (2018) showed the East Fork to be a highly productive ecosystem with high rates of primary production and a P/R ratio generally above 1. While SAMs do contribute to the seasonally dependent primary production in the East Fork, increases in estimated GPP do not correlate strongly with changes in stoichiometry or SAM biomass as shown by Thompson et al. (2019). Changes in the GPP estimates by Reale et al. (2018) were more likely driven by other primary producers, including filamentous green algae (*Cladophora* sp.) that were abundant in the earlier portion of the growing season (March-June). Summers et al. (2020) also did not find a clear relationship between GPP and turbidity, conductance or temperature during spring-fall in the East Fork, which is the growth period of SAMs in this location. This supports the hypothesis that SAMs are not the primary drivers of GPP in the East Fork during much of the growing season.

Surface-based inputs mobilized by ecohydrology appear to be key in increasing available pools of nutrients that the SAMs can utilize to increase biomass and accelerate growth over time, especially during periods in which increased in-channel discharge may create scour that decreases the amount of SAM biomass left in the stream channel. While SAMs can still access essential nutrients from rooting in the benthos (Carignan and Kalff, 1980), these inputs allow for increased periods of production and regrowth that can have cascading effects on the ecosystem through enhanced nutrient cycling, dissolved oxygen creation, provision of refugia and food, and changes to flow and geomorphological characteristics of the stream.

The East Fork is a highly productive stream ecosystem during the growing season (Reale et al. 2018). SAMs present in the river are major contributors to this high level of productivity and exert strong influences in many aquatic ecosystems well beyond the Jemez Mountains. Mountain headwater areas similar to the East Fork are commonly vital water sources for communities and cities worldwide that use surface water that has traveled downstream through the catchment for human consumption. When present in headwater stream ecosystems, SAMs are major contributors to ecosystem primary production, nutrient cycling and water quality improvement. We have shown that SAMs are also responsive to major disturbance events, including nutrient and sediment inputs from flow events after catastrophic forest fires, thunderstorms, and strong precipitation events. As forest fires are increasing in intensity, size, and duration throughout the western United States (Westerling et al., 2006; Vose et al., 2012), the frequency of these input events will increase, and understanding the effects these water quality events have on SAMs elucidates another pathway that energy can move through an aquatic ecosystem after these flow events.

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TABLES

Table 1. F-and P-values for General Linear Models with dependent variables of mean percent carbon (%C), percent nitrogen (%N) and percent phosphorus (%P) content in macrophyte tissues and independent disturbance group (pre- and post-fire, pre- and post-flood). Percentages were arcsine square root transformed prior to analysis.

	<u>Df</u>	<u>F-value</u>	<u>P-value</u>
% C	3, 235	2.10	0.10
% N	3, 235	2.33	0.07
% P	3, 235	19.17	< 0.001

Table 2. Means and standard deviations for %C, %N, %P, C:N, C:P and N:P, when all taxa are pooled. Data are grouped in relation to disturbance events.

	Pre-Fire	Post-Fire	Pre-Flood	Post-Flood
%C	41.5 ± 4.3	39.3 ± 6.6	40.0 ± 4.7	42.3 ± 3.5
%N	2.2 ± 0.5	2.7 ± 0.7	2.0 ± 0.4	2.2 ± 0.4
%P	0.22 ± 0.05	0.33 ± 0.08	0.22 ± 0.06	0.24 ± 0.03
C:N	21 ± 6.6	22 ± 4.9	22 ± 6.2	25 ± 5.5
C:P	288 ± 81.8	246 ± 81.5	318 ± 121.7	222 ± 38.5
N:P	14 ± 4.4	11 ± 4.0	15 ± 7.1	9 ± 2.5

Table 3. Means and standard deviations for %C, %N, %P, C:N, C:P and N:P for *Elodea canadensis*. Data are grouped in relation to disturbance events.

