

Controls on productivity of submerged aquatic vegetation in 2 spring-fed rivers

Jennifer McBride^{1,3} and Matthew J. Cohen^{2,4}

¹School of Natural Resources and Environment, 106 Black Hall, University of Florida, Gainesville, Florida 32611 USA

²School of Forest Resources and Conservation, 328 Newins-Ziegler Hall, University of Florida, Gainesville, Florida 32611 USA

Abstract: Submerged aquatic vegetation (SAV) is an important structural component of many aquatic ecosystems that also affects a broad array of biogeochemical and ecological processes. In the spring-fed rivers of Florida, where SAV is the foundation of healthy community structure and function, environmental controls on SAV growth remain poorly understood. This lack of knowledge complicates the evaluation and prioritization of management and restoration activities. Our goal was to explore the relative influences of environmental drivers on annual patterns of SAV productivity in 2 spring-fed rivers (Silver River and Alexander Springs Creek) with contrasting nitrate concentrations (1.4 vs 0.05 mg N/L, respectively) but otherwise similar physical and chemical attributes. We used monthly measurements from 16 fixed plots in each river to observe spatial and temporal heterogeneity in SAV growth. Mean growth rates between the rivers were statistically indistinguishable, suggesting that SAV growth is not controlled primarily by water column N concentrations. Despite representing most of the autotroph biomass, measured SAV growth rates were only 25% of contemporaneous estimates of open-channel net primary production (i.e., gross primary production minus autotrophic respiration). This result indicates that the epiphytic assemblages that grow primarily on SAV dominate overall ecosystem metabolic activity. Pairwise associations between measured SAV growth and a suite of physical (light, redox potential, temperature, sediment texture) and chemical (porewater and water column solutes) variables revealed that no single factor can accurately predict SAV growth. Instead, 2 complementary multivariate approaches (regression trees, general linear models) yielded useful models to predict SAV growth. While we constructed models independently for each river, their best-fit model formulations were remarkably similar—light (+), sediment redox potential (–), and porewater orthophosphate (–) predicted over 50% of the variation in SAV growth. System managers could use these model results to aid in screening restoration sites for SAV suitability. Further, these results underscore the need for a broad systems approach to springs management.

Key words: submerged aquatic vegetation growth, eutrophication, redox potential, restoration, Florida springs

Submerged aquatic vegetation (SAV) is a critical component of many low-relief river systems (Butcher 1933, Carpenter and Lodge 1986, Canfield and Hoyer 1988, Hoyer et al. 2004). SAV provides refuge and forage habitat for fishes, insects, and birds (Jeppesen et al. 1998, Persson and Crowder 1998); controls flowing water hydraulics (Hensley and Cohen 2012); influences water column chemistry (Wetzel and Søndergaard 1998, Caraco and Cole 2002); and stabilizes sediments against resuspension and erosion (Barko and James 1998). SAV productivity and composition are thus important measures of ecosystem condition (Dennison et al.

1993), which highlights the need to quantify the relative importance, interactions, and generality of factors affecting SAV growth to inform river management and restoration.

North Florida has the highest density of 1st-magnitude ($Q > 2.8 \text{ m}^3/\text{s}$) springs in the world (Scott et al. 2004). Like other freshwater ecosystems globally, springs are altered by human activities that modify species composition, nutrient loads, flow, and ecosystem physical conditions (Smith 2003, Dudgeon et al. 2006, Quinlan et al. 2008). These springs historically supported dense SAV beds (Odum 1957a, Canfield and Hoyer 1988, Duarte and Canfield 1990) that were the

E-mail addresses: ³Present address: Arcadis US Inc., 630 Plaza Drive, Highlands Ranch, Colorado 80129 USA, jamcbride92@gmail.com; ⁴To whom correspondence should be addressed, mjc@ufl.edu

energetic and structural basis of well-studied (Odum 1957b) aquatic food webs. However, the combined impacts of diminished flows (Heffernan et al. 2010, King 2014), aquifer nitrate (NO_3^-) enrichment (Jones et al. 1996, Katz 2004), and changing water clarity (Hensley and Cohen 2017, Luzius et al. 2018) have increased filamentous macroalgal abundance. These changes have contemporaneously decreased SAV growth and cover (Mattson et al. 1995). SAV growth is an important indicator of ecosystem condition (Crowder and Cooper 1982, Camp et al. 2014), and declines in SAV have important and potentially long-lasting ecological consequences. However, the physical, chemical, and biological factors that control SAV productivity remain poorly understood, which limits management and restoration effectiveness.

Light is a dominant factor influencing SAV distribution, abundance, and productivity in both marine and fresh water (Odum 1957a, Duarte 1991, Dobberfuhl 2007) because most SAV taxa have high light requirements (Kirk 1994). SAV abundance varies in springs (Stevenson et al. 1993, Quinlan et al. 2008) in response to light attenuation (Gallegos 1994, Hauxwell et al. 2007), particularly of blue light ($\lambda \sim 400$ nm; Szafraniec 2014). Light attenuation in springs is driven by dissolved (Kirk 1994, Gallegos 2005) and suspended (Hauxwell et al. 2001, 2007) materials. Canopy self-shading (Titus and Adams 1979, Zimmerman 2003) and light-attenuating impacts of epiphytic biomass (Hauxwell et al. 2004, Jacoby et al. 2007, Liebowitz et al. 2014) underscore the primacy of light limitation (Odum 1957a, Sand-Jensen and Borum 1984, Dennison et al. 1993, Hauxwell et al. 2006) for understanding patterns of SAV growth and abundance.

Nutrient availability can also influence SAV distribution, abundance, and productivity. Nutrient requirements, particularly of N and P, vary across SAV and algal taxa (Nifong et al. 2014), suggesting that nutrient enrichment can adjust relative growth rates of algae and macrophytes, ultimately affecting autotrophic assemblage composition and abundance (Maberly et al. 2002, James et al. 2005). Soluble reactive P (SRP) is often a limiting nutrient in freshwater ecosystems. However, concentrations of SRP in springs in Florida are generally high enough to satisfy plant demand (Cohen et al. 2013) and have remained stable at historic levels. In contrast, NO_3^- concentrations in most springs (Scott et al. 2004) currently exceed historic levels of ~ 0.05 mg N/L (Munch et al. 2006). This increased NO_3^- has been implicated in SAV loss and algal proliferation. One mechanism by which NO_3^- enrichment can affect SAV is direct growth inhibition via enzymatic processes (Burkholder et al. 1992, Boedeltje et al. 2005). However, experimental and observational studies suggest this mechanism is unlikely in springs (Osborne et al. 2017). Instead, SAV loss may be the result of indirect effects from increased epiphytic biomass (and competition for light). NO_3^- concentrations are weakly linked to in situ autotroph composition and structure (Canfield and

Hoyer 1988, Stevenson et al. 2007), so the role of NO_3^- in algal proliferation remains unresolved (Heffernan et al. 2010). However, recent adoption of numeric nitrate criteria (0.35 mg N/L) specific to springs (Rule 62-302.531 Florida Administrative Code, <https://www.flrules.org/gateway/ruleno.asp?id=62-302.531>) makes lowering N loads the dominant management goal for springs restoration.

SAV establishment, composition, and structure are influenced by channel hydraulics (Butcher 1933, Madsen and Søndergaard 1983, Heffernan et al. 2010) because flow velocity, shear stress, drag, and turbulence influence epiphyte abundance (Biggs 1996, Stevenson 1996) and mechanical damage to rooted plants (Madsen et al. 2001). Reduced discharge in springs lowers flow velocity (Copeland et al. 2009), which creates favorable conditions for epiphyte and filamentous algal accumulation (King 2014, Reaver et al. 2019), reduces leaf gas exchange (Sand-Jensen 1977), and alters hydraulic drag (Dunn et al. 2008). Dense SAV beds can also alter river hydraulics by changing channel velocity, sedimentation, and turbidity (Petticrew and Kalff 1992, Doyle 2000). These impacts may manifest as a negative correlation between SAV density and mean flow velocity in springs (Hensley and Cohen 2012).

Sediment properties (composition, particle size) affect nutrient availability (Barko et al. 1991) and redox potential (Laing 2016), both of which can influence SAV growth and energy allocation. For example, SAV root-to-shoot biomass ratios respond to sediment nutrient availability (particularly for trace elements such as Fe, Mn, P), which vary with texture and organic matter in springs (Aung 1974, Barko and Smart 1986). Moreover, fine-grained organic sediments typical in springs preclude oxygen transport and, thus, induce low redox ($E_h < 0$ mV) conditions. Sediment redox potential influences SAV establishment and productivity (Santschi et al. 1990) via production of sulfide, reduced iron, and ammonium (Hauxwell et al. 2007, Sederias and Colman 2009).

Our objective was to understand direct and interactive controls on SAV biomass accrual in Florida springs to aid management and restoration efforts. To address this objective, we measured intra-annual dynamics of SAV productivity in 2 spring-fed rivers in north Florida (Silver River and Alexander Springs Creek). These rivers have similar physical attributes but different NO_3^- concentrations. The difference in NO_3^- allowed us to test the hypothesis that physical metrics (i.e., light, sediment redox, channel hydraulics) can better predict SAV growth than chemical metrics (i.e., nutrient availability).

METHODS

We measured in situ shoot elongation rates and above-ground primary productivity of SAV monthly at 16 sites in Silver River and 16 sites in Alexander Springs Creek. Sites

varied in light, flow velocity, and sediment characteristics. These rivers are both spring fed but differ in average NO_3^- concentrations (Silver Springs: ~ 1.35 mg N/L vs Alexander Springs: ~ 0.05 mg N/L). We also measured other physical environmental covariates (redox potential, water column, and porewater chemistry) at each site.

Site description

Silver River is a large, entirely spring-fed river that flows into Ocklawaha River in Marion County, Florida (Fig. 1A–C). The 12-km river is fed by 30 springs with a combined mean discharge of $21.7 \text{ m}^3/\text{s}$. Silver River has stable discharge, temperature, and chemistry like other spring-fed rivers in the region (Odum 1957a, Munch et al. 2006). Land-use change has elevated NO_3^- concentrations from 0.06 mg N/L (Munch et al. 2006) in the early 20th century to >1.3 mg N/L today (Munch et al. 2006, Quinlan et al. 2008). P concentrations, dominated by orthophosphate (OrthoP), have remained unchanged at 0.05 mg P/L (Scott et al. 2004).

Alexander Springs Creek is an entirely spring-fed tributary of the St Johns River in Ocala National Forest in Lake County, Florida (Fig. 1A, B, D). Mean discharge (1956–2010) in this 16-km-long river is $2.9 \text{ m}^3/\text{s}$. Mean NO_3^- (0.05 mg N/L) and OrthoP (0.04 mg P/L) concentrations have remained low, reflecting low intensity land use in the recharge area. Electrical conductivity in Alexander Springs Creek ($1070 \mu\text{S}/\text{cm}$) is higher than Silver River ($463 \mu\text{S}/\text{cm}$) (Cohen et al. 2017).

