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ORIGINAL PAPER

Measuring Bulrush Culm Relationships to Estimate Plant Biomass Within a Southern California Treatment Wetland

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Abstract Assessment of emergent vegetation biomass can be time consuming and labor intensive. To establish a less onerous, yet accurate method, for determining emergent plant biomass than by direct measurements we collected vegetation data over a six-year period and modeled biomass using easily obtained variables: culm (stem) diameter, culm height and culm density. From 1998 through 2005, we collected emergent vegetation samples (*Schoenoplectus californicus* and *Schoenoplectus acutus*) at a constructed treatment wetland in San Jacinto, California during spring and fall. Various statistical models were run on the data to determine the strongest relationships. We found that the nonlinear relationship: $CB = \beta_0 DH^{\beta_1} 10^{\varepsilon}$, where CB was dry culm biomass (g m^{-2}), DH was density of culms × average height of culms in a plot, and β_0 and β_1 were parameters to estimate, proved to be the best fit for predicting dried-live above-ground biomass of the two *Schoenoplectus* species. The random error distribution, ε, was either assumed to be normally distributed for mean regression estimates or assumed to be an unspecified continuous distribution for quantile regression estimates.

Keywords Aquatic vegetation · Non-destructive sampling · *Schoenoplectus acutus* · *Schoenoplectus californicus* · Wetland plant biomass · Wetland plant density

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Introduction

Processes that occur in wetlands are complex and interrelated. In order to evaluate overall performance of a wetland, hydrology, vegetation, and soils all need to be considered (Reddy and D'Angelo 1994). Although the hydrologic cycle is the primary factor affecting vegetation growth, microbial activity, and soil biogeochemical processes (Reddy and D'Angelo 1994; Kadlec and Knight 1996; Mitsch and Gosselink 2000), vegetation productivity and general overall macrophyte health are also important in maintaining the sustainability of the wetland and the health of the ecosystem (Balcombe et al. 2005).

Treatment wetlands are constructed systems designed to maximize wetland functions to achieve specific outcomes (Howard-Williams 1985; Kadlec and Knight 1996; Thullen et al. 2005). Constructed treatment wetland design is often restricted by the area of the available land parcel, the existing topography, soil type and texture, previous uses, water quantity, and water quality. The wetland design must provide dependable water flow, water depth, loading rates, and retention time, while insuring proper mixing, adequate aerobic or anoxic zones depending on the goals of the project, and little or no short-circuiting, all within the template of the existing space and climatic conditions (IWA 2000). In short, proper design is important to ensure that essential components are functioning properly for the natural processes to occur at their optimum (Mitsch and Gosselink 2000).

Vegetation is also an extremely important element in the proper design and functioning of a treatment wetland (Thullen et al. 2005). Location of vegetation stands, the particular plant species in those stands, individual plant or culm size and density, and the health of the aquatic vegetation may all play a role in treatment efficiency. It is important to plant appropriate plant species in suitable locations to encourage their growth, proliferation, and sustainability (Thullen et al. 2005).

Vegetation status should therefore be evaluated as one indicator of wetland function. Sampling methods can be destructive and differ in labor intensity and cost. We wanted to determine whether routinely obtained non-destructive measurements can accurately predict biomass when biomass sampling is too destructive, logistically difficult, or too costly This paper provides information on whether non-destructive sampling provides accurate estimates for the above-ground emergent biomass in our wetland system through time.

Study Site

We worked at a 9.9-ha surface-flow wetland constructed in 1994 to create migratory bird habitat and to reduce the ammonium-nitrogen (NH_4-N) levels of secondary-treated wastewater from the San Jacinto Valley Regional Water Reclamation Facility (Facility), located about 135 km southeast of Los Angeles, California. The wetland was planted with two indigenous bulrush species, *Schoenoplectus californicus* (C.A. Meyer) (Galen Smith 1997, personal communication) and *S. acutus* (G.H.E. Muhlenberg ex J. Bigelow) (Smith 1995), and has the general outline of a hand with five inlet fingers. Water enters the wetland at the tip of each finger and exits through four outlets in the thumb (illustrated in Sartoris et al. 2000a; Thullen et al. 2008). During the summers of 1998 and 2002, the wetland was drained and allowed to dry in order to burn off the above-ground vegetation. Subsequently, portions of the marsh bottom were deepened to create additional water depths of 2 m, changing the original vegetated-marsh to open-water ratio of 80:20 (Configuration 1) to 50:50 in 1998 (Configuration 2), and then to 30:70 in 2002 (Configuration 3). Details of the various configurations, operations, and investigations that have occurred at this site have been reported by Walton et al. (1997), Sartoris et al. (2000a), Smith et al. (2000), Thullen et al. (2002, 2005, 2008), Andersen et al. (2003), and Nelson and Thullen (2008). In addition to water quality and flow measurements, monitoring the growth characteristics of the two plant species (discussed here) as well as plant and sediment elemental analyses were done biannually and annually, respectively.