	Pre-Fire	Post-Fire	Pre-Flood	Post-Fire
%C	37.6 ± 2.1	38.9 ± 3.8	36.0 ± 4.1	37.6 ± 2.2
%N	2.2 ± 0.59	2.3 ± 0.66	2.1 ± 0.46	1.9 ± 0.44
%P	0.25 ± 0.04	0.33 ± 0.06	0.23 ± 0.06	0.27 ± 0.03
C:N	21 ± 6.2	21 ± 5.5	21 ± 6.9	23 ± 6.2
C:P	276 ± 53.8	221 ± 68.3	293 ± 147.2	223 ± 38.1
N:P	13 ± 2.8	11 ± 2.9	14 ± 9.6	10 ± 2.9

Table 4. Means and standard deviations for %C, %N, %P, C:N, C:P and N:P, for *Ranunculus aquatilis*. Data are grouped in relation to disturbance events.

	Pre-Fire	Post-Fire	Pre-Flood	Post-Flood
%C	36.9 ± 5.4	33.4 ± 6.9	37.1 ± 4.5	37.8 ± 4.9
%N	1.8 ± 0.36	1.8 ± 0.61	1.9 ± 0.38	1.7 ± 0.41
%P	0.29 ± 0.05	0.25 ± 0.08	0.22 ± 0.06	0.28 ± 0.03
C:N	26 ± 7.5	22 ± 4.3	23 ± 6.3	26 ± 4.3
C:P	336 ± 88.5	252 ± 98.3	307 ± 93.6	221 ± 40.6
N:P	14 ± 4.8	11 ± 5.0	13 ± 4.0	9 ± 1.9

Table 5. P-values from Two-Way ANOVA analyses to explain variation in nutrient content and nutrient stoichiometry of SAM tissues among species and disturbances types.

	%C	%N	%P	C:N	C:P	N:P
Species	0.02	< 0.001	< 0.001	0.07	0.1	0.15
Disturbance	0.16	0.03	< 0.001	0.07	0.01	< 0.001
Species*Disturbance	0.01	0.01	0.01	0.22	0.139	0.69

Table 6. Pearson's correlations (r^2) comparing % C, % N and %P data to abiotic data. Values marked * are $P < 0.05$ and values marked ** are $P < 0.01$.

	%C	%N	%P	C:N	C:P	N:P	Turbidity (NTU)	DO (mg/L)	Discharge (m ³ /sec)	NO3-N (water)	PO4-P (water)	GPP	Biomass (g/m ²)
%C	--	0.413**	0.379**	0.128*	-0.031	-0.105	0.205*	-0.290**	0.193*	0.163	0.240	-0.0296**	0.070
%N		--	0.282**	-0.814**	-0.103	0.355**	0.123	-0.386**	0.216**	0.058	0.195	-0.110	-0.024
%P			--	-0.093	-0.732**	-0.574**	0.116	-0.106	0.179*	0.333**	0.315	-0.178	0.355**
C:N				--	0.109	-0.413**	-0.015	0.243**	-0.121	0.033	-0.110	-0.083	0.0530
C:P					--	0.822**	-0.017	-0.041	-0.107	-0.154	-0.262	0.012	-0.224**
N:P						--	-0.010	-0.197*	0.006	-0.149	-0.181	0.081	-0.207**
Turbidity							--	-0.676**	0.448**	0.410**	0.600**	-0.343**	0.044
DO								--	-0.0361**	-0.295**	-0.763**	0.162	0.032
Discharge (Estimated)									--	0.250*	0.373*	-0.0525**	0.100
NO3-N										--	0.717**	0.094	0.289**
PO4-P											--	-0.035	0.351*
GPP												--	-0.064

Table 7. F-and P-values for General Linear Models where the first two Principal Components (PC) are created by Principal Components Analyses using abiotic and biotic data. Samples are grouped by disturbance (pre- and post-fire, pre- and post-flood)

	df	F-value	P-value
Abiotic PC1	3, 98	50.59	< 0.0001
Abiotic PC2	3, 98	6.28	< 0.0001
Biotic PC1	3, 235	11.64	< 0.0001
Biotic PC2	3, 235	3.91	0.0090