Both rivers are sourced from the karst Floridan aquifer with the spring vents fed by conduits dissolved into the Ocala Formation that accumulate recharge from their respective springheds. Longitudinal flow accumulation from diffuse seepage is low, but both systems are fed by small surface drainage tributaries (Half Mile Creek on Silver River, Nine Mile Creek on Alexander Springs Creek) that deliver tannic water during rain events. Alexander Springs Creek is wider than Silver River (mean widths of 45 vs 30 m, respectively) and therefore has slightly less riparian shading. Flooding on both systems is controlled entirely by variation in downstream water body stage (Ocklawaha River

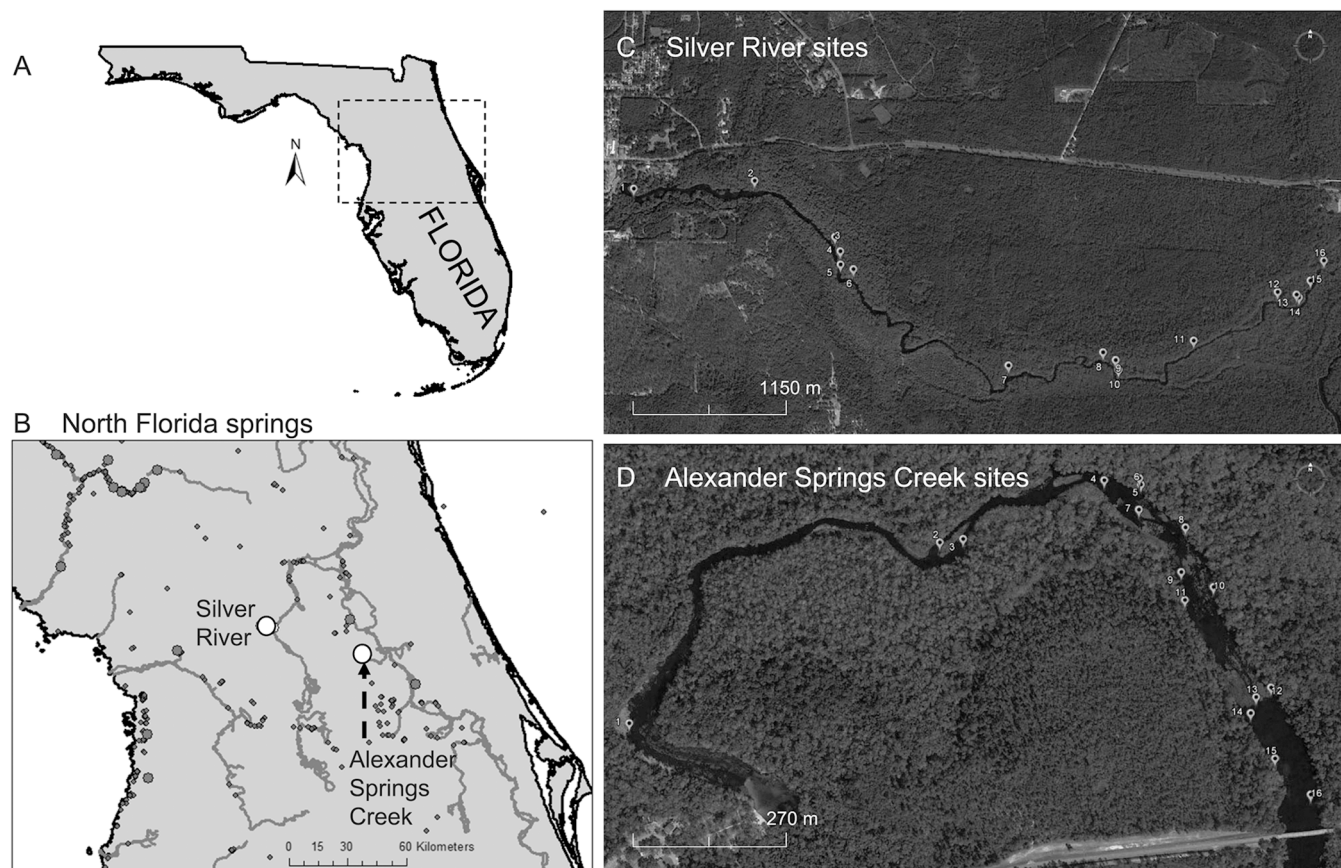


Figure 1. Study sites located in Florida, USA (A), which has the highest density of 1st-magnitude ($Q > 2.8 \text{ m}^3/\text{s}$; Scott et al. 2004) springs in the world (large gray dots; B) as well as many smaller springs (small gray dots; B). The 2 spring-fed rivers studied here (white dots; B) are Silver River (C) and Alexander Springs Creek (D). Locations of submerged aquatic vegetation growth plots ($n = 16$ in each river) are shown in panels C and D.

for Silver River and Lake Dexter for Alexander Springs Creek). Silver River floods more frequently than Alexander Springs Creek.

Study species

Florida springs support relatively few submerged vascular taxa and have only 2 dominant species. *Vallisneria spiralis* is a perennial rooted macrophyte distributed in freshwater to mesohaline environments (Korschgen and Green 1988). Its ribbon-like leaves with rounded tips grow in individual ramets >2 m from a basal meristem, and linear extension occurs via rhizomes and stolons (Korschgen and Green 1988). *Vallisneria spiralis* grows in both study rivers. *Sagittaria arifolia* is a rooted submersed macrophyte that has dark green, ribbon-like leaves, often >1 m in length, with pointed tips and prominent longitudinal ridges. *Sagittaria arifolia* is found in fast-flowing freshwaters throughout central and northern Florida but was present only at Silver River during this study.

High SAV turnover (growth and vegetative propagation) in Silver River is enabled by clear water and abundant nutrients (Odum 1957b). Indeed, rapid growth enables persistently epiphyte-free leaves and recovery from intense grazing and disturbance. SAV can acquire nutrients from the sediments (Chambers et al. 1989, Cedergreen and Madsen 2003) and via water column foliar absorption (Brabandere et al. 2007, Cohen et al. 2012) depending on the relative supply rates. Ammonium (NH_4^+) is the preferred N form used by macrophytes, but low NO_3^- can be the dominant N source when NH_4^+ concentrations are persistently low (Nichols and Keeney 1976). Biomass can be produced with stored rhizome carbohydrates (Titus and Adams 1979), masking growth seasonality (Hauxwell et al. 2007).

We selected growth measurement sites in each river to span the range of observed lateral and longitudinal variation in vegetation and algal cover by species, riparian shading, water velocity, sediment attributes, and porewater chemistry obtained from previous survey measurements (100 plots across 20 transects; Cohen et al. 2017). We selected 16 sites in each river with dense and homogenous SAV beds where water depth was <1.5 m. This depth allowed us to clip vegetation without the use of SCUBA equipment. We chose sites to represent all permutations of high and low values for epiphytic algal cover (high $\geq 75\%$ vs low $\leq 25\%$), canopy cover (high >60% vs low <40%), flow velocity (high >0.15 m/s vs low <0.1 m/s), and sediment organic matter (Silver River: high >20% vs low <10%; Alexander Springs Creek: high >15% vs low <5%).

Clipping technique

SAV grows from a basal meristem, so biomass accrual is often measured with leaf marking techniques (Odum 1957b, Zieman and Wetzel 1980, Hauxwell et al. 2007). In-

dividual leaves grow irregularly with the youngest leaves growing fastest (Tomlinson 1974, Jacobs 1979), but mean growth rates of leaves of different ages are still informative (Odum 1957b). However, we elected to measure SAV growth in experiments by leaf clipping (Kowalski et al. 2009) after testing multiple leaf tagging methods (e.g., hole punch, various thread techniques). Leaf clipping is a method often used to estimate shoot elongation and primary productivity (Dunton 1990, Lapointe et al. 1994). This clip and reharvest technique requires periodic biomass harvest of shoots at a height of 2 cm above the basal meristem. This technique can underestimate productivity and regrowth because repeated loss of photosynthetic tissue depletes belowground reserves and may keep plants from reaching pre-disturbance productivity (Morgan and Kitting 1984, Tomasko and Dunton 1995). However, several studies suggest clipping effects are minimal (Greenway 1974, Dawes and Lawrence 1979). We used this approach because it is the most repeatable and robust for high drag environments such as our study sites. We applied this technique uniformly across our study sites, which allowed us to directly compare production between sites.

Sampling methods

We installed a fixed, 1-m² quadrat divided into four 0.25-m² sections at each of 16 plots in each river. These quadrats were installed parallel to the bank so that 2 sections were on the upstream end of the quadrat and 2 sections on the downstream end. We regularly clipped the vegetation surrounding each plot to ensure light reached the plot vegetation unobstructed. We began the experiment by clipping standing biomass to 2 cm above the basal sheath across the entire plot. This initial biomass was sorted by species, and we measured shoot width and length characteristics to assess biomass recovery and turnover as well as to characterize SAV morphology and tissue element composition. Ground and homogenized tissue samples were analyzed for foliar composition (%C, %N, %P). We measured %C and %N with an elemental analyzer (CarloErba NA1500) in the University of Florida Light Stable Isotope Mass Spectrometry Laboratory and %P (Method 365.1; USEPA 1993d) post-Kjeldahl digestion in the University of Florida Analytical Research Laboratory.

We measured leaf blade elongation and biomass production at 1-mo, 3-mo, and 6-mo intervals for 18 mo (May 2015–December 2016) in Silver River and 12 mo (January 2016–January 2017) in Alexander Springs Creek. We collected SAV in upstream plot quarters at 1-mo and 3-mo intervals to examine short-term growth responses and seasonal variation, as well as from the downstream plot half at 6-mo intervals to assess long-term production. After each collection, harvested biomass was stored on ice until it was washed to remove epiphytic algae, separated by species, and measured for shoot length. We dried biomass (dry mass, or dm) at

70°C to constant mass (≥ 24 hr) and normalized to clipped area (g dm/m^2).

We calculated shoot elongation rates (cm/d) for the 2 species at each site from the mean length of clipped leaves for each sampling interval (1, 3, and 6 mo). Aboveground biomass growth rates ($\text{g m}^{-2} \text{d}^{-1}$) were obtained from SAV dm adjusted for sampling interval. We used aboveground biomass accrual rates in most analyses because we judged them to be more reliable and repeatable than shoot elongation rates, which were susceptible to broken leaves during sampling. Shoot elongation and biomass accrual were positively correlated (Pearson's r) for both *S. kurziana* ($r^2 = 0.44$, $p < 0.001$) and *V. americana* ($r^2 = 0.15$, $p < 0.001$). We estimated daily biomass turnover for each site by dividing initial SAV biomass (g dm/m^2 ; measured May 2015 in Silver River and January 2016 in Alexander Springs Creek) by mean biomass accrual rate ($\text{g dm m}^{-2} \text{d}^{-1}$). We divided this turnover rate by 365 to yield an annual biomass turnover frequency. Monthly growth rates were mean centered by site and log-transformed to explore seasonal growth patterns.

At each site, we measured water depth, velocity, SAV cover, epiphytic algal cover, and light availability at 1-mo intervals and sediment properties, water column chemistry, and porewater chemistry at 3-mo intervals. Water velocity was estimated at 60% of stream depth with a Sontek acoustic doppler velocimeter (San Diego, California), and water depth was obtained from the stadia rod of that device. SAV density and epiphyte cover were estimated visually by a single researcher with a 5-point Braun-Blanquet scale (0 = <1%, 1 = 1–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75% and 5 = 75–100% cover). We estimated stream surface light from both seasonal densiometer (% canopy cover) measurements in each cardinal direction as well as open-sky irradiance (W/m^2) measurements from a nearby weather station (<http://fawn.ifas.ufl.edu/>; Ocklawaha station).

We field filtered (0.45 μm) porewater and water column samples and stored them frozen in acid-washed 20-mL scintillation vials until laboratory analysis of $\text{NO}_x\text{-N}$ (Method 353.2; USEPA 1993c), $\text{NH}_3\text{-N}$ (Method 350.1; USEPA 1993b), OrthoP (Method 365.1; USEPA 1993d), Ca^{+2} (Method 200.7; USEPA 1994), and Cl^- concentrations (Method 300.0; USEPA 1993a) at the University of Florida Analytical Research Laboratory.

