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Physical variables driving epiphytic algal biomass in a dense macrophyte bed of the St. Lawrence River (Quebec, Canada)

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Abstract

The variables affecting epiphyton biomass were examined in a sheltered, multispecies macrophyte bed in the St. Lawrence River. Alteration of light penetration, resulting from the presence of dense macrophytes forming a thick subsurface canopy, primarily determined epiphyton biomass. Seasonal decrease of water levels also coincided with major increases in biomass. Plant morphology was the next important variable influencing epiphytic biomass, whereas the contribution of other variables (sampling depth, macrophyte species, relative abundance of macrophytes, and temperature) was low. Groups of lowest epiphyte biomass (0.1–0.6 mg Chl*a* g^{-1} DW) were defined by the combination of a low percentage of incident light (<13% surface light) and simple macrophyte stem types found below the macrophyte canopy. Highest epiphyte biomass (0.7–1.8 mg Chl*a* g^{-1} DW) corresponded to samples collected in mid-July and August, under high irradiance (>20% surface light) and supported by ramified stems. Our results suggest that epiphyton sampling should be stratified according to the fraction of surface light intensity, macrophyte architecture, and seasonal water level variations, in decreasing order of influence.

Introduction

Epiphytic algae are major contributors to the primary production of wetlands, rivers and lakes (Hooper & Robinson, 1976; Cattaneo & Kalff, 1980; Goldsborough & Robinson, 1996) and thus support littoral food chains (Vadeboncoeur et al., 2002). The quantification of epiphyte algal biomass has been hindered by their notorious variability that has been reported at small (m) and large (km) spatial scales (Cattaneo et al., 1993; Lalonde & Downing, 1991).

Variability in periphytic assemblages has been attributed to water movement, temperature, nutrients, and grazers (Cattaneo & Kalff, 1980; Kairesalo, 1983; Wetzel, 1983; Steinman & McIntire, 1986; Lowe, 1996; Saravia et al., 1998). Available light (incident radiation and water transparency) is crucial since it regulates production and biomass (Wetzel, 1983; Hill, 1996; Pillsbury & Lowe, 1999), species composition (Steinman & McIntire, 1986) and succession (Tuji, 2000) of epiphytic algae. Plant architecture also plays a role in variability of epiphytic algal biomass; macrophytes with finely dissected leaves, such as *Myriophyllum* sp., tend to develop greater epiphytic biomass than simpler plants, partly due to their high surface-to-biomass ratio (Cattaneo &

Kalff, 1980; Lalonde & Downing, 1991) or to their fractal dimension (Jeffries, 1993). Contrasting plant growth forms influence small scale water circulation and hence colonization rate, sediment resuspension, and water transparency (Vermaat et al., 2000). Plants affect their physical and chemical environment to different degree according to their density per unit of water volume (O'Neill-Morin & Kimbal, 1983) and their capacity to form a canopy (Frodge et al., 1990). The influence of the host plant has been difficult to separate from other environmental variables that may lead to differences in the biomass or composition of epiphytic algae (e.g. Moss, 1976).

This study quantifies the relative importance of physical variables affecting variability of epiphytic algal biomass at an intermediate spatial scale (1–100 m), by considering a single, sheltered, densely canopied multispecific macrophyte bed in the St. Lawrence River (Canada). We hypothesized that variables affecting the biomass of submerged macrophytes (plant architecture, water depth, and light; Hudon et al., 2000) would also affect the biomass of their epiphytes. Our study also contrasted the effects of host plant species and architecture. These results may allow us to identify the most efficient way to quantify and predict epiphyte biomass in a structurally heterogeneous environment.

Study site

The study site is located in a large, protected St. Lawrence River wetland (154 ha) at the western (upstream) tip of the Boucherville islands, 1 km across from the Montreal Harbour (Latitude 45° 60′ N, Longitude 73° 49′ W). The submerged macrophyte bed (14.5 ha) under study is located on the downstream side of a 300-m jetty that shelters the site from prevailing southwesterly winds. Water depth at this site ranges from 0 to 3 m and is characterized by low water velocities (0–0.4 m s^{-1}); the area is primarily influenced by water originating from the Great Lakes, with high conductivity, a slightly basic pH and high water clarity (Table 1). The St. Lawrence River is characterized as a meso-eutrophic system (Hudon, 2000). As a result of these water characteristics and the sheltered situation of the bed, abundant macrophytes form a dense subsurface canopy among which metaphyton (filamentous algae) can form dense patches in summer.