During the course of our investigations, we documented several specific differences between the two plant species. Morphological differences between *S. acutus* and *S. californicus* during the middle of the growing season are subtle. Identifications are verified by comparing their seed morphology (Correll and Correll 1975), but *S. californicus* generally has more triangularly shaped culms that are basic green in color, while *S. acutus* culms are round and bluish-green in color. The allometric relationships between the two species can vary significantly, however, between late fall through early spring due to the phenology of the two species. *Schoenoplectus acutus*, a ubiquitous wetland plant throughout North America, senesces every winter and new shoots emerge from the rhizomes each spring. *Schoenoplectus californicus* occurs in generally warmer climates of the south and western U.S. (http://www.ars-grin.gov/cgi-bin/npgs/html/taxon.pl?409604 2009) and does not senesce each winter when healthy, but instead loses individual culms intermittently. Due to this seasonal difference, culm heights, diameters, and therefore biomass, can differ significantly between the two species. Consequently biomass predictions for the two species were calculated separately.

Methods

Vegetation Monitoring

Vegetation monitoring was routinely done during the spring and fall of the collection years as a way to establish how plant growth was initiating in the spring and then to determine the maximum growth of the season. *Schoenoplectus californicus* (California bulrush) and *S. acutus* (hardstem bulrush) were sampled in May 1998, May and September 1999, May and September 2000, May and October 2001, June and October 2003, June and October 2004, and June and October 2005.

Vegetation coverage for each species during each sampling period was estimated using a geographical information system (GIS) based on aerial photography (1:2400) obtained near the time of sampling. The area estimates were used for determining total plant biomass within the wetland at specific times (Table 1) and using those values to compare treatment capabilities related to plant coverage (see Sartoris et al. 2000a, b).

We measured above-ground and below-ground plant biomass, culm density, diameter, and height. Initially (1998–2000), culm biomass and morphological data were collected by destructive sampling within 10–14 0.25-m^2 quadrats randomly located within the treatment wetland. Live above-ground vegetation (culms), dead culms (detritus), and root/rhizome biomass were separately weighed first as fresh weights (with adherent water removed) and

Table 1 Areal vegetation coverage by species during biannual sampling events

		S. californicus	*S. acutus*
Sampling dates	Wetland configuration	Coverage (ha)	Coverage (ha)
May-98	1	6.89	0.73
May-99	2	0.03	0.00
Sep-99	2	2.13	0.00
May-00	2	3.05	0.00
Sep-00	2	3.34	0.00
May-01	2	3.77	0.00
Oct-01	2	4.11	0.00
Jun-03	3	1.77	0.13
Oct-03	3	2.16	0.18
Jun-04	3	2.70	0.26
Oct-04	3	2.55	0.25
Jun-05	3	3.02	0.23
Oct-05	3	2.88	0.29

then after air drying to constant weight, i.e., dry weight. Prior to the biomass collection, diameters and heights of 10 culms within the quadrats were measured and all culms were counted. Height measurements were taken from the sediment line to the culm tip and diameters were measured just above the sediment line.

Beginning in May 2000, we reduced the quadrat size to 0.06 m^2. Due to time and budget constraints, biomass samples were not taken in May and October 2001, but culm density, diameters, and heights were measured in a separate set of 14 0.25 m^2 quadrats. After 2003, the number of quadrats was reduced to seven and the 0.06 m^2 quadrat was used. Above-ground biomass was measured in June and October 2003 and 2004, but root material was not sampled in 2004. Culm density, diameters, and heights were measured and recorded from 14 0.06 m^2 quadrats in June and October 2005, but biomass was not measured.