FIGURES

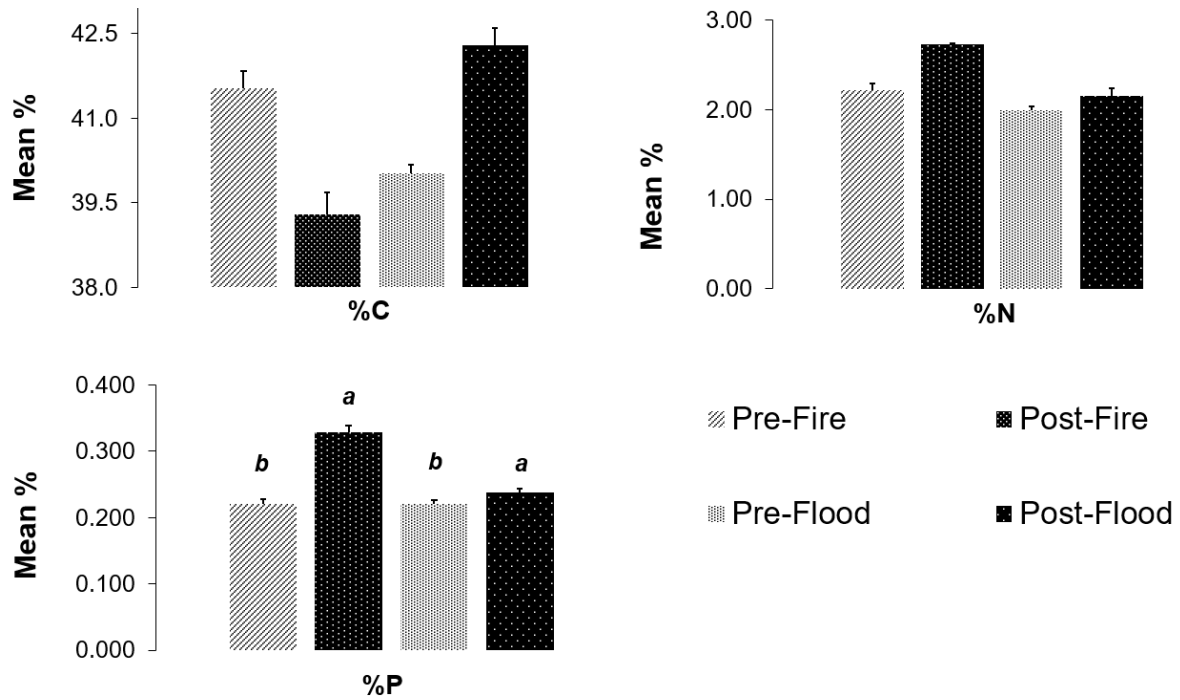


Figure 1. Mean percent % content of carbon (%C), nitrogen (%N) and phosphorus (%P) found in Submerged Aquatic Macrophyte tissues during Pre-Fire, Post-Fire, Pre-Flood and Post-Flood periods. Changes in mean %P content were significantly different between pre- and post- fire and flood periods. No significant differences were noted in %C and %N contents among periods. Error bars represent standard error.