Materials and methods

Sampling

Epiphytes growing on submerged macrophytes were sampled on 13 occasions during the growing season, between June 15 and October 1, 1999, usually over 2 days every second week. On each sampling day, about ten samples were collected at pre-selected random locations and depths within the gridded study area. Samples ($n = 126$) were collected by a diver, by gently enclosing sections of macrophyte in a 600-ml hinged cylindrical Plexiglas box (15 cm high × 7.5 cm diameter), thus quantitatively retrieving all tightly and loosely attached epiphytic algae. The random design and high macrophyte biomass, sometimes, made it impossible to enclose in the sampler a single macrophyte species without disturbing the epiphyton assemblage. Accordingly, 33 out of the 126 (26%) samples contained several species. The submerged plant sections, their epiphytes and enclosed water were funneled into a 1-l jar and kept cool until the return to the laboratory for further processing on the same day.

The temperature was continuously recorded at an elevation of 0.8 m below chart datum (CD), outside of the dense macrophyte bed, for the entire study period. Daily water level data for Montreal Harbour (Jetty No. 1, gauging station No. 15520) were obtained from the Department of Fisheries & Oceans (2000). For each sample, water temperature, pH, specific conductivity, and dissolved oxygen (Hydrolab H_2O) were measured at the depth of epiphyte/macrophyte sampling. Spatial coordinates (D-GPS Marconi/Loktor), total and sampling depth, and characteristics of the plant stand around the sampling point (dominant taxa and relative abundance, on a scale of 1–3, for sparse to high plant abundance) were also recorded. Water velocity was estimated using either a mechanical flow meter (Global Water Flow Probe, model FP201) or, for slow currents or dense plant stands, from the drift of a floating sphere.

Table 1. Physical and chemical characteristics recorded during the 1999 sampling season at Boucherville wetlands

Variable (units)	Mean (s.d., *n*)
Water depth (m)	1.26 (0.73, 133)
Current speed (m s^{-1})	0.09 (0.09, 43)
Conductivity (μS cm^{-1})	273.6 (7, 120)
pH	8.3 (0.3, 120)
Light extinction coefficient in open water (K, m^{-1})	0.72 (0.5, 5)
Total dissolved phosphorus (μg P l^{-1})	10 (2.2, 35)
Total phosphorus (μg P l^{-1})	28.5 (19.1, 39)
Silicate (μg SiO_2 l^{-1})	629.0 (110.9, 39)
Nitrate (μg $N{-}NO_3^-$ l^{-1})	138.2 (67.3, 39)
Ammonium (μg $N{-}NH_4^+$ l^{-1})	15.4 (6.2, 39)

Incident solar photosynthetically available radiation (PAR, LI-COR LI-190SB) was continually recorded in the Montreal Harbour. In the field, underwater PAR (LI-COR LI-193SA 4π probe) at sampling depth was measured for each sample. Precise measurement of light within dense macrophyte beds was achieved by mounting the underwater light probe with a pressure gauge at the end of a 3-m-long retractable pole. The pole was entered obliquely through the submerged macrophytes, thus ensuring that the plants disturbed by the introduction of the pole would not alter light above the sampling location. PAR measurements were used to calculate the fraction of surface irradiance (I_0) reaching the sampling depth z (I_z). The PAR light extinction coefficient (K, m^{-1}) of open water was also measured outside the macrophyte bed.

Laboratory analyses

In the laboratory, the epiphytic algae were removed from the macrophytes by intense and regular manual shaking (9 min at 80 beats min^{-1}). Chlorophyll-*a* (Chl*a*) was measured from known filtered volumes (50–100 ml) of resuspended epiphytes (Whatman GF/C); filters were kept frozen at −15 °C for 2–9 days. Chl*a* was extracted in hot 95% ethanol (Nusch, 1980) and the spectrophotometric absorbance was measured at 665 and 750 nm, before and after acidification (Sartory & Grobbelaar, 1984).