During the September 1998 burn we did not measure sediment temperatures. However, due to the number of plants which were negatively affected by that burn, we deployed Omegapellets®, a temperature melt material in pellet form, (manufactured by Omega Engineering, Stamford, CT) prior to the July 2002 burn. Pellets with melting temperatures of 66°, 79°, 93°, 149°, and 177°C were placed in terra cotta plates and secured at the sediment surface or buried under 10 cm of soil at 14 marsh locations throughout the wetland. Six weeks later, they were retrieved and melting results were recorded.

Statistical Analyses

The biomass of culms in a plot is a function of density and culm size (diameter and height). We considered two forms of nonlinear, multiplicative statistical models: (1) $CB = \beta_0 DH^{\beta_1} 10^{\varepsilon}$ and (2) $CB = \beta_0 DH^{\beta_1} + \varepsilon$, where CB was dry culm biomass (g m^{-2}), DH was density of culms × average height of culms on a plot, β_0 and β_1 were intercept and slope parameters to estimate, and ε was a random error distribution either assumed to be normally distributed for mean regression estimates or assumed to be an unspecified continuous distribution for quantile regression estimates. Model (1) assumes a multiplicative error structure with variance changing with the mean of culm biomass and was the model form selected because it was more consistent with the observed heterogeneous variance pattern (Fig. 1). This model was easily estimated in its linearized form with

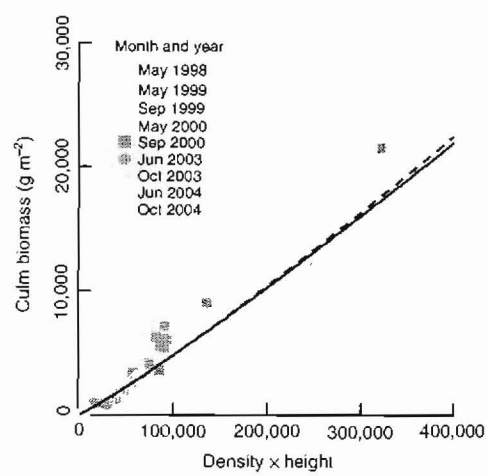

Fig. 1 Culm biomass (g dry weight m^{-2}) and density × height (DH) for n=61 plots by year and month for *Schoenoplectus californicus*. Dotted line is estimated mean regression and solid line is estimated median (0.50 quantile) regression assuming a common model (1) for all seasons and years