We collected ~ 1 L of sediment at each site to assess root zone conditions. Samples were dried at 60°C for 72 h, then ground and homogenized to pass through a 2-mm sieve, and analyzed for %C, %N, and %S with an elemental analyzer (Carlo Erba NA1500). We extracted sediment metals (P, K, Ca, Mg, Mn, and Fe) with a Mehlich-1 solution and measured them with an ICP-MS (Method 200.7; USEPA 1994). We estimated loss on ignition or % organic matter from mass loss following combustion of 5 g of dried sample at 450°C for 6 h.

We measured sediment redox potential (Eh) at 15-min intervals for 1 wk at each site with nine 8-mm submersible

platinum redox electrodes (Paleo Terra, Amsterdam, The Netherlands) installed at each of 3 sediment depths (shallow = 1.5 cm, medium = 4.5 cm, and deep = 7.5 cm). This replication was vital to capture heterogeneity in redox potential through the root zone (Vepraskas et al. 2001, Laing 2016). We fastened electrodes to PVC stands surrounding each plot to minimize sediment disturbance and maintain vertical electrode position. Eh initially declined with time because of sediment disturbance during installation, so we only analyzed Eh values after all electrodes had equilibrated (Laing 2016). We defined electrode equilibration as the point at which the slope of Eh vs time in a 3-h moving window (12 readings) was ≥ 0 . Eh values were normalized for pH (6.8) and temperature (22°C). All 3 depths were included in all subsequent prediction models.

Statistical analysis

We assessed if chemical and physical properties (e.g., flow velocity, light, sediment and water column solute composition, sediment Eh) differed between rivers with the Student's t -test applied to the mean observed values observed at all 32 sites. No transformations were necessary prior to comparisons of river physicochemical attributes.

To quantify the impact of repeated clipping on SAV biomass accrual, we evaluated SAV growth rates ($\text{g m}^{-2} \text{d}^{-1}$) as a function of time since initial harvest (mo). The resulting fitted slopes quantify changes in site productivity over the sampling period ($\text{g m}^{-2} \text{d}^{-1} \text{mo}^{-1}$), with negative values indicating that repeated clipping lowers site productivity.

We evaluated differences in growth rate between species with a 2-sample t -test on mean measured 1-mo shoot elongation rates. Temporal variability in SAV growth (log-normalized productivity rates) was assessed on a monthly basis across all sites over the sampling duration.

We used analysis of variance (ANOVA) to determine if SAV growth rates differed by site in each river and Tukey's honest significant difference (HSD) post-hoc contrasts to identify significant pairwise site differences to characterize spatial heterogeneity in growth. We used R for both tests (aov function for ANOVA; *lsmeans* with cld function for post-hoc Tukey's HSD; version 3.2.2; R Project for Statistical Computing, Vienna, Austria).

We used a 2-sample t -test to determine if SAV growth differed between rivers, and thereby, the potential NO_3^- effects on SAV growth. We used bivariate correlations (Pearson's r) to obtain preliminary insights about links between chemical and physical variables at each site and SAV growth. To specifically test the hypothesis that SAV growth is controlled primarily by physical attributes rather than by chemical and biological conditions, we evaluated multivariate relationships between SAV biomass accrual and environmental variables with both regression trees and general linear mixed-effects models. Regression trees use recursive binary partitioning of predictor variables, selecting each split

to maximize homogeneity of the response variable in the resulting nodes (Clark and Pregibon 1992). We implemented regression trees separately for each river with the *rpart* function (Therneau et al. 2015) in R. One advantage of this package is that it uses 10-fold cross-validation to reduce model overfitting. Given the relatively low sample sizes in this study, we further pruned the resulting trees based on the criterion that the selected simpler tree produced cross-validation errors within 1 standard deviation of the best fit tree.

We used general linear mixed-effects models (GLMM) to test for associations between SAV and different environmental predictors. This approach allows for fixed (e.g., environmental covariates such as light, depth, sediment redox, surface water and porewater chemistry) and random (site) effects. The slopes of the site effects indicate the sign and sensitivity of SAV growth responses to variation in the predictor variable. We used the *lmer* function in the *lme4* package (Bates and Sarkar 2007) in R for this analysis. To limit model complexity given the low power in our cross-site comparison, we initially selected those variables which were significantly ($p < 0.05$) correlated with SAV growth. We then iteratively omitted variables based on model performance, selecting the subset of covariates that best described SAV growth based on minimizing the Akaike information criterion (AIC).

Regression tree and GLMM models are complementary rather than redundant. Regression trees provide simple, non-parametric, and visually-intuitive predictions that help identify threshold behaviors in growth responses. However, the model output of regression trees can be sensitive to data idiosyncrasies, particularly for small datasets, leading to unwarranted confidence in the specific threshold values. Moreover, in contrast to regression trees, fitted GLMM slopes can provide information on the sensitivity of SAV growth to environmental variation.

RESULTS

River characteristics

We observed significant differences between rivers for only a few variables, most notably for canopy cover, water column NO_3^- , sediment Ca, and chloride concentrations (Table 1). Most variables, including water depth, flow velocity, algal cover, OrthoP, sediment organic matter, and redox potentials, did not differ significantly between rivers.

Sampling interval

Mean aboveground SAV biomass accrual (i.e., daily productivity) diminished with longer sampling intervals (1, 3, and 6 mo) as plots approached the biomass of the initial standing crop. These results indicate that intervals >1 mo between clippings underestimate maximum growth rates (Fig. 2A). Recovery time to initial biomass varied between

Table 1. Summary of river characteristics (mean $\pm$ SD) for 16 sites measured from May 2015 through December 2016 in Silver River and January through December 2016 in Alexander Springs Creek. Bolded variables indicate statistically-significant differences between rivers based on a Student's *t*-test ($p < 0.05$). BDL indicates measurements below analytical detection limits.

	Silver River	Alexander Springs Creek
Water depth (m)	0.64 $\pm$ 0.22	0.62 $\pm$ 0.13
Water velocity (m/s)	0.16 $\pm$ 0.11	0.1 $\pm$ 0.07
Incident light (W/m^2)	90.21 $\pm$ 54.50	148.67 $\pm$ 65.32
Canopy cover (%)	57.3 $\pm$ 23.4	34.9 $\pm$ 25.4
Algal cover (Braun–Blanquet)	3.0 $\pm$ 2.0	4.0 $\pm$ 1.0
Water column Ca^{+2} (mg/L)	80.8 $\pm$ 3.1	52.9 $\pm$ 15.0
Water column Cl^- (mg/L)	11.9 $\pm$ 0.9	305.4 $\pm$ 124.6
Water column $\text{NH}_3\text{-N}$ (mg/L)	0.17 $\pm$ 0.24	0.04 $\pm$ 0.01
Water column $\text{NO}_x\text{-N}$ (mg/L)	1.31 $\pm$ 0.23	0.14 $\pm$ 0.11
Water column OrthoP ($\mu\text{g/L}$)	37.7 $\pm$ 30.1	37.4 $\pm$ 6.7
Porewater Ca^{+2} (mg/L)	91.1 $\pm$ 21.7	63.9 $\pm$ 25.0
Porewater Cl^- (mg/L)	14.2 $\pm$ 4.3	367.8 $\pm$ 186.3
Porewater $\text{NH}_3\text{-N}$ (mg/L)	0.27 $\pm$ 0.34	0.27 $\pm$ 0.52
Porewater $\text{NO}_x\text{-N}$ (mg/L)	0.81 $\pm$ 0.42	0.12 $\pm$ 0.08
Porewater OrthoP ($\mu\text{g/L}$)	223.0 $\pm$ 414.4	101.7 $\pm$ 78.6
Sediment P (mg/kg)	13.2 $\pm$ 10.4	226.1 $\pm$ 194.8
Sediment K (mg/kg)	24.68 $\pm$ 14.4	62.0 $\pm$ 86.9
Sediment Ca (mg/kg)	6338.0 $\pm$ 1168.0	4185.0 $\pm$ 1606.0
Sediment Mg (mg/kg)	236.4 $\pm$ 121.9	707.0 $\pm$ 468.2
Sediment Mn (mg/kg)	0.29 $\pm$ 0.3	0.48 $\pm$ 0.42
Sediment Fe (mg/kg)	BDL	10.5 $\pm$ 11.2
Sediment %C	16.4 $\pm$ 6.2	8.5 $\pm$ 7.9
Sediment %N	0.6 $\pm$ 0.5	0.5 $\pm$ 0.5
Sediment %S	0.5 $\pm$ 0.5	0.3 $\pm$ 0.5
Sediment organic matter (%)	14.8 $\pm$ 11.7	13.5 $\pm$ 13.4
Shallow redox potential (mV) ^a	-115.8 $\pm$ 170.4	-151.1 $\pm$ 56.6
Medium redox potential (mV) ^a	-107.4 $\pm$ 163.2	-155.6 $\pm$ 86.9
Deep redox potential (mV) ^a	-175.5 $\pm$ 139.8	-175.8 $\pm$ 55.5

^a Redox probe depths: shallow (1–2 cm), medium (4–5 cm), and deep (7–8 cm).

rivers, with 72% recovery of initial biomass within 6 mo in Silver River but full recovery of initial biomass within 6 mo in Alexander Springs Creek (Fig. 2B).

The impact of repeated clipping on biomass recovery was negligible based on fitted slopes between time and mean site productivity over the sampling period (Fig. 2C). The mean slope across all sites was $0.09 \text{ g m}^{-2} \text{ d}^{-1} \text{ mo}^{-1}$ (± 0.09), and most of the slopes in both rivers were positive, suggesting that repeated clipping did not inhibit growth and may have modestly stimulated growth. We hereafter report results for only 1-mo clipping interval data.

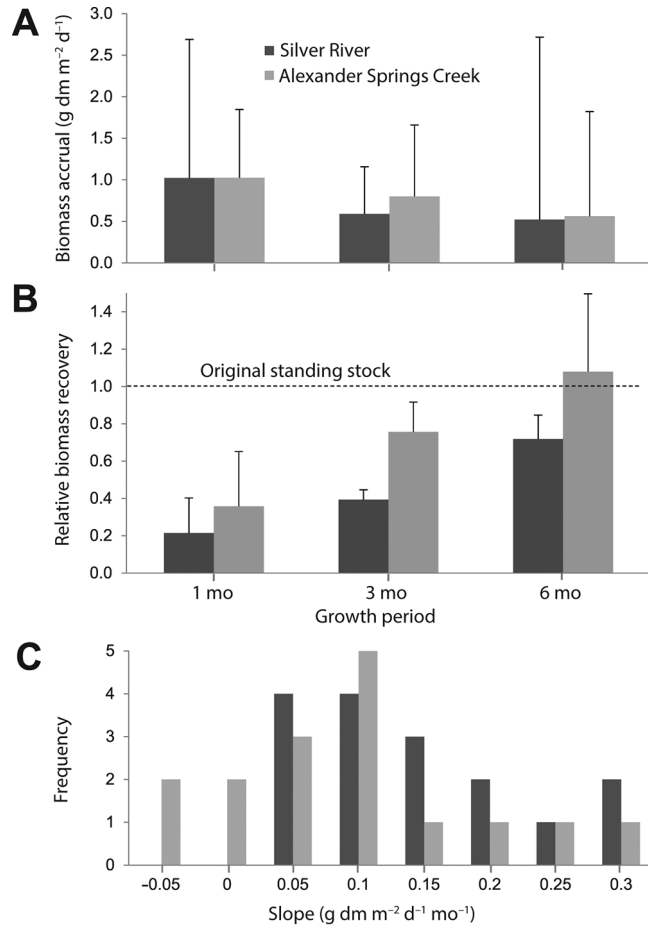


Figure 2. Summary of sampling impacts. A.—Mean ($\pm 95\%$ confidence interval) aboveground biomass accrual for 3 growth periods. B.—Aboveground biomass recovery relative to initial standing crop ($\pm 95\%$ confidence interval) vs time. C.—Frequency distributions of the slopes of monthly mean site productivity estimates ($\text{g dm}^{-2} \text{d}^{-1} \text{mo}^{-1}$) used to assess repeated clipping effects. Positive slopes indicate increasing SAV growth with repeated clipping.