The presence of abundant metaphyton complicated the analysis of epiphytic (microscopic) biomass somewhat, since it greatly increased the range of biomass and yet could not always be accounted for in a separate group, especially at low filament biomass. The following rule was thus established: (1) when samples contained filamentous algae in sufficient abundance to be quantified as a separate category, they were considered as a substratum for microscopic epiphytes; their Chl*a* concentration was subtracted from total epiphyte biomass and the corresponding dry weight of filaments was added to the dry weight of macrophytes; (2) when filamentous metaphyton were present but not abundant enough to be separated from the epiphytes in a given sample, they were considered as epiphytes.

Macrophytes from which epiphytic algae were removed were identified, assigned a stem type (from 0 for a bare stem to 3 for densely foliated stems, Fig. 1), dried to a constant mass at 60 °C, and weighed (± 0.0001 g). Epiphyte biomass (mg or μg Chl*a*) was expressed per unit of macrophyte dry weight (g^{-1} DW).

Nutrient (total P, total dissolved P, NO_3^-, NH_4^+, SiO_2) concentrations in the water were measured every other sampling date (7 dates) on subsurface water collected within the macrophyte bed. Total (TP) and dissolved phosphorus (filtered samples, TDP) were measured using the molybdenum blue method (Stainton et al., 1977) after autoclaving 50-ml samples with 0.5 g of potassium persulfate for 1 h at 120 °C. NO_3^-, NH_4^+ (whole samples) and SiO_2 (filtered samples) were measured by automated flow injection analysis (Lachat methods 10-107-04-1-B, 10-107-06-1-F and 31-114-27-1-A, respectively).

Aboveground biomass of macrophytes and metaphyton serving as epiphyte support was

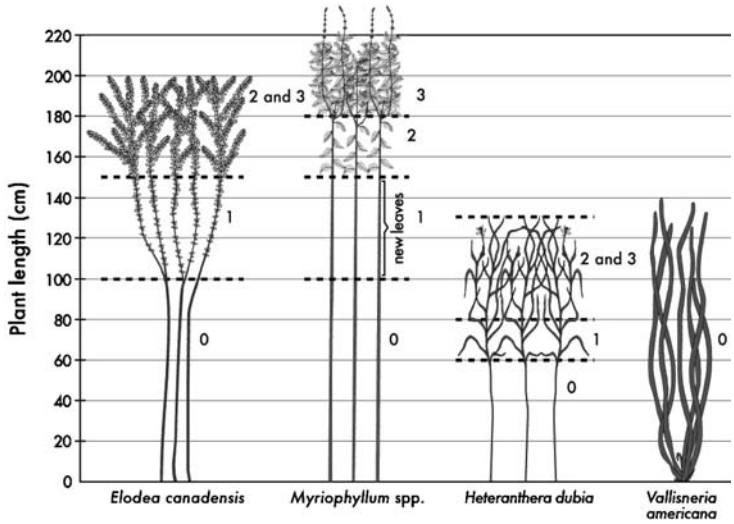

Figure 1. Schematic representation of the four types of macrophyte stems, according to density of leaves: bare stems (0); few leaves (1); moderate leaves (2); dense leaves (3).

quantified by hand collecting plants in 25 × 25 cm quadrats every 2 weeks, in shallow (<1 m) and deep (2 m) waters. In the laboratory, individual plant species were identified and processed separately. Metaphyton (various species of blue-green and green filamentous algae) was set aside as a separate category whenever found in sufficient amount. Loose detritus, microscopic periphyton and sediment were carefully washed off the plants, which were subsequently dried to a constant mass and weighed (±0.001 g).

Data analyses

Differences in mean epiphytic biomass between sampling dates and depths were tested using Kruskal–Wallis non-parametric and parametric analyses of variance (STATGRAPHICS Plus 4.0). Parametric analyses were carried out on $\log_{10}$ transformed values, in order to ensure homogeneity of variances among groups.