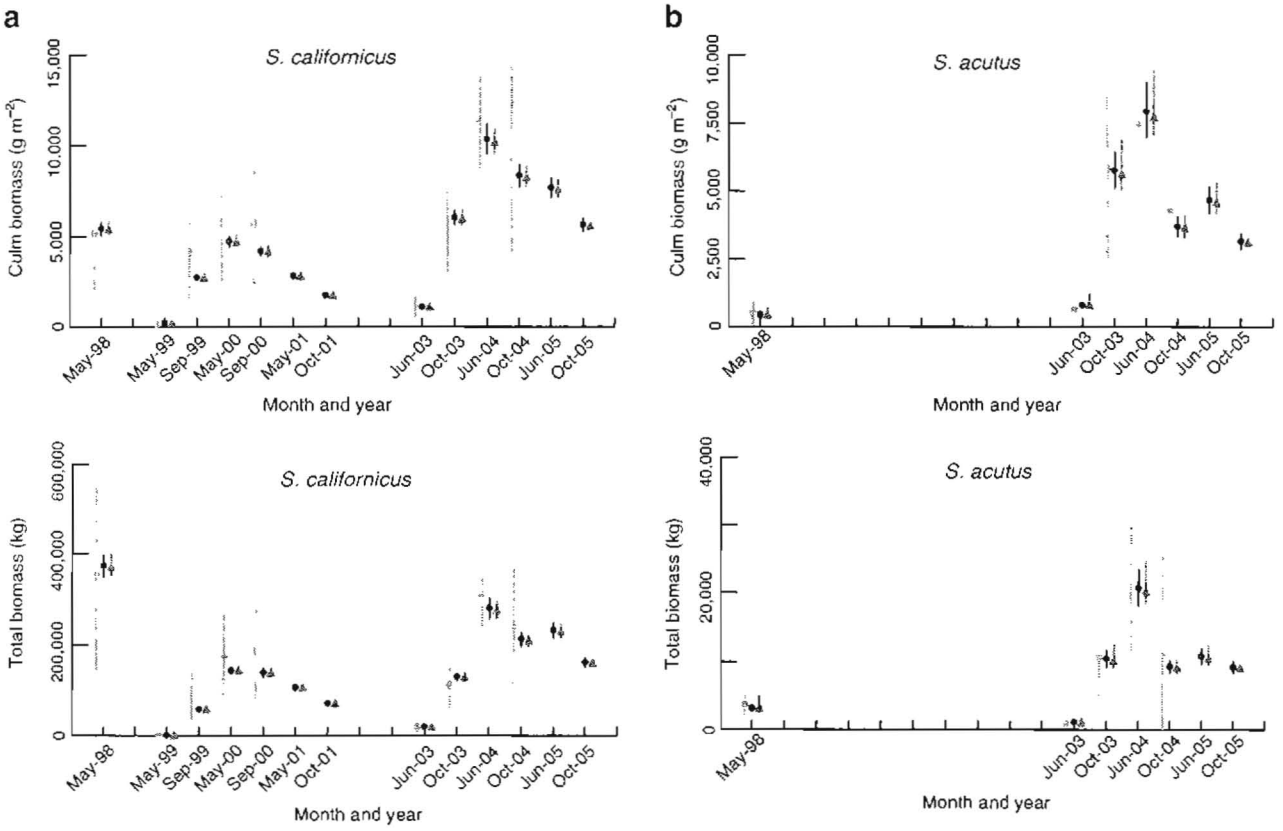

Fig. 2 Average live culm biomass (g dry weight m^{-2}) and total live culm biomass (total dry weight of species in kg × total area covered by the species within the wetland) of (a) *S. californicus* and (b) *S. acutus* within the San Jacinto Wetland Research Facility during the investigation period. Solid red circles are sample estimates, open black circles are back-transformed OLS mean regression estimates, and solid blue triangles are back-transformed 0.50 quantile regression estimates. Bars are 95% (*S. californicus*) or 90% (*S. acutus*) confidence intervals

linear regression by taking logarithms (base 10), $\log_{10}(CB) = \log_{10}\beta_0 + \beta_1(\log_{10}DH) + \varepsilon$. Model (2) was estimated in its multiplicative form with nonlinear regression but was not selected because the additive, homogeneous variance pattern was not consistent with the observed data (Fig. 1). Although the observed relationship between culm biomass and density × height was nearly linear over 80% of the range of the data (Fig. 1), nonlinearity was evident near the origin where culm biomass and density × height both approached zero. Because culm diameter was strongly correlated with culm height (r=0.75 for *S. californicus* and r=0.73 for *S. acutus*), including diameter as a multiplicative function of *DH* never improved model fit and was not considered further.

We used both ordinary least squares (OLS) regression to estimate changes in mean biomass with *DH* and linear quantile regression (Cade and Noon 2003; Koenker 2005) to estimate changes in the percentiles of biomass with *DH*. The quantile regression estimates provide a natural accommodation of additional heterogeneity in the response not reflected by the multiplicative error term in model (1) because it allows unequal slopes (rates of change) in the additive log-log scale not accounted for by the mean regression model. Additionally, the quantile regression estimates are not based on an assumed parametric error distribution as are OLS estimates of the mean regression. The predicted values for an upper and lower quantile regression estimate at any selected *DH* provide a distribution-free approach to estimating prediction intervals for a single new observation, e.g., 0.95 and 0.05 quantile regressions estimate endpoints for a 90% prediction interval. Furthermore, because the quantile regression estimates are equivariant to monotonic transformations like $\log_{10}$, it is possible to back-transform estimates to the original data scale without bias, something that is not true for the estimated mean regression. We estimated 90% prediction intervals for a single new plot observation for *S. californicus* based on back-transforming estimated 0.05 and 0.95 quantile regressions and by back-transforming estimated prediction intervals from the mean regression model.

