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The effects of a catastrophic forest fire on the biomass of submerged stream macrophytes

Virginia F. Thompson*, Diane L. Marshall, Justin K. Reale, Clifford N. Dahm

Department of Biology, University of New Mexico, MSC03 2020, Albuquerque, NM, 87131-0001, United States

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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).

* Corresponding author.
E-mail address: gin2001@unm.edu (V.F. Thompson).

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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 (United States Department of Agriculture (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 3400 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 exclosure 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 (United States Department of Agriculture (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 h (Western Regional Climate Center (WRCC), 2018). This unusually strong regional storm from dissipating tropical storms resulted in a long-duration flood with a peak discharge of ~3.6 $m^3 s^{-1}$, 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 above-ground 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 cm^2 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 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 min to remove epiphytic organisms. After sonication, samples were dried at 60 °C for 48 h 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-min intervals within the exclosure 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 Team, 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

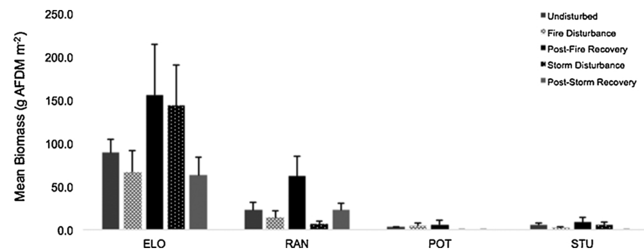

Fig. 1. Calculated means of biomass data in g AFDM m^{-2} for *Elodea canadensis* (ELO), *Ranunculus aquatilis* (RAN), *Potamogeton richardsonii* (POT), and *Stuckenia pectinata* (STU). Variables are designated based on the timing and type of disturbance that occurred and are broken into three major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

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 (Fig. 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 (United States Department of Agriculture (USDA) and National Resources Conservation Service (NRCS), 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

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

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 ± 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 (Fig. 2). 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 (Fig. 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 (Fig. 1), no pairwise comparisons among disturbance type groupings (e.g., Undisturbed vs Flood Disturbance, Post-Fire Recovery vs Post-Flood Recovery, etc.) using Tukeys Studentized Range tests showed statistically significant effects on biomass (P-values all > 0.05). The lack of significant pairwise

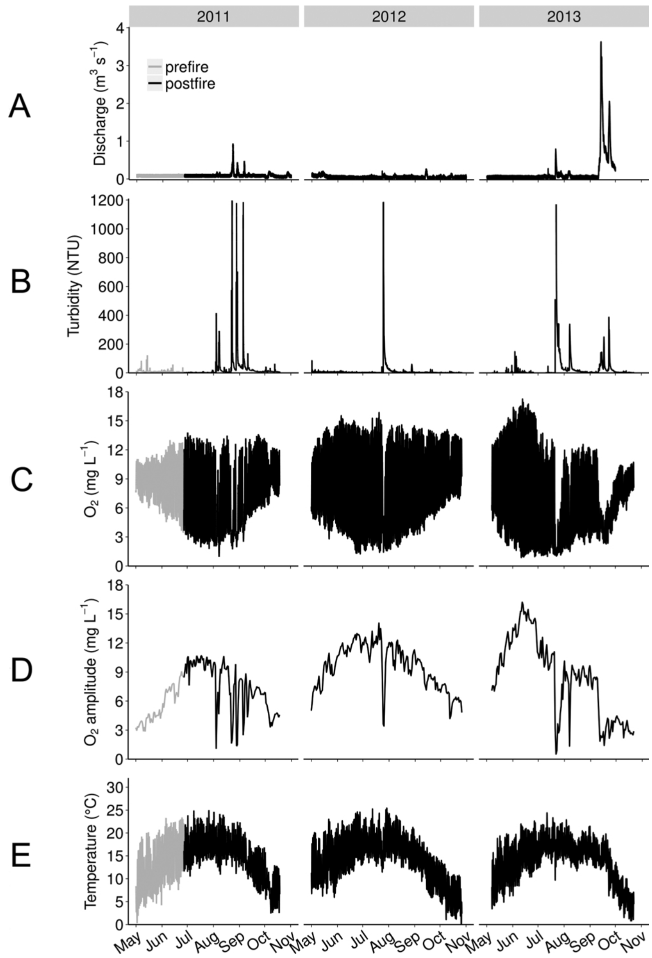

Fig. 2. (A) Stream discharge ($m^3 s^{-1}$), (B) turbidity (NTU) (C) dissolved oxygen (mg L^{-1}), (D) daily amplitude of dissolved oxygen (mg L^{-1}) and (E) stream temperature (°C) measured in 15-minute increments during much of the growing season (May to November) at the East Fork for 2011-2013.