The CART analysis (Breiman et al., 1984) was selected to relate epiphyte biomass to a subset of environmental variables, whose rank of inclusion reflects their level of importance as predictor variables within our sample space. Factors which co-varied significantly (e.g. sampling date and water level) were prevented from appearing together in the final model-building process. Such multivariate non-parametric, non-linear models are particularly appealing since they can deal equally well with quantitative (I_z/I_0, depth, temperature) and categorical (stem type, plant relative abundance, support species) variables in a way that is easily interpreted. This analysis recursively identifies the variables and thresholds which split the data into the most homogeneous subgroups, so that different predictors may be chosen for different subsets of observations. Furthermore, statistical interpretation is improved when resulting groups have residuals of homogeneous variance, which was achieved by carrying out all analyses of epiphyte biomass on $\log_{10}$ transformed Chl*a* values.

Epiphyte biomass was modeled first on samples exclusively dominated by *Myriophyllum* spp. (CART-Myr), a morphologically variable macrophyte species (Fig. 1) that was dominant in our study area ($n = 41$ samples) (Fig. 3). Second, to expand the range of plant morphology and the effect of macrophyte species, an additional model of epiphyte biomass (CART-All) was elaborated considering all macrophyte species. In this instance, we utilized only samples in which a single host species was dominant, representing >80% of total DW ($n = 93$). Physical variables included sampling depth (m), relative irradiance at sampling depth (I_z/I_0), date, and water temperature. Macrophyte species, stem type, and relative abundance of the macrophyte stand were also included into

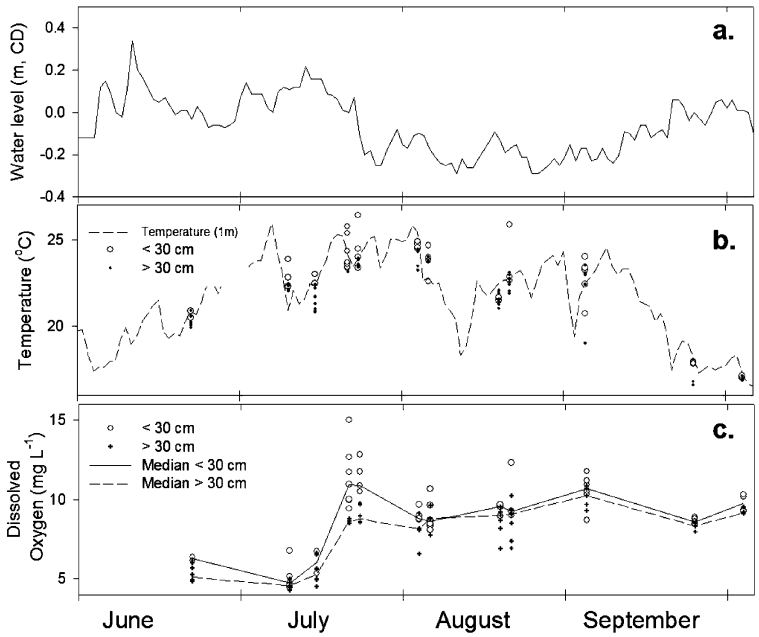

Figure 2. Seasonal variations of physical characteristics measured at the time of epiphyte sampling in the dense, multispecific macrophyte bed at Boucherville in 1999. (a) Daily water level at Montreal Harbour. (b) Water temperature (°C) in the upper 30 cm (+) and at depth >30 cm (O). Seasonal variation in water temperature outside the dense macrophyte bed from a continuous recorder (– –; −0.8 m CD). (c) Dissolved O_2 concentration (mg l^{-1}) in the upper 30 cm (+) and at depth >30 cm (O).

CART models. Variables not included in the analyses either followed a strong diurnal cycle (absolute irradiance, pH, and dissolved O_2) or were measured at different spatial and temporal scales (nutrients).

The predictions of the CART-All model were tested on samples in which a mixture of different macrophyte species occurred without clear dominance ($n = 33$). Predicted versus observed epiphyte biomass ($\log_{10}$ transformed) were compared (Sign test, STATSGRAPHICS Plus 4.0) and the error of the prediction was expressed as the root mean square (RMS) of the relative errors.

Results

Environmental conditions

The 1999 season (April 1–September 30) was characterized by extremely low water levels (0.18 m above chart datum, Fig. 2) and unusually warm (mean monthly air temperature 22.9 °C) and sunny (average of 8.3 h of daily sunshine) weather conditions, relative to the 1989–1998 period (level of 1.03 m above chart datum, 20.8 °C and 7.2 h of sunshine, respectively; Environment Canada, 2000).