Although the back-transformed estimate of the mean from the mean regression model is inherently biased, back-transformed estimates of the prediction intervals from the mean regression model are not biased because they are quantiles of a normal distribution. Because our sample size was so much smaller for *S. acutus*, we only estimated 80% prediction intervals from either the regression quantile or mean regression approach. All statistical models were estimated with functions available in R (R Development Core Team 2008; lm() for the linear mean regression model and rq() in the quantreg package for linear quantile regression). Confidence intervals on quantile regression estimates were based on inverting a rank score test with the default weighting to account for heterogeneity.

The median (0.50 quantile) regression estimate provides an alternative to the mean as a point estimate of predicted culm biomass. However, because neither the median (0.50 quantile) nor mean regression models in the logarithmic scale provide estimates of mean biomass when back-transformed to the arithmetic scale (both are estimates of the median), we used the nonparametric smearing estimate of Duan (1983) to provide unbiased estimates of mean biomass, similar to implementations in Runkel et al. (2004). The smearing estimate multiplies the exponentiated estimates (and confidence interval endpoints) of the mean or median regressions made in the logarithmic scale by the average of the exponentiated residuals, $10^{\hat{y}} \times n^{-1} \sum_{i=1}^{n} 10^{e_i}$, where $\hat{y}$ and e are the predicted values and residuals, respectively, from the mean or median regressions. Mean biomass was estimated for each month and year combination from smearing estimates for both the mean and median (0.50 quantile) regression models by obtaining regression estimates and confidence intervals corresponding to the mean of *DH* for that time period. This provided model-based estimates of mean biomass for time periods both when culm biomass was and was not measured, based both on an assumed normal distribution and with the less restrictive assumption of an unspecified continuous distribution.

Results

Throughout the entire study period, overall total wetland plant biomass differed between the two species due to the larger proportion of *S. californicus* relative to *S. acutus* in the total wetland vegetative cover (Fig. 2a and b). Additionally, the 1998 September burning of the above-ground vegetation negatively affected *S. acutus* more than *S. californicus*. Temperatures were not measured at that time, but sediment surface temperature sample results monitored during the June 2002 burn did not exceed 93°C with the exception of one sample. Even so, many *S. acutus* rhizomes just under, or on, the sediment surface were killed. *Schoenoplectus acutus* was further disadvantaged because water depths in the marsh areas were maintained at an average 27 cm, which is generally too deep for survival of new shoots, particularly when the parent plants are already stressed. Most of the *S. acutus* coverage during 2003–2005 was due to plants that had survived the burn and were located along the wetland perimeter in shallower standing water or in saturated soil conditions. As they recovered after the burn they expanded laterally into the marsh areas.

Although our initial modeling efforts for *S. californicus* suggested some differences among year (1998, 1999, 2000, 2003, and 2004) and season (spring months of May and June and fall months of September and October) combinations, much of this difference was driven by the restricted range of density × height measured for each of the nine combinations of season and year (Fig. 1). We explored an option of expanding model (1) to include separate slopes and intercepts for spring and fall months, ignoring annual differences. The joint test of the hypothesis that these two additional parameters were zero (P=0.068 for mean regression and P=0.316 for median regression) and the reduction in Akaikie Information Criterion (Burnham and Anderson 1998, difference in AICc = (−101.35) − (−100.28) = −1.07) indicated only weak support for selecting the model with separate slopes and intercepts by season. An examination of predictions for the model with separate slopes and intercepts for seasons also indicated poor model fit for fall at *DH* <60,000 due to few (3) observations in this range. The model fit for spring was very good for *DH* <60,000 because of many observations in this range and the model with common slopes and estimates for both seasons yielded comparable fit. We, therefore, chose to make predictions and estimate prediction intervals based on the model that ignored seasonal differences. There were too few observations for *S. acutus* to consider models that differed among seasons.