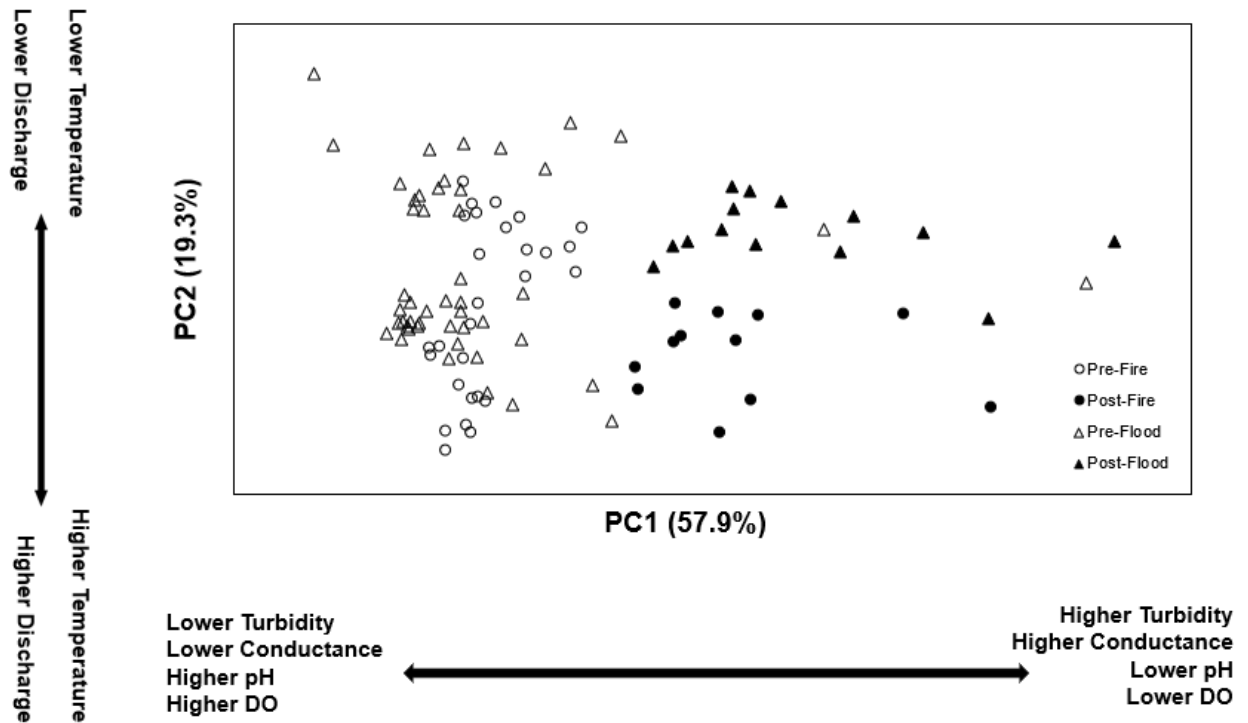


Figure 2. Principal Components Analysis of sites using abiotic data ([turbidity (NTU), specific conductance ($\mu\text{S}/\text{cm}$), pH, dissolved oxygen (DO) (mg/L), temperature ($^{\circ}\text{C}$) and estimated discharge (m^3/sec) showing clustering of samples. There are distinct clusters of pre-(fire/flood) and post-(fire/flood) data. Principal Component 1 is associated with dissolved oxygen, pH, specific conductance and turbidity and Principal Component 2 was associated with temperature and estimated discharge. These two principal components accounted for 77.2% of the variance in the data.