Standing crop and growth rates

We observed high spatial heterogeneity in SAV standing crop and productivity across sites. Initial standing crop (dm) ranged from 40.9 to 394.7 g/m^2 (mean = 165.0) in Silver River and 34.6 to 371.2 g/m^2 (mean = 126.5) in Alexander Springs Creek. Site mean SAV productivity (dm) ranged from 0.11 to 2.31 $\text{g m}^{-2} \text{d}^{-1}$ (mean = 1.02) in Silver River and 0.39 to 1.89 (mean = 1.02) in Alexander Springs Creek. ANOVA revealed significant differences in mean productivity among sites within each river (Silver River: $F = 12.01$, $\text{df} = 15/184$, $p < 0.001$; Alexander Springs Creek: $F = 7.98$, $\text{df} = 15/131$, $p < 0.001$; Fig. 3A). Initial standing crop was weakly correlated with site productivity in Silver River ($r^2 = 0.36$, $p = 0.01$) but not in Alexander Springs Creek ($r^2 = 0$, $p = 0.83$; Fig. 3C).

Annual biomass turnover (mean growth:initial standing crop; y^{-1}) was positively correlated with productivity in Alexander Springs Creek (range = 0.78–9.70/ y ; $r^2 = 0.33$, $p = 0.02$) and Silver River (range = 0.89–4.94/ y ; $r^2 = 0.48$, $p < 0.01$; Fig. 3B). Mean SAV biomass turnover in Alexander Springs Creek (4.16/ y) was significantly higher ($p = 0.04$) than in Silver River (2.25/ y).

Mean shoot elongation in Silver River was 0.49 cm/d (range = 0.10–1.50 cm/d) for *S. kurziana* and 0.61 cm/d (range = 0.12–1.92 cm/d) for *V. americana*. In Alexander Springs Creek, where *V. americana* was the only SAV species, mean shoot elongation was 0.57 cm/d . Shoot elongation rates were significantly higher for *V. americana* than *S. kurziana* ($p = 0.03$) in Silver River. However, based on a *t*-test, *V. americana* growth rates did not differ between rivers ($p = 0.42$). Mean aboveground biomass accrual (1-mo growth period) was 1.02 $\text{g dm}^{-2} \text{d}^{-1}$ in both Silver River and Alexander Springs Creek (Fig. 2A).

Minimum growth was observed for both *S. kurziana* and *V. americana* in winter, and maximum growth for both species occurred in summer (Fig. 3D). Notably, only January and September (in Alexander) and July (in Silver) were significantly different from the annual mean. In Silver River, the monthly growth minimum occurred in January (0.83 $\text{dm m}^{-2} \text{d}^{-1}$; 64% of mean growth) and the maximum occurred in July (2.08 $\text{g dm}^{-2} \text{d}^{-1}$; 160% of mean growth). In Alexander Springs Creek, minimum growth occurred in January (0.78 $\text{g dm}^{-2} \text{d}^{-1}$; 76% of mean growth) with maximum growth in September (1.31 $\text{g dm}^{-2} \text{d}^{-1}$; 127% of mean growth).

Drivers of SAV growth

Based on bivariate correlations, few environmental factors were associated with SAV productivity. Sediment redox potential was the best univariate predictor of SAV in both rivers. In Silver River, the best single predictors were sediment redox potential ($r = +0.64$), canopy cover ($r = -0.62$), porewater Cl^- ($r = -0.37$), and epiphytic algal cover ($r = -0.36$). In Alexander River, the best predictors included sediment redox potential ($r = +0.49$), sediment Fe ($r = +0.32$), water column OrthoP ($r = -0.28$), and porewater Cl^- ($r = -0.24$).

The initial regression tree models that included every parameter were unstable and difficult to interpret, indicating overfitting and, thus, limited utility for predicting SAV growth. We therefore developed regression tree models with the subset of measured predictors (light, water velocity, algal cover, water depth, sediment organic matter, redox potential, $\text{NO}_x\text{-N}$, Cl^- , and OrthoP) that were most promising based on bivariate correlations. We included Cl^- in these models because its values varied within and across sites. Water column and porewater NH_4^+ were omitted because values were consistently near analytical detection limits. Even the cross-validated trees were likely to be overfitted and

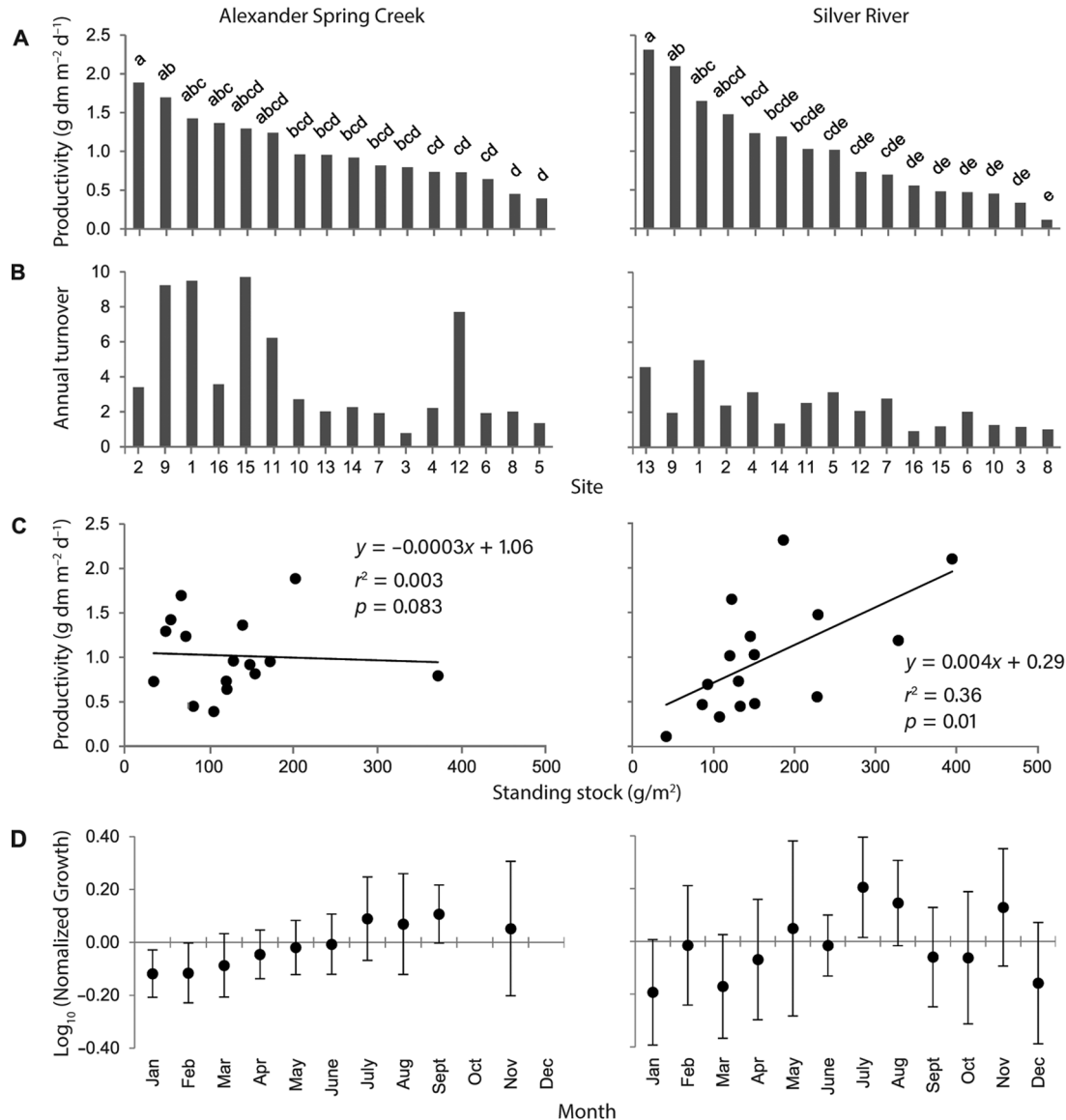


Figure 3. A.—Mean aboveground biomass accretion ranked by productivity. Different lowercase letters indicate significant differences (Tukey's HSD) between sites ($p < 0.05$). B.—Annual frequency of biomass turnover across all sites. C.—Relationship between initial standing crop and productivity at each site. D.—Mean-centered log₁₀-normalized daily SAV growth (+95% confidence interval) from January through December 2016.

unstable because of our limited sample size, so we focused on the primary and secondary splits as most informative for assessing SAV growth. In Silver River, low canopy cover (<33.3%) and high sediment redox potential (>−214 mV at 1.5-cm depth) predicted high SAV productivity (2.33 g dm m⁻² d⁻¹). Water velocity and sediment organic matter were also important factors in the regression trees (Fig. 4A). In Alexander Springs Creek, high sediment redox potential (>−141.3 mV at 4.5-cm depth) and low canopy cover (<42.2%) predicted high SAV productivity (2.01 g dm m⁻² d⁻¹). Water column Cl⁻, water depth, algal cover, and porewater OrthoP also influenced the prediction of SAV

productivity (Fig. 5A). Tree-based model goodness-of-fit for SAV growth was similar in both Silver River (Fig. 4; $R^2 = 0.53$, RMSE = 0.65 g dm m⁻² d⁻¹) and Alexander Springs Creek (Fig. 5; $R^2 = 0.57$, RMSE = 0.44 g dm m⁻² d⁻¹).

We considered multiple GLMM model configurations, including main effects and 2-way interactions. However, we only report the selected main effects results because 2-way interactions were inconsistent and weak, and including them uniformly produced higher AIC scores. The model with the lowest AIC in Silver River explained 50% of the SAV growth variation based on significant main effects of canopy cover,

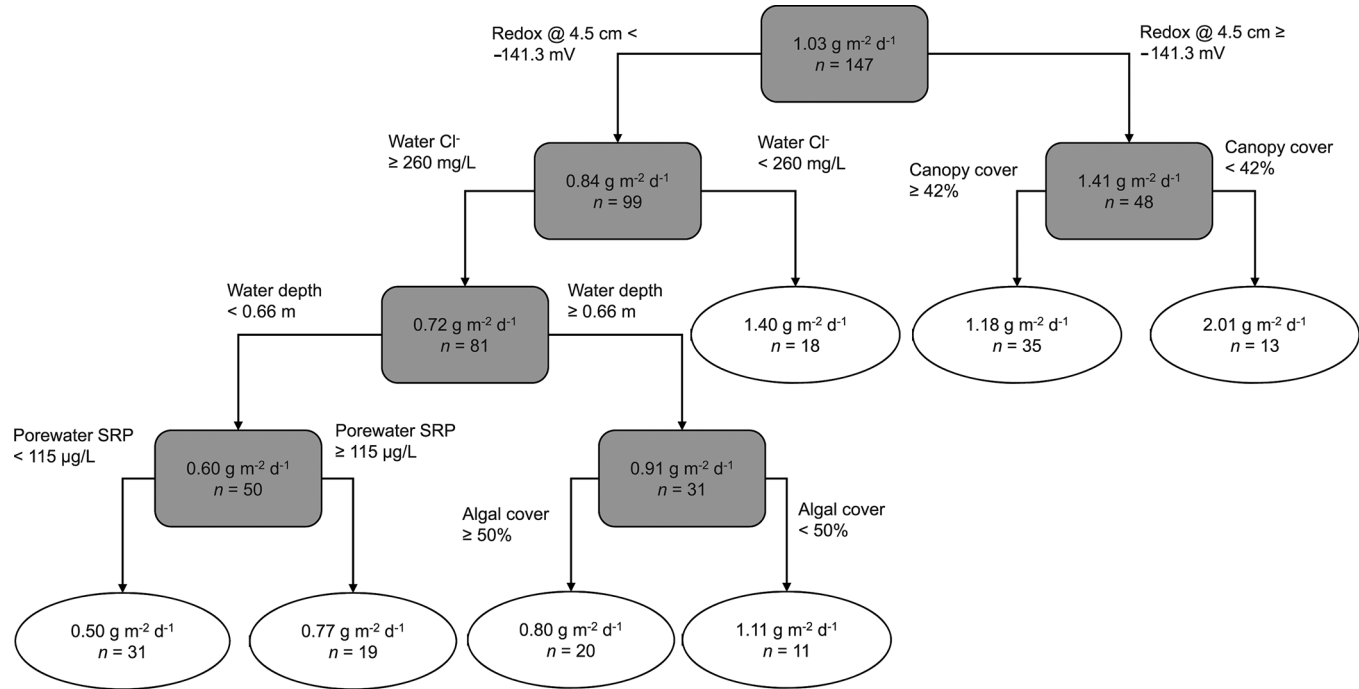


Figure 4. Regression tree for SAV growth in Silver River. Estimated aboveground productivity ($\text{g dm m}^{-2} \text{d}^{-1}$) and sample size (n) are included in decision and terminal nodes. At each decision node, an observation is assigned to daughter nodes based on a predictor variable threshold (e.g., canopy cover above or below 33%). Overall model $R^2 = 0.53$, with a root-mean squared error of $0.65 \text{ g m}^{-2} \text{d}^{-1}$.