The regression models for *S. californicus* all indicated relationships with an increasing rate of change in culm biomass with increasing *DH* as all the estimated exponents for model (1) were >1.0 (Fig. 3, Table 2). The 90% prediction intervals for *S. californicus* culm biomass at *DH* <100,000 differed less than for *DH* >100,000 for the quantile regression and mean regression models (Fig. 3), but were narrower for the quantile regression estimates at high *DH*. For example, at *DH*=20,000, the 90% prediction interval based on the quantile regression estimates was [466, 1183] g m^{-2} and based on normal distribution estimates was [521, 1244] g m^{-2}. At *DH*=200,000, the quantile regression interval was [7469, 14890] g m^{-2} and the normal distribution interval was [7370, 17441] g m^{-2}. This can be attributed both to the improved modeling of heterogeneity with the quantile regression approach and as

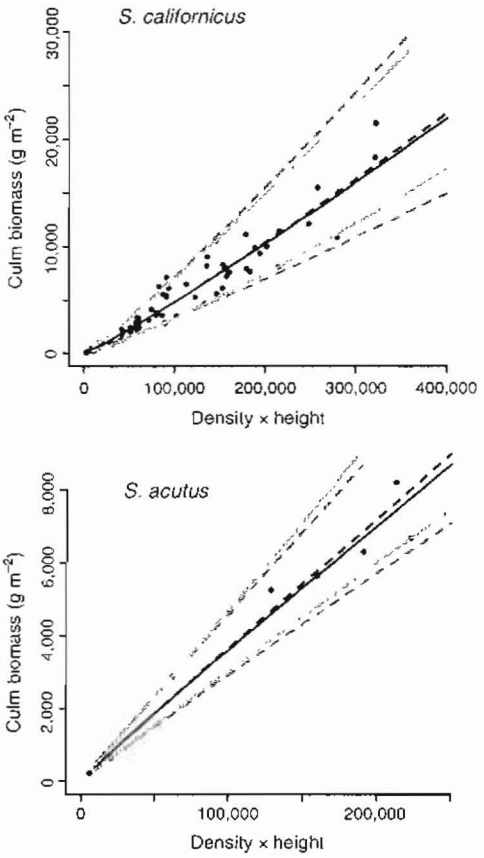

Fig. 3 Culm biomass (g dry weight m^{-2}) and density × height (*DH*) for n=61 plots for *S. californicus* and for n=10 plots for *S. acutus*. Dashed black lines are estimated mean regressions and upper and lower dashed blue lines define 90% (*S. californicus*) or 80% (*S. acutus*) prediction intervals based on a normal distribution assumption and the mean regression estimates for model (1). Solid black lines are estimated median (0.50 quantile) regressions for model (1). Solid upper and lower red lines are estimated 0.95 and 0.05 quantile regressions for *S. californicus* forming 90% prediction intervals or 0.90 and 0.10 quantile regressions for *S. acutus* forming 80% prediction intervals

a consequence of the normal distribution being a poor approximation of the error distribution in the mean regression model. Point estimates of predicted culm biomass for *S. californicus* were similar whether based on the mean or median (0.50 quantile) regression models, consistent with the symmetric nature of the error distribution. The median predicted values at *DH*=20,000 and *DH*=200,000 were 813 and 10,242 g m^{-2}, respectively, and the mean predicted values were 805 and 11,337 g m^{-2}, respectively. These both are estimates of median biomass in the back-transformed arithmetic scale. Estimates of mean and total biomass and their confidence intervals from the smearing estimate on back-transformed mean and median regression estimates were very similar and are graphed in Fig. 2a. The model based estimates had much narrower confidence intervals than the simple, sample estimates of biomass of *S. californicus*, both because of the additional information provided by the modeled relationship with *DH* and because samples across all months and years contributed to the estimated sampling variation. Note that the wide confidence intervals of the simple, sample estimates of mean and total biomass overlap the model based estimates (Fig. 2a).