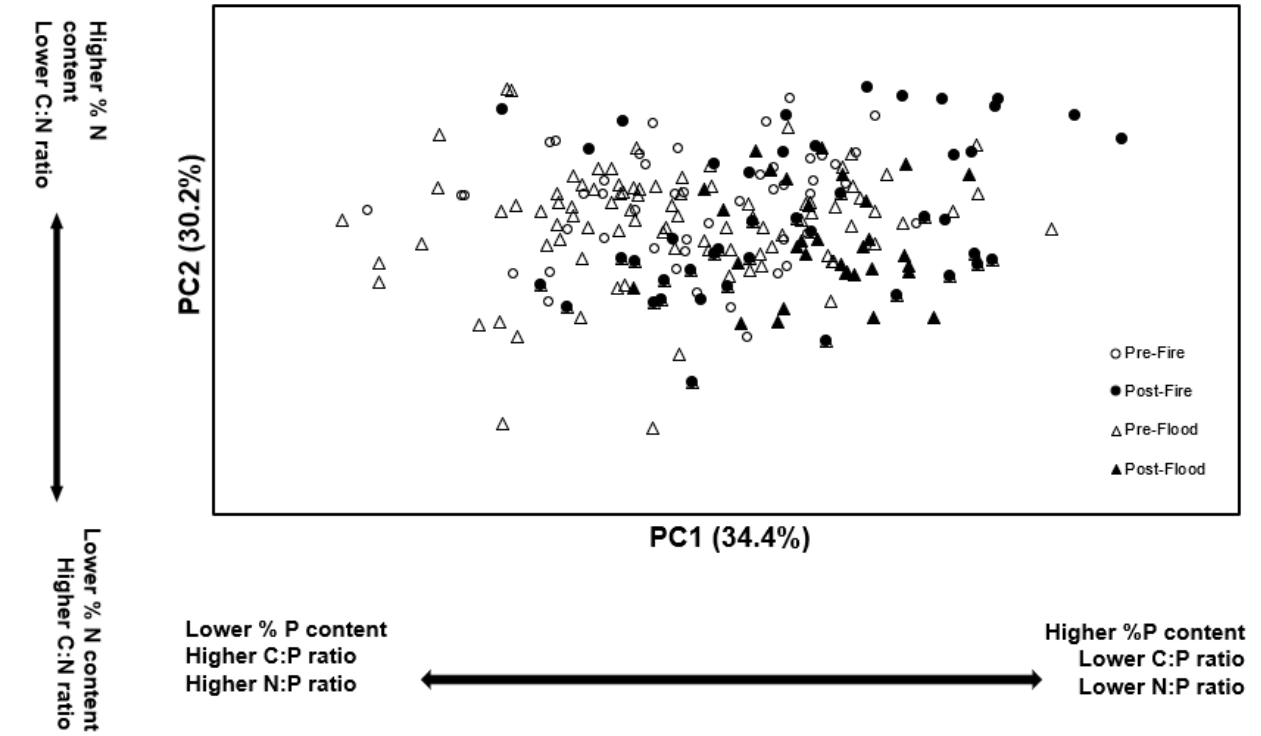


Figure 3. Principal Components Analysis of samples using biotic data. There is a distinct rightward shift in post-fire and post-flood sample clustering compared to pre-fire and pre-flood samples. Principal Component 1 illustrates clustering of sites with higher tissue %P content and lower C:P and N:P ratios. Principal Component 2 groups samples along a gradient of tissue %N content and C:N ratio. These two principal components accounted for 76.4% of the variation in the data.

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EPILOGUE

The research throughout these studies was centered around one predominant question: What affects the occurrence, biomass, and growth of submerged aquatic macrophytes (SAMs) in these high elevation mountain streams and rivers? While not ubiquitous in all aquatic ecosystems in the Jemez Mountains, SAMs can have major effects on ecosystem structure and function when present in abundance. For example, SAMs improve water quality, provide food and refugia, affect water velocity, and both retain and facilitate nutrient cycling in aquatic ecosystems.

In **Chapter 1**, the following questions were asked: 1.) What physical factors are associated with SAM presence or absence in these high elevation stream and river sites in the Jemez Mountains? 2.) Do these drivers differ from factors influencing patterns in SAM presence/absence in better-studied lower elevation areas? We found that SAMs were most likely to be found in streams that were deeper, narrower, lower velocity and lower gradient. These abiotic conditions are similar to conditions controlling presence/absence of SAMs at lower elevations streams where SAMs are prevalent, suggesting that these controls affect SAMs globally regardless of elevation. We also found three SAM species to be present in the Jemez Mountains: *Elodea canadensis* (Michx.), *Ranunculus aquatilis* (L.), and *Stuckenia pectinata* (L.) Boerner. All species are native to the United States. *Stuckenia pectinata* was only encountered twice at our sampling sites and was therefore excluded from statistical analyses on presence and absence. The presence and absence studies focused on *E. canadensis* and *R. aquatilis*.