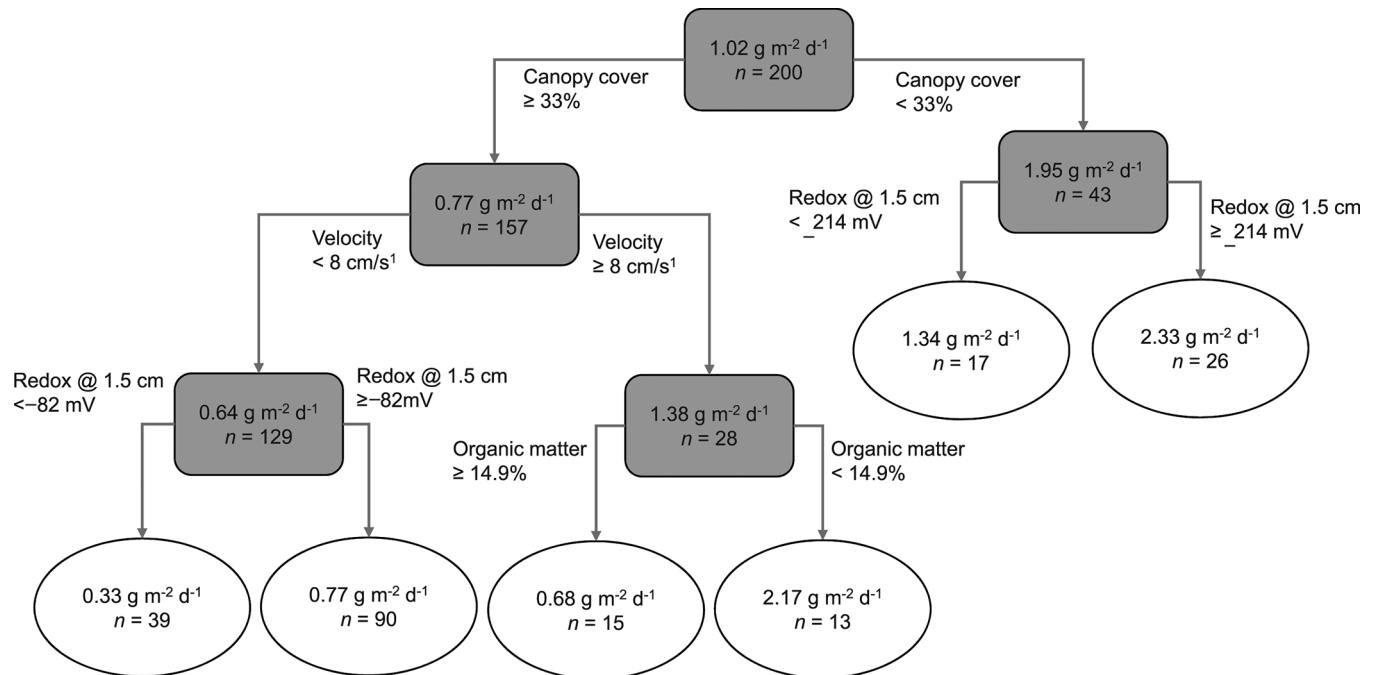


Figure 5. Regression tree for SAV growth at Alexander Springs Creek. Estimated aboveground productivity ($\text{g dm m}^{-2} \text{d}^{-1}$) and sample size (n) are shown for decision and terminal nodes. At each decision node, an observation is assigned to daughter nodes based on a predictor variable threshold (e.g., redox potential above or below -141.3 mV). Overall model $R^2 = 0.57$, with a root-mean squared error of $0.44 \text{ g m}^{-2} \text{d}^{-1}$.

Table 2. A.—Fitted model comparisons for SAV productivity in river from which the best model was selected (bold) based on minimum Akaike information criterion (AIC). Other variables (flow velocity, sediment OM, porewater and surface water Cl, algal cover) were rejected prior to model construction based on weak pairwise correlation with SAV growth. B.—Summary of the best-fit model goodness of fit and values of fitted main effects identified for each river, along with mean-centered standardized slope, standard error, and *t*-value. The Silver River model was statistically significant ($p < 0.001$) with a conditional R^2 of 0.50. The Alexander Springs Creek model was also significant ($p < 0.001$) with a conditional R^2 of 0.37.

A. Model comparisons						
Model Form	Silver AIC	Alexander AIC				
~f (Canopy)	536.7	303.7				
~f (PW_OrthoP)	567.9	303.5				
~f (SW_NO3)	574.8	303.5				
~f (PW_NO3)	562.2	296.9				
~f (Redox)	299.1	271.7				
~f (Canopy + Redox)	281.1	269.1				
~f (Canopy + Redox + PW_OrthoP)	265.6	251.2				
~f (Canopy + Redox + PW_NO3)	269.0	267.2				
~f (Canopy + Redox + PW_NO3 + PW_OrthoP)	267.8	254.1				
~f (Canopy + Redox + SW_NO3)	272.9	269.8				
~f (Canopy + Redox + PW_OrthoP + SW_NO3)	268.9	253.3				
B. Best Fit Model Summary						
	Silver River		Alexander Springs Creek			
Main effect	Standardized slope	Standard error	<i>t</i> -value	Standardized slope	Standard error	<i>t</i> -value
Canopy	−0.30	0.11	−2.65	−0.19	0.08	−2.43
Redox @ 4.5 cm	0.35	0.17	2.07	0.47	0.11	4.16
PW_OrthoP	−0.65	0.19	−3.44	−0.30	0.10	−2.88

sediment redox potential (at 4.5-cm depth), and porewater OrthoP (Table 2). We note that none of these predictor variables were significantly correlated, so variance inflation due to multicollinearity was negligible (variance inflation factor = 1.10, 1.13, and 1.04 for canopy, redox, and porewater SRP, respectively, where values >5 are considered cause for concern; Belsley et al. 1980). The lowest AIC model for Alexander Springs Creek explained 37% of the variation and, like the Silver River model, included significant main effects of canopy cover, sediment redox potential (at 4.5-cm depth), and porewater OrthoP (Table 2). No significant multicollinearity was evident (variance inflation factor = 1.26, 1.95, and 1.66 for canopy, redox, and porewater SRP, respectively). Comparisons among model candidates indicated that a similar model form yielded the lowest AIC for both rivers. Inclusion of site random effects ($n = 16$) yielded models for both rivers with slightly higher predictive power but also higher AIC, suggesting improved performance was due to overfitting. In both rivers, redox potential at the same depth (4.5 cm) was the strongest predictor with strong positive slopes indicating that higher Eh (more oxidized conditions)

leads to faster SAV growth—notably, inclusion of the other 2 redox depths (1.5 and 6 cm) yielded poorer models. Similarly, both models imply that light likely exerts a strong control on growth. SAV growth was negatively related to canopy cover on both rivers. Finally, SAV growth was negatively related to OrthoP, indicating that higher P concentrations inhibit SAV growth via mechanisms that are, as yet, unclear.

DISCUSSION

Spatial and temporal heterogeneity in SAV growth

The substantial spatial heterogeneity in SAV initial standing crop (40.9–394.7 g dm/m² in Silver River, 34.6–371.2 g dm/m² in Alexander Springs Creek) and mean growth (0.11–2.31 g m^{−2} d^{−1} in Silver River, 0.39–1.89 g m^{−2} d^{−1} in Alexander Springs Creek) underscores the need to understand SAV growth controls. Restoration success is frequently assessed by comparing ecosystem structure to reference conditions, and our findings reveal how spatially variable SAV growth and establishment can be. These results highlight the risk that poor growth responses following SAV restoration plantings may occur, particularly if we

fail to recognize critical site-specific factors that may actually influence growth (e.g., light, redox potential).

Growth was less variable over time than across space, although there was some evidence for consistent but subtle annual growth variation with peaks occurring in summer. Modest temporal variation in growth is consistent with relatively-constant stream surface light, which can occur when open sky irradiance and canopy cover vary inversely. This pattern of growth is also consistent with the chemical and thermal stability of spring ecosystems (Odum 1957b) because temperature strongly controls growth of these taxa elsewhere (Hauxwell et al. 2007). Most importantly, modest temporal variation in SAV growth suggests that the factors that control growth at a location are stable over time. Pre-restoration sampling of these specific environmental conditions is likely to be informative for predicting restoration success.

The mean measured SAV biomass we measured (165 g/m^2 in Silver River; 127 g/m^2 in Alexander Springs Creek) was lower than SAV biomass measured in previous studies. Quinlan et al. (2008) found Silver River biomass standing stocks of $584 \pm 402 \text{ g dm/m}^2$ in summer and $426 \pm 323 \text{ g dm/m}^2$ in winter. Odum (1957b) found 578 g dm/m^2 standing crop in upper Silver River. These studies imply that the distribution and abundance of SAV biomass has not changed significantly over the last 60 y despite significant increases in NO_3^- loading and changes in flow, recreation, and epiphyte cover. Similarly, the wet mass estimated by Canfield and Hoyer (1988) was 4400 g/m^2 in Alexander Springs Creek, roughly twice what we observed (after adjusting our dm measurements 1:10 for dry:wet mass; Cohen et al. 2017). In contrast, Nifong (2017) observed a mean wet mass standing crop of 1720 g/m^2 , and Hauxwell et al. (2007) measured total dm of *V. americana* (above and below ground, assuming 70% is aboveground) between 162 and 1013 g dm/m^2 in a spring-fed estuary in Florida. These studies are more closely aligned with our measured mean values and the high spatial variation in SAV standing crop.

The discrepancy between our low standing crop measurements and prior studies of the same systems (Odum 1957b, Duarte and Canfield 1990, Quinlan et al. 2008) is probably the result of sampling different types of sites. Our clipping method required sites to be shallow ($<1.5 \text{ m}$) to avoid use of SCUBA, necessitating the use of sites on channel margins. Channel margins may exhibit naturally lower standing crops and biomass accrual rates because of their substrate and light conditions (e.g., lower redox, high canopy cover). Despite this possible sampling effect, our uniform sampling approach across sites remains useful for comparing drivers of SAV growth.