In contrast to *S. californicus*, all but the 0.90 quantile regression for *S. acutus* indicated slightly decreasing rates of change in culm biomass with increasing *DH* as the estimated exponents were <1.0 (Fig. 3, Table 2). The 80% prediction intervals for *S. acutus* culm biomass were of similar length for the quantile regression and mean regression estimates, but the estimates for the quantile regression prediction intervals were shifted to slightly higher biomass values compared to the intervals from the mean regression (Fig. 3). For example, at *DH*=20,000, the 80% prediction interval based on the quantile regression estimates was [623, 905] g m^{-2} and based on normal distribution estimates was [606, 959] g m^{-2}. At *DH*=200,000, the quantile regression interval was [6008, 9554] g m^{-2} and the normal distribution interval was [5721, 9110] g m^{-2}. The median predicted values at *DH*=20,000 and *DH*=200,000 were 774 and 7,013 g m^{-2}, respectively, and the mean predicted values were 762 and 7,219 g m^{-2}, respectively. With an n=10 it is difficult to expect the normal distribution to be a very good approximation but it is also unreasonable to expect the quantile regression estimates to be very precise. Estimates of mean and total biomass and their confidence intervals from the smearing estimate on back-transformed mean and median regression estimates were very similar (Fig. 2b). The model based estimates had narrow confidence intervals but sample sizes for measured biomass of *S. acutus* were insufficient to provide useable confidence intervals for simple, sample estimates of mean biomass in most month and year combinations.

Discussion

We measured various morphological characteristics of two species of bulrush within our site twice per year for six years to assess their rate of establishment and determine vegetation productivity and sustainability under three wetland configurations. During several of these sampling events we were physically or financially unable to collect biomass samples but proceeded to collect the other less costly and less physically challenging measurements that were available to us. Regression analyses were then used to develop biomass estimates from the non-destructive sampling methods in order to predict dry weight of the above-ground emergent vegetation.

Table 2 Parameter estimates for mean, and quantile regressions for *S. californicus* (n=61 plots) and for *S. acutus* (n=10 plots) for model (1) estimated in linearized form by using $\log_{10}$ transformation of culm biomass as a function of density × height. Probabilities for coefficient of determinations test the null hypothesis that $\beta_1=0$.

Parameter	Estimate	Lower 95% CI	Upper 95% CI	Coefficient of determination
S. californicus				
Mean				R^2=0.96, P<0.001
β_0	−1.89633	−2.17956	−1.61309	
β_1	1.11527	1.05767	1.17387	
0.05 quantile				
β_0	−2.51639	−8.10569	−1.77821	
β_1	1.20537	1.04255	1.58087	
0.50 quantile				R^1=0.79, P<0.001
β_0	−1.82230	−2.15945	−1.47705	
β_1	1.10030	1.03076	1.15545	
0.95 quantile				
β_0	−1.65725	−2.01215	0.46360	
β_1	1.09981	0.73509	1.18961	
S. acutus				
Mean				R^2=0.99, P<0.001
β_0	−1.31670	−1.72573	−0.90767	
β_1	0.97626	0.89066	1.06186	
0.10 quantile				
β_0	−1.43758	na	na	
β_1	0.98401	na	na	
0.50 quantile				R^1=0.90, P=0.021
β_0	−1.22864	−1.62052	−0.83169	
β_1	0.95728	0.88036	1.01880	
0.90 quantile				
β_0	−1.44685	na	na	
β_1	1.02377	na	na	

True plant production is difficult to measure and there is a need for standardization of productivity estimation techniques (Hopkinson et al. 1978; Good et al. 1982; Gross et al. 1991). Various methods for estimating emergent aquatic vegetation biomass using non-destructive sampling techniques coupled with various statistical models have been used with various outcomes. Teal and Howes (1996) found their allometric equations could yield accurate estimates of aboveground biomass in their salt marsh investigations and found that measurements taken in any single year could be applied to other years with suitable precautions to account for seasonal cycles. However, Clarke and Jacoby (1994) found "no distinct seasonal patterns for *Juncus kraussii*'s above-ground biomass" when evaluating the biomass and above-ground productivity of salt-marsh plants in Australia. After collecting shoot density, and above- and below-ground biomass, Tanner (1996) found that *Schoenoplectus validus* showed a near linear growth of new culms, reaching an above-ground biomass of about 1.65 kg m^{-2}, but his data were from a 4-month mesocosm study in 190-l polyethylene tanks and therefore couldn't be extrapolated to longer term. Gouraud et al. (2008) found that measuring only 20 shoots of *Schoenoplectus maritimus* (*Bolboschoenus maritimus*) for height and diameter was adequate as an appropriate non-destructive method for quantifying primary production in a marsh in southern France. However, they found that their non-destructive sampling underestimated biomass particularly at low levels. In contrast, Giroux and Bédard (1988) reported an overestimation of *Schoenoplectus americanus* biomass by non-destructive sampling. But as Gouraud et al. (2008) point out, non-destructive methods can offer an alternative to destructive sampling especially when morphometric parameters and shoot biomass are used to create allometric equations of aboveground biomass.