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 $m^3 s^{-1}$, 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 (Fig. 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 (Fig. 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 (Fig. 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 $m^3 s^{-1}$ 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 $m^3 s^{-1}$) and smaller (> 0.5 $m^3 s^{-1}$ and < 1.0 $m^3 s^{-1}$) 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 (Fig. 2C,D). 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 to 2013 (Fig. 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 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 (Fig. 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 (Fig. 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 (Fig. 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 (Fig. 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, Fig. 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 (Fig. 2B). TThese pulses also decreased DO concentrations (Fig. 2C) and DO daily amplitudes (Fig. 2D). Sherson et al. (2015) also measured increases in turbidity, specific conductance, nitrogen (as $N\text{-}NO_3^-$), and phosphorus (as $P\text{-}PO_4^{3-}$) 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; Fig. 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 ($N\text{-}NH_4^+$), nitrate ($N\text{-}NO_3^-$), and orthophosphate $P\text{-}PO_4^{3-}$ (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 (Fig. 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 (Fig. 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 (Fig. 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 (Fig. 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, Fig. 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 (Fig. 2C,D). Diurnal DO amplitudes were reduced, suggesting lower in-stream primary production (Fig. 2C). In addition, DO amplitudes did not recover post-flood in the way diurnal DO concentrations did after shorter duration spates (Fig. 2D), 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 to 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.

5. 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.

6. CRediT author statement

Virginia F. Thompson: Conceptualization, Methodology, Formal Analysis, Investigation, Data Curation, Writing—Original Draft, Review & Editing, Visualization. **Diane L. Marshall**: Formal Analysis, Writing—Review & Editing, Supervision. **Justin K. Reale**: Investigation, Formal Analysis, Visualization, Writing– Review & Editing. **Clifford N. Dahm**: Conceptualization, Resources, Writing– Review & Editing, Supervision.

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References

Bixby, R.J., Cooper, S.D., Gresswell, R.E., Brown, L.E., Dahm, C.N., Dwire, K.A., 2015. Fire effects on aquatic ecosystems: an assessment of the current state of the science. Freshwater Sci. 34, 1340–1350.

Bowen, B.M., 1996. Rainfall and climate variation over a sloping New Mexico plateau during the North American monsoon. J. Clim. 9, 3432–3442. https://doi.org/10.1175/1520-0442(1996)009<3432:RACVOA>2.0.CO;2.

Carignan, R., Kalff, J., 1980. Phosphorus sources for aquatic weeds: Water or sediment? Science 207, 987–989. https://doi.org/10.1126/science.207.4434.987.

Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1–10. https://doi.org/10.1007/s00442-004-1788-8.

Dahm, C.N., Candelaria-Ley, R.I., Reale, C.S., Reale, J.K., Van Horn, D.J., 2015. Extreme water quality degradation following a catastrophic forest fire. Freshwater Biol. 60, 2584–2599.

Earl, S.R., Blinn, D.W., 2003. Effects of wildfire ash on water chemistry and biota in south-western USA streams. Freshwater Biol. 48, 1015–1030. https://doi.org/10.1046/j.13652427.2003.01066.x.

Franklin, P., Dunbar, M., Whitehead, P., 2008. Flow controls on lowland river macrophytes: a review. Sci. Total Environ. 400, 369–378.

Goff, F., Gardner, J.N., Reneau, S.L., Goff, C.J., 2006. Preliminary Geologic Map of the Redondo Peak Quadrangle, Sandoval County, New Mexico. New Mexico Bureau of Geology and Mineral Resources Open File Geologic Map OF-GM 111. Accessed 13 April 2016. http://geoinfo.nmt.edu/publications/maps/geologic/ofgm/downloads/111/Redondo%20Peak%20Report.pdf.

Gresswell, R.E., 1999. Fire and aquatic ecosystems in forested biomes of North America. Trans. Am. Fish Soc. 128 193-221.e.

Henry, C.P., Amoros, C., Bornette, G., 1996. Species traits and recolonization processes after flood disturbances in riverine macrophytes. Vegetatio 122, 13–27.

Koehl, M.A.R., 1984. How do benthic organisms withstand moving water? Am. Zool. 24, 57–70.

Lacoul, P., Freedman, B., 2006. Environmental influences on aquatic plants in freshwater ecosystems. Environ. Rev. 14, 89–136. https://doi.org/10.1139/a06-001.

Lake, P.S., 2000. Disturbance, patchiness, and diversity in streams. J. N. Am. Benthol. Soc. 19, 573–592.

Luo, L., Tang, Y., Zhong, S., Bian, X., Heilman, W.E., 2013. Will future climate favor more erratic wildfires in the Western United States? J. Appl. Meteorol. Clim. 52, 2410–2417.

Muldavin, E., Tonne, P., 2003. A vegetation survey and preliminary ecological assessment of Valles Caldera National Preserve, New Mexico. Report for Cooperative Agreement 01CRAG0014. University of New Mexico, Albuquerque, NM.

Nichols, S.A., Shaw, B.H., 1986. Ecological life histories of the three aquatic nuisance plants, *Myriophyllum spicatum*, *Potamogeton crispus* and *Elodea canadensis*. Hydrobiologia 131, 3–21. https://doi.org/10.1007/BF00008319.