Multivariate controls of SAV productivity

Both multivariate approaches were significantly more successful in predicting SAV growth than simple bivariate

predictors, indicating that controls on growth are complex. This result has important implications for management decision-making because it suggests a nuanced perspective is needed to understand the likelihood of site-based restoration success. Moreover, the 2 multivariate models offer complementary information relevant to managers. In one case (regression trees) the resulting model is intuitive and highly applicable, but threshold estimates are likely far more uncertain than estimated. The GLMM models are less intuitive, but the fitted slopes allow us to better explore the sensitivities of measured responses to continuous variation in the controlling variables, rather than overemphasizing threshold effects.

Notably, the central inference from both multivariate model types was similar across both rivers. SAV growth in springs appears to be controlled by light (positive effect), sediment redox conditions (positive effect), and porewater OrthoP (an unexpected negative effect). Water column Cl^- concentrations, water depth, flow velocity, and sediment organic matter composition were less important predictors. Given that the 2 river models were constructed independently, their convergence in structure, parameterization, and goodness-of-fit suggests some important generality for predicting SAV growth. This result is relevant for future management actions because it suggests our models may be used to predict SAV planting success at new sites.

Existing literature suggests light is the main factor controlling SAV distribution, abundance, and growth (Canfield and Hoyer 1988, Duarte and Canfield 1990, Hauxwell et al. 2007), but our results and those of others suggest that other factors may be of similar importance. Notably, Canfield and Hoyer (1988) suggested that substrate type, water depth, and water velocity influence growth. Butcher (1933) found that water velocity and substrate type in addition to light availability were key factors driving SAV growth. Our results suggest that researchers should continue to focus on light and flow velocity as well as redox potential and, by extension, sediment texture.

The mechanisms by which light and redox potential influence SAV growth are relatively well understood (Duarte 1991, Dennison et al. 1993, Sederias and Colman 2009), but the mechanism by which elevated OrthoP might have a negative effect on SAV growth is less clear. P is critical to plant growth, and increased P availability often results in accelerated production, but our models showed that increased P had a negative influence on SAV growth. This association could be the result of covariation of P with an unmeasured environmental parameter. Plants require a wide range of elements (e.g., N, P, K, Ca, Fe), so SAV growth may be limited by nutrients, such as Fe, that are depleted or absent in many springs (Kurz et al. 2015). OrthoP-caused growth inhibition may also result from indirect or interaction effects with sediment redox conditions or light. In oxidized sediments with high redox potential, phosphate complexes with Fe, reducing the amount of P available to plants

(Moore and Reddy 1994). As such, the presence of rooted macrophytes may inhibit porewater OrthoP availability via root zone oxidation. High levels of OrthoP do not cause decreased growth, but rather decreased growth (and attendant reduction in root zone oxidation) allows locally-lower redox conditions which, consequently, enhance P availability. However, we observed the OrthoP effect after including the direct effect of redox potential. Finally, diminished SAV productivity could result from indirect effects of elevated P availability on periphyton increases and the resulting reductions in light inputs (Dierberg et al. 2002). Further investigation of P inhibition is needed, even though systematic increases in P loads to springs have been observed in these spring ecosystems (Scott et al. 2004).

Redox potential

Despite marked spatial heterogeneity in redox conditions, mean site redox potential values (-306.6 to 172.2 mV in Silver River and -235.2 to -72.2 mV in Alexander Springs Creek) confirm highly reducing conditions (< -100 mV). These conditions could enable accumulation of phytotoxic compounds such as sulfide in the root zone (Reddy and DeLaune 2008). Redox potential was the best bivariate predictor of aboveground SAV productivity and the strongest predictor variable in both multivariate models. Indeed, we estimate that SAV productivity increases by $1 \text{ g m}^{-2} \text{ d}^{-1}$ for a redox potential increase of 200 mV in Alexander Springs Creek (slope = 0.005) and 350 mV in Silver River (slope = 0.0028). In short, our study suggests sediment redox conditions are required for successfully predicting site suitability for SAV planting.

However, the mechanisms behind the strong association between redox potential and SAV growth are not entirely clear. Redox potential controls nutrient availability and abundance of phytotoxic compounds in aquatic ecosystems (Reddy and DeLaune 2008). Our results support this as a mechanism because higher growth rates were associated with redox potentials in which phytotoxic compounds (e.g., sulfide and NH_4^+) are less likely to accumulate. SAV can alter sediment conditions and protect against phytotoxic compounds via rhizosphere oxidation (Sand-Jensen et al. 1982, Carpenter et al. 1983, Wigand et al. 1997). This aerated root zone may explain high microscale heterogeneity of sediment redox conditions, and further suggests that declines in SAV distribution and abundance for any reason (e.g., shading, disturbance, overgrazing) may alter redox potential. Thus, decreases in SAV cover could influence the growth and vigor of the remaining SAV as well as efforts to restore SAV assemblages via replanting.

Nitrate effects

NO_3^- was not associated with SAV growth in our study. Water column NO_3^- was uncorrelated with aboveground

SAV productivity across rivers ($r^2 = 0.00$, $p = 0.94$), and there was no significant difference ($p = 0.88$) in mean SAV biomass accrual between rivers. Together, these results support the hypothesis that SAV growth does not depend on NO_3^- and add to growing evidence that growth primary production (GPP) and SAV growth in these ecosystems are not, and historically were not, nutrient limited (Duarte and Canfield 1990, Heffernan et al. 2010, Nifong et al. 2014). SAV are stoichiometrically homeostatic across 3 orders of magnitude of N concentrations (Nifong et al. 2014), and autotrophic N demand is saturated via advection even at low concentrations (King et al. 2014). In light of weak evidence for N controlling growth rates, the regulatory emphasis on N concentration for SAV management overshadows the far clearer role of other drivers. Instead, a systems perspective (Odum 1957b) on SAV growth controls that explicitly considers light (Odum 1957a), redox potential (Laing 2016), herbivory (Liebowitz et al. 2014), water velocity (King 2014, Hensley and Cohen 2017), and micronutrients (Kurz et al. 2015) is crucial for effective spring ecosystem management.

Gross primary production

Primary production and respiration (i.e., metabolism) play a central role in ecosystem energy flow and elemental processing (Bernhardt et al. 2018). GPP, the aggregate photoautotroph fixation of C, is often measured at the reach scale by diel oxygen variation (Odum 1957a, b, Appling et al. 2018), but this approach does not readily reveal contributions from different vegetation types. We estimated SAV contributions to GPP (GPP_{sav}) based on measurements of aboveground SAV biomass accrual rates, which measures net primary production (defined as GPP less autotroph respiration, R_a). These estimates required several assumptions, all of which we estimated with ranges, from which we extracted uncertainty using a Monte Carlo simulation (10,000 permutations of parameters). Specifically, we estimated aboveground net primary production by multiplying aboveground net primary production by SAV root-to-shoot biomass ratios measured during vegetation surveys on Silver River (Cohen et al. 2017) and in other similar studies (Wigand et al. 1997, Van den Berg et al. 1999). For this parameter, we used a uniform distribution of ratios between 1.1 and 1.5. We then converted net primary production to GPP by assuming autotrophic respiration was 50% of GPP (Hall and Tank 2003, Hall and Beaulieu 2013; Monte Carlo uniform distribution range = 40–60%), which yielded GPP estimates ($\text{g biomass m}^{-2} \text{ d}^{-1}$). We converted GPP estimates to C fluxes ($\text{g C m}^{-2} \text{ d}^{-1}$) based on mean foliar C content for *S. kurziana* and *V. americana* blades of 36.8 and 34.2%, respectively, (uniform distribution range = 30–40%) from the same vegetation survey (Cohen et al. 2017). Finally, we converted GPP from C to O_2 with molecular weights, assuming a photosynthetic quotient of 1.0 (uniform distribution range = 0.9–1.1).

We estimate that SAV contributes 2.43 and 2.47 g O₂ m⁻² d⁻¹ to GPP in Silver River and Alexander Springs Creek, respectively. In Silver River, estimates of GPP_{SAV} ranged from 0.27 to 5.67 g O₂ m⁻² d⁻¹ across sites, with no systematic longitudinal variation. In Alexander Springs Creek, GPP_{SAV} estimates had a similar range of 0.95 to 4.57 g O₂ m⁻² d⁻¹, but upstream GPP_{SAV} exceeded downstream GPP_{SAV} (3.32 g O₂ m⁻² d⁻¹ vs 2.27 g O₂ m⁻² d⁻¹).

These GPP_{SAV} estimates were lower than open channel measurements made during the same period (Cohen et al. 2017). From May 2015 through December 2016, mean open-channel GPP was 8.76 g O₂ m⁻² d⁻¹ (±2.79 g O₂ m⁻² d⁻¹) in Silver River and 10.62 g O₂ m⁻² d⁻¹ (±3.28 g O₂ m⁻² d⁻¹) in Alexander Springs Creek (Cohen et al. 2017). We therefore estimate SAV accounts for ~25% of ecosystem GPP. Propagating uncertainties in the variable range estimates using the Monte Carlo simulation suggests SAV contributes between 12 and 40% of GPP in these rivers. These values are surprisingly low given the dominance of SAV in spring-river submerged biomass (Hoyer et al. 2004) and historical estimates of standing stock biomass (Odum 1957b, Munch et al. 2006).

Our estimates of relative SAV contribution to ecosystem GPP in Silver River and Alexander Springs Creek are consistent with findings from the St Lawrence River, where SAV accounted for 27% of the annual C budget (Vis et al. 2007). In the St Lawrence River, annual primary production is nearly equally distributed between submerged macrophytes, phytoplankton (34%), epiphyton (16%), and emergent macrophytes (23%).

Two plausible explanations exist for the surprisingly small fraction of open-channel GPP attributed to SAV growth. First, benthic and epiphytic algae may dominate GPP. Rapid biomass turnover rate (Odum 1957b) and relative abundance in many of the springs in Florida, both today and under historical conditions, may enable a metabolic contribution disproportionate to their standing stock. Second, systematic bias in our site selection process would lead to underestimates of the SAV contribution to GPP. Specifically, the densest SAV is typically in deep, well-lit parts of the channel, but our measurements were taken in shallow water near channel margins. These results suggest microflora are an important component of spring ecosystem productivity, although we likely underestimated SAV productivity by a factor of 2 or more, which implies that GPP_{SAV} is more important than our study suggests.

Our findings that SAV growth is likely controlled by local variation in light and sediment redox conditions and is independent of N concentrations underscore the need for a broadened scope of environmental management in Florida's springs. The fact that the underlying factors of light and sediment properties were consistent across both rivers will be useful for practitioners interested in maximizing the success of SAV restoration. Given the importance of SAV restoration to spring ecosystem management, expeditious

field-scale management experiments to validate the findings of this study are clearly warranted.

ACKNOWLEDGEMENTS

Author contributions: JM and MJC designed the study and wrote the paper. JM collected field measurements and analyzed results.

We gratefully acknowledge site access to Alexander Springs Creek provided by Ocala National Forest and to Silver River by Florida Department of Environmental Protection and Silver River State Park. Larry Korhnak and Chad Foster were tireless support during field data collection, and Joelle Laing provided assistance with redox measurements. Funding was provided by the St Johns River Water Management District under the auspices of the Collaboration Research Initiative for Springs Protection and Sustainability (CRISPS; Contract number 27789).