In **Chapter 2**, the following questions were asked: 1.) Do flood events following a major catastrophic wildfire and a decadal-scale regional precipitation event reduce standing SAM biomass through scour from elevated sediment loads and high flows? 2.) Do fire-linked flood events provide a fertilizer effect that stimulates biomass accrual during baseflow conditions after monsoonal storms? We found that SAMs were affected by wildfire-associated inputs differently than from a large regional precipitation event from dissipating tropical storms. SAM recovery, as shown by increases in standing biomass, was significantly higher after the fire-associated floods that delivered nutrient rich ash and soils into the stream channel than in the flood event that delivered extremely high flows but lower levels of turbidity. We found four species present (*Elodea canadensis* (Michx.), *Ranunculus aquatilis* (L.), *Potamogeton richardsonii* (Benn.) Rydb., and *Stuckenia pectinata* (L.) Boerner) at the research site. All species are native to the United States. Two species accounted for 90% of the biomass found (*E. canadensis* and *R. aquatilis*). *Elodea canadensis* showed the greatest biomass fluctuations before and after disturbance events. *Ranunculus aquatilis* added biomass following higher flow conditions in 2011 and 2013. Rapid recovery from flood pulses immediately after catastrophic wildfire lasted until the end of the 2011 growing season. There was a more typical growing season in 2012 and a less dramatic recovery of both taxa after the major flood disturbance in September of 2013.

In **Chapter 3**, the following questions were asked: 1.) Was the percent nitrogen (%N) and percent phosphorus (%P) content in SAM tissues different after a catastrophic fire compared to the nutrient content of pre-fire SAM tissues? 2.) Did nutrient content of SAM tissues

respond to a decadal large-scale multi-day flood two years after the wildfire? 3.) Did the type of disturbance (catastrophic fire versus major flood) alter nutrient content and stoichiometric ratios in SAM tissues compared to tissue nutrient content before the disturbances? We found that SAM tissue nutrient content in post-fire tissues differed from pre-fire tissues, including increases in %N and %P content. There were also significant differences in the N:P stoichiometric ratios before and after these disturbance events. The type of disturbance did make a difference in regard to the amount of increase in %N and %P content in post-event (fire/flood) tissues as compared to pre-event tissues. While SAM tissues increased in %N and %P content after both fire-impacted small floods in 2011 and a major multiday regional flood in September 2013, the increase in %N and %P was far more modest in the tissues after the large regional flood as compared to the immediate post-fire tissues. Reductions in N:P ratios were seen after the disturbance events. There also were correlations between increases in water column inorganic N and P and increases in SAM tissues of %N and %P content and decreases in N:P ratios.

Climate change has brought an increase in the frequency, intensity, and duration of forest fires throughout the western United States (Westerling 2016, Vose et al. 2012, Luo et al. 2013). This, in turn, has greatly increased both direct and indirect effects on stream ecosystems, including increased flooding, erosion, and altered hydrologic regimes (Vose et al. 2012). Erosive processes are a common source of nutrient introduction in lotic ecosystems, especially in areas prone to strong monsoonal storms that mobilize large amounts of sediment into stream channels. Monsoon-prone regions like the southwestern US tend to get high-intensity, short duration rainfall (Neary et al. 2003, Verkaik et al. 2013) in

the summer that can boost peak flows. Such events are accentuated from severely burned catchments (Neary et al. 2003, Reale et al. 2015). These types of short-term pulse disturbances (e.g., flash floods from monsoon precipitation) have potential long-term effects on stream ecosystems and their overall structure and function.

Wildfire induced changes in water quality, especially changes such as much increased turbidity and decreased or zero dissolved oxygen, can have significant and far-reaching effects. These effects occur both in the areas that were burned and in downstream areas many kilometers downstream from the fire. This can include urban areas far from the forested watershed where wildfire occurs (Dahm et al. 2015, Reale et al. 2015). These effects from wildfires on stream ecosystems occur when precipitation events mobilize ash, charcoal, soil, and solutes (Gresswell 1999; Verkaik et al. 2013) and transport these materials into stream and river ecosystems. Because SAMs can potentially help mitigate these negative effects through provision of ecosystem services such as water quality improvements, sediment retention, and nutrient cycling, understanding their roles can be helpful in managing catchments where catastrophic wildfires are becoming more frequent and destructive.

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