We found that using the nonlinear multiplicative statistical model, $CB = \beta_0 DH^{\beta_1} 10^{\varepsilon}$, avoided problems of under- or overestimating biomass that were evident if we attempted to use a linear model due to the fact the relationship was not strictly linear, especially as DH approached zero. However, productivity among individual small quadrats might vary over a range >4,000 g m^{-2} at DH >110,000 for *S. californicus*, as indicated by our model based prediction intervals. However, our back-transformed model estimates of mean (or total) biomass were relatively precise, whether estimated with median or mean regression in the logarith-

mic scale. A comparison of the model estimates of means with those from the simple. sample estimates (Fig. 2a and b) suggest some over and under estimation that might be due to model lack-of-fit. Some model lack-of-fit is expected because we lacked sufficient sample sizes to estimate models by month and year combinations, and yet there was some evidence that the multiplicative relations were not consistent across all years and seasons. The degree to which this is an issue can only be resolved by obtaining larger samples within each season and year.

Under-ground biomass was impossible to predict at this site because wetland burn events at different times affected the below-ground material in different ways at different locations within the wetland. This was probably due to variation in the temperatures reached at different wetland locations [likely determined by the above-ground detrital mass, soil moisture, and microclimatic conditions at any given location (Brooks 2002)] and whether rhizomes were above or below the sediment. In addition to fire impacts, very deep water depths (exceeding the sampler's reach) prevented the collection of root and rhizome biomass material during several sampling events.

While seasons and variations in nutrient loading from wastewater treatment plant operations or agricultural activities can significantly influence variations in nitrogen removals (Gottschall et al. 2007; Thullen et al. 2008), the two seasons sampled at this site (spring and fall) did not prove to be important in predicting significant changes in biomass production and did not add any strength to the model. Longer-term growth patterns of the plant community played a more important role based on the general sigmoid (S-shaped) plant growth curves exhibited by the two species (Fig. 2a and b). These logistic curves do not conform perfectly to the typical S-shaped growth curve reaching a maximum standing crop, but instead the growth pattern of our bulrush follows a curve representing a more complex life cycle within a limited environment (Krebs 1972). We found that predicting aquatic plant biomass using the nonlinear regression models described above proved to explain the growth curves more accurately.

Since plant densities and harvesting frequency have significant effects on biomass yields (Reddy et al. 1983), it stands to reason that with extensive destructive sampling (removing the biomass and thus reducing the regenerative capacity of the community) growth decreases. Coupled with the time required to collect all the above- and below-ground plant material within the quadrat, clean off soil, algal, and detrital material, and appropriately dry the material for weighing, requires a great deal of time just for one sample. It necessitates a fraction of the time to count culms and measure a sub-sample of the culm heights. Provided the density and height model is adjusted for each particular site, the model should provide the necessary information for a fraction of the cost of collecting biomass. So, in evaluating treatment capabilities and relating them to the existing macrophyte biomass within the wetland, we have found that the model can accurately predict above-ground biomass using the non-destructive sampling data we collected during every sampling event.

Conclusions

Biomass can vary significantly between the two otherwise similar bulrush species, *Schoenoplectus californicus* and *S. acutus*, depending upon the time of year. This is largely due to the marked difference in their annual phenological responses. However, during the growing season, the morphology of the species is very similar. Measuring their establishment, biomass production, and survival over 6 years has provided the data to establish some morphological and allometric relationships. Using the nonlinear, multiplicative statistical model, $CB = \beta_0 DH^{\beta_1} 10^{\varepsilon}$, and in agreement with Gouraud et al. (2008), the estimate can be used provided it is tested and adjusted appropriately for each study. Estimates were obtained both from a regression model that relied on an assumed parametric (normal) error distribution and from a quantile regression model that only assumed some unspecified continuous distribution. The prediction intervals for individual quadrats for the latter regression approach tended to be narrower than for the parametric model, especially at larger biomass values, but differences between confidence intervals on estimated means were less pronounced.

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