LITERATURE CITED

- Appling, A. P., J. S. Read, L. A. Winslow, M. Arroita, E. S. Bernhardt, N. A. Griffiths, R. O. Hall, J. W. Harvey, J. B. Heffernan, E. H. Stanley, E. G. Stets, and C. B. Yackulic. 2018. The metabolic regimes of 356 rivers in the United States. *Scientific Data* 5:180292.
- Aung, L. H. 1974. Root-shoot relationships. Pages 29–61 in E. W. Carson (editor). *The plant root and its environment*. University Press of Virginia, Charlotte, Virginia.
- Barko, J. W., and W. F. James. 1998. Effects of submerged aquatic macrophytes on nutrient dynamics, sedimentation, and resuspension. Pages 197–214 in E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christoffersen (editors). *The structuring role of submerged macrophytes in lakes*. Springer-Verlag, New York, New York.
- Barko, J. W., and R. M. Smart. 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecology* 67:1328–1340.
- Barko, J. W., R. M. Smart, and D. G. McFarland. 1991. Interactive effects of environmental conditions on the growth of submersed aquatic macrophytes. *Journal of Freshwater Ecology* 6:199–207.
- Bates, D. M., and D. Sarkar. 2007. *lme4*: Linear mixed-effects models using Eigen and R. (Available from: <https://cran.r-project.org/src/contrib/>)
- Belsley, D. A., E. Kuh, and R. E. Welsch. 1980. *Regression diagnostics: Identifying influential data and sources of collinearity*. John Wiley & Sons, New York, New York.
- Bernhardt, E. S., J. B. Heffernan, N. B. Grimm, E. H. Stanley, J. W. Harvey, M. Arroita, A. P. Appling, M. J. Cohen, W. H. McDowell, R. O. Hall, J. S. Read, B. J. Roberts, E. G. Stets, and C. B. Yackulic. 2018. The metabolic regimes of flowing waters. *Limnology and Oceanography* 63:99–118.
- Biggs, B. J. F. 1996. Hydraulic habitat of plants in streams. *Regulated Rivers: Research & Management* 12:131–144.
- Boedeltje, G., A. J. Alfons, J. P. Smolders, and J. G. M. Roelofs. 2005. Combined effects of water column nitrate enrichment, sediment type and irradiance on growth and foliar nutrient concentration of *Potamogeton alpinus*. *Freshwater Biology* 50:1537–1547.
- Brabandere, L. D., T. K. Frazer, and J. P. Montoya. 2007. Stable nitrogen isotope ratios of macrophytes and associated periphyton

- along a nitrate gradient in two subtropical, spring-fed streams. *Freshwater Biology* 52:1564–1575.
- Burkholder, J. M., K. M. Mason, and H. B. Glasgow. 1992. Water column nitrate enrichment promotes decline of eelgrass *Zostera marina*: Evidence from seasonal mesocosm experiments. *Marine Ecological Progress Series* 81:163–178.
- Butcher, R. W. 1933. Studies on the ecology of rivers: I. On the distribution of macrophytic vegetation in the rivers of Britain. *Journal of Ecology* 21:58–91.
- Camp, E. V., C. L. Staudhammer, W. E. Pine, J. C. Tetzlaff, and T. K. Frazer. 2014. Replacement of rooted macrophytes by filamentous macroalgae: Effects on small fishes and macroinvertebrates. *Hydrobiologia* 722:159–170.
- Canfield, D. E., and M. V. Hoyer. 1988. Influence of nutrient enrichment and light availability on the abundance of aquatic macrophytes in Florida streams. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1467–1472.
- Caraco, N. F., and J. J. Cole. 2002. Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. *Ecological Applications* 12:1496–1509.
- Carpenter, S. R., J. J. Elser, and K. M. Olson. 1983. Effects of roots of *Myriophyllum verticillatum* L. on sediment redox conditions. *Aquatic Botany* 17:243–249.
- Carpenter, S. R., and D. M. Lodge. 1986. Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany* 26:341–370.
- Cedergreen, N., and T. V. Madsen. 2003. Nitrate reductase activity in roots and shoots of aquatic macrophytes. *Aquatic Botany* 76:203–212.
- Chambers, P. A., E. E. Prepas, M. L. Bothwell, and H. R. Hamilton. 1989. Roots versus shoots in nutrient uptake by aquatic macrophytes in flowing waters. *Canadian Journal of Fisheries and Aquatic Sciences* 46:435–439.
- Clark L. A., and D. Pregibon. 1992. Tree-based models. Pages 377–419 in J. M. Chambers and T. J. Hastie (editors). *Statistical models in S*. Chapman Hall/CRC Press, Boca Raton, Florida.
- Cohen, M. J., J. B. Heffernan, A. Albertin, and J. B. Martin. 2012. Inference of riverine nitrogen processing from longitudinal and diel variation in dual nitrate isotopes. *Journal of Geophysical Research: Biogeosciences* 117:G01021.
- Cohen, M. J., M. J. Kurz, J. B. Heffernan, J. B. Martin, R. L. Douglass, C. R. Foster, and R. G. Thomas. 2013. Diel phosphorus variation and the stoichiometry of ecosystem metabolism in a large spring-fed river. *Ecological Monographs* 83:155–176.
- Cohen, M. J., J. A. McBride, R. T. Hensley, C. Reijo, L. V. Korhnak, C. R. Foster, L. Kirk, and S. Power. 2017. Nitrogen dynamics and metabolism. Section ES.4.2.1 in Collaborative research initiative on sustainability and protection of springs, CRISPS. Final report 2014–2017. St Johns River Water Management District, Palatka, Florida. (Available from: https://www.sjrwmd.com/static/waterways/springs-science/CRISPS_Final_Report-All_Sections.pdf)
- Copeland, R., N. A. Doran, A. J. White, and S. B. Upchurch. 2009. Regional and statewide trends in Florida's spring and well groundwater quality (1991–2003). Bulletin 69. Florida Geological Survey, Tallahassee, Florida. (Available from: <https://ufdc.ufl.edu/UF00095137/00001>)
- Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813.
- Dawes, C. J., and J. M. Lawrence. 1979. Effects of blade removal on the proximate composition of the rhizome of the seagrass *Thalassia testudinum* Banks ex König. *Aquatic Botany* 7:255–266.
- Dennison, W. C., R. J. Orth, K. A. Moore, J. C. Stevenson, V. Carter, S. Kollar, P. W. Bergstrom, and R. A. Batiuk. 1993. Assessing water quality with submersed aquatic vegetation: Habitat requirements as barometers of Chesapeake Bay health. *Bioscience* 43:86–94.
- Dierberg, F. E., T. A. DeBusk, S. D. Jackson, M. J. Chimney, and K. Pietro. 2002. Submerged aquatic vegetation-based treatment wetlands for removing phosphorus from agricultural runoff: Response to hydraulic and nutrient loading. *Water Research* 36:1408–1422.
- Dobberfuhl, D. R. 2007. Light limiting thresholds for submerged aquatic vegetation in a blackwater river. *Aquatic Botany* 86:346–352.
- Doyle, R. D. 2000. Effects of sediment resuspension and deposition on plant growth and reproduction. US Army Corps of Engineers, Vicksburg, Mississippi.
- Duarte, C. M. 1991. Seagrass depth limits. *Aquatic Botany* 27:15–26.
- Duarte, C. M., and D. E. Canfield. 1990. Macrophyte standing crop and primary productivity in some Florida spring-runs. *Water Resources Bulletin* 26:927–934.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, M. L. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews* 81:163–182.
- Dunn, A. E., D. R. Dobberfuhl, and D. A. Casamatta. 2008. A survey of algal epiphytes from *Vallisneria americana* Michx. (*Hydrocharitaceae*) in the Lower St Johns River, Florida. *Southeastern Naturalist* 7:229–244.
- Dunton, K. 1990. Production ecology of *Ruppia maritima* L. sl and *Halodule wrightii* Aschers in two subtropical estuaries. *Journal of Experimental Marine Biology and Ecology* 143:147–164.
- Gallegos, C. L. 1994. Refining habitat requirements of submersed aquatic vegetation: Role of optical models. *Estuaries* 17:187–199.
- Gallegos, C. L. 2005. Optical water quality of a blackwater river estuary: The Lower St Johns River, Florida, USA. *Estuarine, Coastal and Shelf Science* 63:57–72.
- Greenway, M. 1974. The effects of cropping on the growth of *Thalassia testudinum* (König) in Jamaica. *Aquaculture* 4:199–206.
- Hall, R. O., and J. J. Beaulieu. 2013. Estimating autotrophic respiration in streams using daily metabolism data. *Freshwater Science* 32:507–516.
- Hall, R. O., and J. L. Tank. 2003. Ecosystem metabolism controls nitrogen uptake in streams in Grand Teton National Park, Wyoming. *Limnology and Oceanography* 48:1120–1128.
- Hauxwell, J., J. Cebrian, J. A. Herrera-Silveira, J. Ramirez, A. Zaldivar, N. Gomez, and N. Aranda-Cirerol. 2001. Measuring production of *Halodule wrightii* Aschers: Additional evidence suggests clipping underestimates growth rate. *Aquatic Botany* 69:41–54.
- Hauxwell, J., J. Cebrian, and I. Valiela. 2006. Light dependence of *Zostera marina* annual growth dynamics in estuaries subject to different degrees of eutrophication. *Aquatic Botany* 84:17–25.