Aboveground macrophyte biomass was >400 g DW m^{-2} between mid-July and early September, reaching values as high as 1.2 kg DW m^{-2} in mid-August (Fig. 3a). Taxa commonly observed at 1-m depth (Fig. 3b) were *Elodea canadensis* Michx., *Hetheranthera dubia* (Jacq.) MacM., *Myriophyllum* spp., and *Vallisneria americana* Michx. *Stuckenia* (*Potamogeton*) *pectinata* L. was less abundant and exhibited a seasonal maximum in late July (Fig. 3b). At 2-m depth, *Myriophyllum* spp. were the most abundant species during the entire growing season, accounting for about 50% of total biomass (not shown). Epiphyton samples were consistently collected on all macrophyte taxa throughout the sampling season. With the exception of *V. americana*, all these submerged macrophytes tended to form thick subsurface canopies which monopolized incident light and generated a sharp decrease in light intensity with depth (Fig. 4). Metaphyton was more important in shallow waters (<1 m), where it reached biomass >30 g DW m^{-2} after

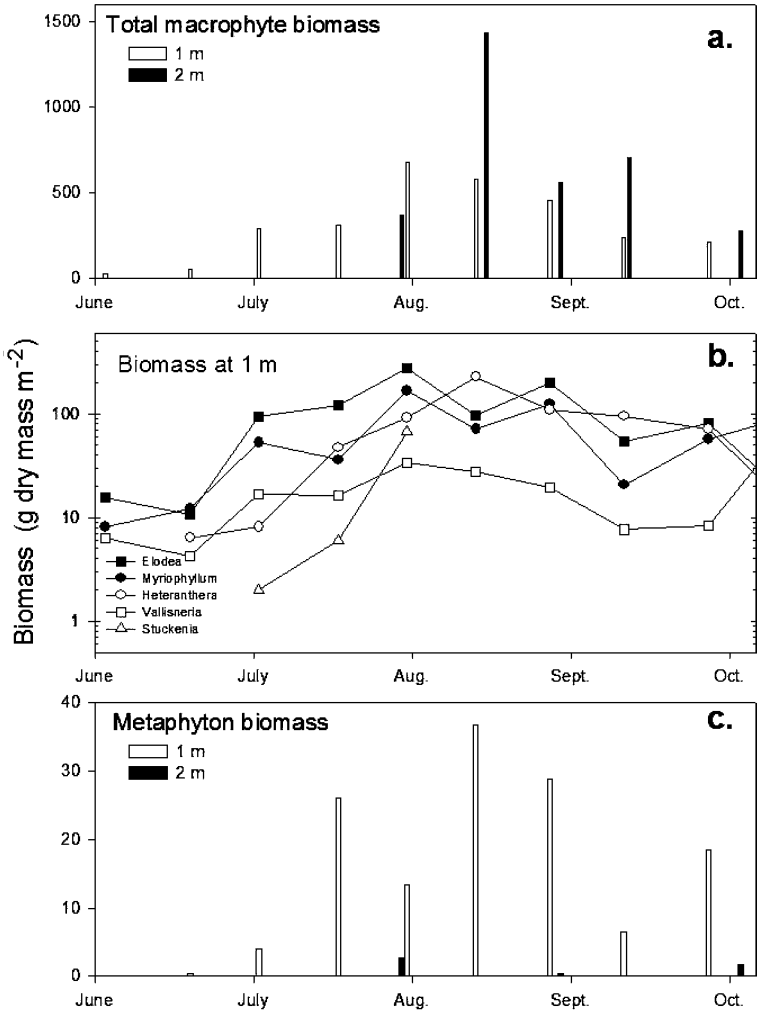

Figure 3. Seasonal variations of vegetation biomass measured in the dense, multispecific macrophyte bed at Boucherville in 1999. (a) Mean (±sd) biomass (kg DW m^{-2}) of aboveground submerged macrophytes for the <1 m (open bars) and 2 m (full bars) depth intervals. (b) Mean macrophyte biomass by taxon (g DW m^{-2}) at 1 m depth. (c) Mean metaphyton biomass (g DW m^{-2}) for the <1 m (open bars) and 2 m (full bars) depth intervals.

mid July and remained conspicuous throughout September (Fig. 3c).