Orem, C.A., Pelletier, J.D., 2015. Quantifying the time scale of elevated geomorphic response following wildfires using the multi-temporal LiDAR data: an example from the Las Conchas fire, Jemez Mountains, New Mexico. Geomorphology 232, 224–238. https://doi.org/10.1016/j.geomorph.2015.01.006.

Osborne, T.Z., Kobziar, L.N., Inglett, P.W., 2013. Fire and water: new perspectives on fire's role in shaping wetland ecosystems. Fire Ecol. 9, 1–5.

Parsons, A., Robichaud, P.R., Lewis, S.A., Napper, C., Clark, J.T., 2010. Field guide for mapping post-fire soil burn severity. General Technical Report RMRS-GTR-243. US Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, CO Retrieved from: www.fs.fed.us/rm/pubs/rmrs_gtr243.pdf.

Raschke, R.L., Rusanowski, P.C., 1984. Aquatic macrophyton field collection and laboratory analyses. In: Dennis, W.M., Isom, B.G. (Eds.), Ecological Assessment of Macrophyton: Collection, Use, and Meaning of Data. American Society for Testing and Materials (ASTM), Baltimore, MD, pp. 16–27.

Reale, J.K., 2018. Evaluating the effects of catastrophic wildfire on water quality, whole-stream metabolism and fish communities (dissertation). University of New Mexico.

Reale, J.K., Van Horn, D.J., Condon, K.E., Dahm, C.N., 2015. The effects of catastrophic wildfire on water quality along a river continuum. Freshwater Sci. 34, 1426–1442. https://doi.org/10.1086/684001.

Riis, T., Biggs, B.J., 2003. Hydrologic and hydraulic control of macrophyte establishment and performance in streams. Limnol. Oceanogr. 48, 1488–1497.

RStudio Team, 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. http://www.rstudio.com/.

Sherson, L.R., Van Horn, D.J., Gomez-Velez, J.D., Crossey, L.J., Dahm, C.N., 2015. Nutrient dynamics in an alpine headwater stream: use of continuous water quality sensors to examine responses to wildfire and precipitation events. Hydrol. Process. 29, 3193–3207. https://doi.org/10.1002/hyp.10426.

Smith, H.G., Sheridan, G.J., Lane, P.N., Nyman, P., Haydon, S., 2011. Wildfire effects on water quality in forest catchments: a review with implications for water supply. J. Hydrol. 396, 170–192.

Spicer, K.W., Catling, P.M., 1988. The biology of Canadian weeds: 88. *Elodea canadensis* Michx. Can. J. Plant Sci. 68, 1035–1051. https://doi.org/10.4141/cjps88-125.

Stephan, K., Kavanagh, K.L., Koyama, A., 2012. Effects of spring prescribed burning and wildfires on watershed nitrogen dynamics of central Idaho headwater areas. For. Ecol. Manage. 263, 240–252. https://doi.org/10.1016/j.foreco.2011.09.013.

Townsend, S., Schult, J., Douglas, M., Lautenschlager, A., 2017. Recovery of benthic primary producers from flood disturbance and its implications for an altered flow regime in a tropical savannah river (Australia). Aquat. Bot. 126, 9–20.

Trenberth, K.E., Fasullo, J.T., Shepherd, T.G., 2015. Attribution of climate extreme events. Nat. Clim. Change. 5, 725–730. https://doi.org/10.1038/nclimate2657.

United States Department of Agriculture (USDA), National Resources Conservation Service (NRCS), 2016. The PLANTS Database (http://plants.usda.gov, 18 November 2016). National Plant Data Team, Greensboro, NC Accessed 9 February 2017.

United States Department of Agriculture (USDA), Forest Service, 2011. Burned-Area Report [Reference FSH 2509.13). Retrieved from. Accessed 27 July 2013. https://inciweb.nwcg.gov/incident/article/2406/12597.

Van Horn, D.J., White, C.S., Martinez, E.A., Hernandez, C., Merrill, J.P., Parmenter, R.R., Dahm, C.N., 2012. Linkages between riparian characteristics, ungulate grazing, and geomorphology and nutrient cycling in montane grassland streams. Rangeland Ecol. Manage. 65, 475–485. https://doi.org/10.2111/REM-D-10-00170.1.

Verkaik, I., Rieradeval, M., Cooper, S.D., Melack, J.M., Dudley, T.L., Prat, N., 2013. Fire as a disturbance in Mediterranean climate streams. Hydrobiologia 719, 353–382. https://doi.org/10.1007/s10750-013-1463-3.

Wang, C., Zheng, S., Wang, P., Hou, J., 2015. Interactions between vegetation, water flow and sediment transport: a review. J. Hydrodyn. Ser. B 27, 24–37.

Westerling, A.L., 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Phil. Trans. R. Soc. B 371, 20150178.

Western Regional Climate Center (WRCC), 2018. Valles Caldera National Preserve Climate Stations. Retrieved from. Accessed 17 July 2018. https://wrcc.dri.edu/vallescaldera/.