- Hauxwell, J., T. K. Frazer, and C. W. Osenberg. 2007. An annual cycle of biomass and productivity of *Vallisneria americana* in a subtropical spring-fed estuary. *Aquatic Botany* 87:61–68.
- Hauxwell, J., C. W. Osenberg, and T. K. Frazer. 2004. Conflicting management goals: Manatees and invasive competitors inhibit restoration of a native macrophyte. *Ecological Applications* 14:571–586.
- Heffernan, J. B., D. M. Liebowitz, T. K. Frazer, J. M. Evans, and M. J. Cohen. 2010. Algal blooms and the nitrogen-enrichment hypothesis in Florida springs: Evidence, alternatives, and adaptive management. *Ecological Applications* 20:816–829.
- Hensley, R. T., and M. J. Cohen. 2012. Controls on solute transport in large spring-fed karst rivers. *Limnology and Oceanography* 57:912–924.
- Hensley, R. T., and M. J. Cohen. 2017. Flow reversals as a driver of ecosystem transition in Florida's springs. *Freshwater Science* 36:4–25.
- Hoyer, M., T. Frazer, and S. Notestein. 2004. Vegetative characteristics of three low-lying Florida coastal rivers in relation to flow, light, salinity and nutrients. *Hydrobiologia* 528:31–43.
- Jacobs, R. 1979. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. *Aquatic Botany* 7:151–172.
- Jacoby, C., T. Frazer, R. Swett, S. Keller, and S. Notestein. 2007. Kings Bay vegetation evaluation. Final report. Southwest Florida Water Management District, Brooksville, Florida. (Available from: <https://www.swfwmd.state.fl.us/sites/default/files/medias/documents/Kings%20Bay%20Vegetation%20Evaluation%2C%202007.pdf>)
- James, C., J. Fisher, V. Russell, S. Collings, and B. Moss. 2005. Nitrate availability and hydrophyte species richness in shallow lakes. *Freshwater Biology* 50:1049–1063.
- Jeppesen, E., T. L. Lauridsen, T. Kairesalo, and M. R. Perrow. 1998. Impact of submerged macrophytes on fish-zooplankton interactions in lakes. Pages 91–114 in E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christoffersen (editors). *The structuring role of submerged macrophytes in lakes*. Springer-Verlag, New York, New York.
- Jones, G. W., S. B. Upchurch, and K. M. Champion. 1996. Origin of nitrate in groundwater discharging from Rainbow Springs, Marion County, Florida. Southwest Florida Water Management District, Brooksville, Florida.
- Katz, B. G. 2004. Sources of nitrate contamination and age of water in large karstic springs in Florida. *Environmental Geology* 46:689–706.
- King, S. A. 2014. Hydrodynamic control of filamentous macroalgae in a sub-tropical spring-fed river in Florida, USA. *Hydrobiologia* 734:27–37.
- King, S. A., J. B. Heffernan, and M. J. Cohen. 2014. Nutrient flux, uptake, and autotrophic limitation in streams and rivers. *Freshwater Science* 33:85–98.
- Kirk, J. T. O. 1994. *Light and photosynthesis in aquatic ecosystems*. Cambridge University Press, Cambridge, UK.
- Korschgen, C. E., and W. L. Green. 1988. American wild celery (*Vallisneria americana*): Ecological considerations for restoration. Technical Report 19. US Fish and Wildlife Service, Fish and Wildlife, Washington DC. (Available from: <https://pubs.er.usgs.gov/publication/2000897>)
- Kowalski, J. L., H. R. DeYoe, C. P. Krull, and T. C. Allison. 2009. Comparison of leaf-clipping and leaf-piercing techniques as applied to the seagrass *Syringodium filiforme*. *Bulletin of Marine Science* 85:159–172.
- Kurz, M. J., J. B. Martin, M. J. Cohen, and R. Hensley. 2015. Diffusion and seepage-driven element fluxes from the hyporheic zone of a karst river. *Freshwater Science* 34:206–221.
- Laing, J. M. 2016. Relationships between sediment redox potential and vegetation characteristics in Florida spring systems: Implications for restoration. PhD Thesis, University of Florida, Gainesville, Florida.
- Lapointe B. E., D. A. Tomasko, and W. R. Matzie. 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. *Bulletin of Marine Science* 54:696–717.
- Liebowitz, D. M., M. J. Cohen, J. B. Heffernan, T. K. Frazer, and L. V. Korhnak. 2014. Environmentally-mediated consumer control of algae proliferation in Florida springs. *Freshwater Biology* 59:2009–2023.
- Luzius, C., F. Guillemette, D. C. Podgorski, A. M. Kellerman, and R. G. M. Spencer. 2018. Drivers of dissolved organic matter in the vent and major conduits of the world's largest freshwater spring. *Journal of Geophysical Research: Biogeosciences* 123:2775–2790.
- Maberly, S. C., L. King, M. M. Dent, R. I. Jones, and C. E. Gibson. 2002. Nutrient limitation of phytoplankton and periphyton growth in upland lakes. *Freshwater Biology* 47:2136–2152.
- Madsen, J. D., P. A. Chambers, W. F. James, E. W. Kock, and D. F. Westlake. 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* 444:71–84.
- Madsen, T. V., and M. Søndergaard. 1983. The effects of current velocity on the photosynthesis of *Callitriche stagnalis* Scop. *Aquatic Botany* 15:187–193.
- Mattson, R. A., J. H. Epler, and M. K. Hein. 1995. Description of benthic communities in karst, spring-fed streams of North Central Florida. *Journal of the Kansas Entomological Society* 68:18–41.
- Moore, A., and K. R. Reddy. 1994. Role of Eh and pH on phosphorus geochemistry in sediments of Lake Okeechobee, Florida. *Journal of Environmental Quality* 23:955–964.
- Morgan, M. D., and C. L. Kitting. 1984. Productivity and utilization of the seagrass *Halodule wrightii* and its attached epiphytes. *Limnology and Oceanography* 29:1066–1076.
- Munch, D. A., E. J. Phelps, M. S. Allen, R. L., Knight, D. J. Toth, C. Huang, J. B. Davis, C. M. Fortich, W. L. Osburn, E. L. Quinlan, M. J. Woods, P. Cooney, R. A. Clarke, and S. L. Knight. 2006. Fifty-year retrospective study of the ecology of Silver Springs, Florida. Publication number SJ2007-SP4. St Johns River Water Management District, Palatka, Florida.
- Nichols, D. S., and D. R. Keeney. 1976. Nitrogen nutrition of *Microphyllum spicatum*: Uptake and translocation of ¹⁵N by ramets and roots. *Freshwater Biology* 6:145–154.
- Nifong, R. L. 2017. Experimental effects of grazers on autotrophic species assemblages across a nitrate gradient in Florida springs. *Aquatic Botany* 139:57–64.
- Nifong, R. L., M. J. Cohen, and W. P. Cropper. 2014. Homeostasis and nutrient limitation of benthic autotrophs in natural chemostats. *Limnology and Oceanography* 59:2101–2111.
- Odum, H. T. 1957a. Primary production measurements in eleven Florida springs and a marine turtle-grass community. *Limnology and Oceanography* 2:85–97.

- Odum, H. T. 1957b. Trophic structure and productivity of Silver Springs, Florida. *Ecological Monographs* 27:55–112.
- Osborne, T. Z., L. H. Placca, T. B. Schafer, and J. Johansen. 2017. Nitrate inhibition of submerged aquatic vegetation. Section ES.4.2.2 in Collaborative research initiative on sustainability and protection of springs, CRISPS. Final report 2014–2017. St Johns River Water Management District, Palatka, Florida. (Available from: https://www.sjrwmd.com/static/waterways/springs-science/CRISPS_Final_Report-All_Sections.pdf)
- Persson, L., and L. B. Crowder. 1998. Fish-habitat interactions mediated via ontogenetic niche shifts. Pages 3–23 in E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christoffersen (editors). *The structuring role of submerged macrophytes in lakes*. Springer-Verlag, New York, New York.
- Petticrew, E. L., and J. Kalf. 1992. Water flow and clay retention in submerged macrophyte beds. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2483–2489.
- Quinlan, E. L., E. J. Philips, K. A. Donnelly, C. H. Jett, P. Sleszynski, and S. Keller. 2008. Primary producers and nutrient loading in Silver Springs, FL, USA. *Aquatic Botany* 88:247–255.
- Reaver, N. G. F., D. A. Kaplan, R. A. Mattson, E. Carter, P. V. Sucsy, and T. K. Frazer. 2019. Hydrodynamic controls on primary producer communities in spring-fed rivers. *Geophysical Research Letters* 46:4715–4725.
- Reddy, K. R., and R. D. DeLaune. 2008. *Biogeochemistry of wetlands: Science and applications*. CRC Press, Boca Raton, Florida.
- Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquatic Botany* 3:55–63.
- Sand-Jensen, K., and J. Borum. 1984. Epiphyte shading and its effect on photosynthesis and diel metabolism of *Lobelia dormanna* L. during the spring bloom in a Danish lake. *Aquatic Botany* 20:109–119.
- Sand-Jensen, K., C. Prahl, and H. Stokholm. 1982. Oxygen release from roots of submerged aquatic macrophytes. *Oikos* 38:349–354.
- Santschi, P., P. Höhener, G. Benoit, and M. Buchholtz-ten Brink. 1990. Chemical processes at the sediment-water interface. *Marine Chemistry* 30:269–315.
- Scott, T., G. Means, R. Meagan, R. Means, S. Upchurch, R. Copeland, R. Jones, and A. Willet. 2004. Springs of Florida. Bulletin Number 66. Florida Geological Survey, Tallahassee, Florida, USA. (Available from: http://aquaticcommons.org/1284/1/bulletin_66.pdf)
- Sederias, J., and B. Colman. 2009. Inhibition of *Chara vulgaris* oospore germination by sulfidic sediments. *Aquatic Botany* 91:273–278.
- Smith, V. H. 2003. Eutrophication of freshwater and coastal marine ecosystems a global problem. *Environmental Science and Pollution Research* 10:126–139.
- Stevenson, J. C., L. W. Staver, and K. Staver. 1993. Water quality associated with survival of submersed aquatic vegetation along an estuarine gradient. *Estuaries* 16:346–361.
- Stevenson, R. J. 1996. The stimulation and drag of current. Pages 321–340 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: Freshwater benthic ecosystems*. Academic Press, San Diego, California.
- Stevenson, R. J., A. Pinowska, A. Albertin, and J. O. Sickman. 2007. Ecological condition of algae and nutrients in Florida springs: The synthesis report. Florida Department of Environmental Protection, Tallahassee, Florida. (Available from: https://www.researchgate.net/publication/238737639_Ecological_Condition_of_Algae_and_Nutrients_in_Florida_Springs_The_Synthesis_Report)
- Szafraniec, M. L. 2014. Spectral distribution of light in Florida spring ecosystems: Factors affecting the quantity and quality of light available for primary producers. PhD Thesis, University of Florida, Gainesville, Florida.
- Therneau, T., B. Atkinson, and B. Ripley. 2015. *rpart*: Recursive partitioning and regression trees. (Available from: <http://CRAN.R-project.org/package=rpart>)
- Titus, J. E., and M. S. Adams. 1979. Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria spiralis* L. *Oecologia* 40:273–286.
- Tomasko, D. A., and K. H. Dunton. 1995. Primary productivity in *Halodule wrightii*: A comparison of techniques based on daily carbon budgets. *Estuaries* 18:271–287.
- Tomlinson, P. B. 1974. Vegetative morphology and meristem dependence—The foundation of productivity in seagrasses. *Aquaculture* 4:107–130.
- USEPA (United States Environmental Protection Agency). 1993a. Method 300.0: Determination of inorganic anions by ion chromatography (Rev 2.1). Environmental Monitoring Systems Laboratory, Office of Research and Development, United States Environmental Protection Agency, Cincinnati, Ohio.
- USEPA (United States Environmental Protection Agency). 1993b. Method 350.1: Determination of ammonia nitrogen by semi-automated colorimetry (Rev 2.0). Environmental Monitoring Systems Laboratory, Office of Research and Development, United States Environmental Protection Agency, Cincinnati, Ohio.
- USEPA (United States Environmental Protection Agency). 1993c. Method 353.2: Determination of nitrate-nitrite by automated colorimetry (Rev 2.0). Environmental Monitoring Systems Laboratory, Office of Research and Development, United States Environmental Protection Agency, Cincinnati, Ohio.
- USEPA (United States Environmental Protection Agency). 1993d. Method 365.1: Determination of phosphorus by semi-automated colorimetry (Rev. 2.0). Environmental Monitoring Systems Laboratory, Office of Research and Development, United States Environmental Protection Agency, Cincinnati, Ohio.
- USEPA (United States Environmental Protection Agency). 1994. Method 200.7: Determination of metals and trace elements in water and wastes by inductively coupled plasma-atomic emission spectroscopy (Rev 4.4). Environmental Monitoring Systems Laboratory, Office of Research and Development, United States Environmental Protection Agency, Cincinnati, Ohio.
- Van den Berg, M. S., M. Scheffer, E. Van Nes, and H. Coops. 1999. Dynamics and stability of *Chara* spp. and *Potamogeton pectinatus* in a shallow lake changing in eutrophication level. *Hydrobiologia* 408:335–342.
- Vepraskas, M. J., M. Polizzotto, and S. P. Faulkner. 2001. Redox chemistry of hydric soils. Pages 85–105 in M. J. Vepraskas and C. B. Craft (editors). *Wetland soils: Genesis, hydrology, landscapes, and classification*. CRC Press, Boca Raton, Florida.

- Vis, C., C. Hudon, R. Carignan, and P. Gagnon. 2007. Spatial analysis of production by macrophytes, phytoplankton and epiphyton in a large river system under different water-level conditions. *Ecosystems* 10:293–310.
- Wetzel, R. G., and M. Søndergaard. 1998. Role of submerged macrophytes for the microbial community and dynamics of dissolved organic carbon in aquatic systems. Pages 133–148 *in* E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christoffersen (editors). *The structuring role of submerged macrophytes in lakes*. Springer-Verlag, New York, New York.
- Wigand, C., J. C. Stevenson, and J. C. Cornwell. 1997. Effects of different submersed macrophytes on sediment biogeochemistry. *Aquatic Botany* 56:233–244.
- Zieman, J. C., and R. G. Wetzel. 1980. Productivity in seagrasses: Methods and rates. Pages 87–116 *in* R. C. Phillips and C. P. McRoy (editors). *Handbook of seagrass biology: An ecosystem perspective*. Garland STPM Press, New York, New York.
- Zimmerman, R. C. 2003. A biooptical model of irradiance distribution and photosynthesis in seagrass canopies. *Limnology and Oceanography* 48:568–585.