Dense macrophyte canopy near the surface reduced water circulation and thus induced vertical differences of water temperature and dissolved oxygen especially on sunny days (Fig. 2). Although water temperature measured in the macrophyte bed during sampling generally agreed with the continuous record in open water, they tended to be more variable, especially after the beginning of July. For a given date, the temperature within the macrophyte bed could differ by as much as 5 °C, depending on depth. Temperatures measured in the upper 30 cm of the water column were generally higher than values recorded in open water, whereas the opposite was true for measurements taken at depths >30 cm. The same pattern was observed for dissolved oxygen concentrations, which were systematically higher in the upper 30 cm of the water column (Fig. 2) by as much as 6.5 mg l^{-1} than in deeper water layers.

In mid-summer, when macrophyte biomass was maximal and water levels were lowest (Figs. 2 and 3), the subsurface canopy became very thick and obstructed most incident light. Consequently, depending on macrophyte abundance, relative

irradiance (I_z/I_0) showed little relationship with depth (Fig. 4a); epiphytes sampled in shallow waters could receive $<20\%$ of the surface radiation whereas samples collected in water ≥ 1 m could receive up to 55% of the surface light. Samples taken in areas of low submerged macrophyte abundance were exposed to nearly the same light attenuation regime as in open water (Fig. 4a).

As expected in the St. Lawrence River, nutrient concentrations did not show significant seasonal variations. The combination of low water levels, sunny and dry climate and relatively high nutrient concentrations (Table 1) resulted in conditions highly conducive to epiphytic growth – namely, warm water temperature, high incident light and high biomass of macrophytic substrate.

Epiphyte biomass

Epiphyte biomass spanned several orders of magnitude (24–5800 μg Chl*a* g^{-1} DW; Fig. 4b). Epiphyte biomass tended to increase with relative irradiance ($p < 0.01$). However, in a simple regression analysis, relative irradiance explained only a small fraction of the total variance of epiphyte biomass (17%), suggesting the additional effects of other environmental factors.

No seasonal pattern of mean epiphyte biomass (μg Chl*a* g^{-1} DW) could be discerned when all samples were considered together (Kruskal–Wallis, $p > 0.05$; not shown); the date of October 1 was omitted from this seasonal analysis of variance because of macrophyte decay and consequent contamination of epiphyte chlorophyll by plant tissue. Temporal variation was then examined separately for samples exposed to low (<13%) and high (>13%) relative irradiance (Fig. 5). This threshold was selected because it coincided with the lower threshold value identified in the CART models as explaining maximum variance (see text below for more details). At low relative irradiance ($I_z/I_0 < 13\%$), epiphyte biomass remained in a narrow range (0.39 ± 0.21 mg Chl*a* g^{-1} DW) for the entire sampling period (Fig. 5a) and did not differ among sampling dates (Kruskal–Wallis; $p > 0.05$). In contrast, under higher relative irradiance ($I_z/I_0 > 13\%$), epiphyte biomass followed distinct seasonal changes (Kruskal–Wallis, $p < 0.05$; Fig. 5b). Epiphyte biomass was highest in mid-summer (Kruskal–Wallis, $p < 0.05$), reaching an average of 1.8 mg Chl*a* g^{-1} DW. The presence of metaphytic filamentous algae in small amounts probably increased Chl*a* values in the samples, especially under high irradiance.

Prediction of epiphyte biomass

To predict epiphyton biomass, we examined two CART models, which were based solely on samples from *Myriophyllum* spp. (CART-Myr) or on all monospecific samples (CART-All). Both models of epiphyte biomass responded to the same variables although thresholds varied somewhat between models (Table 2). The fraction of incident relative irradiance (I_z/I_0) and sampling date respectively explained >20% and >6% of the variance in epiphyte biomass and contributed consistently to both CART models. Stem type contributed 8 and 11% of variance of the CART-All and CART-Myr models, respectively. The contribution of the remaining variables (plant species, relative abundance of macrophytes and temperature) represented $<5\%$ (Table 2). As a result, groups of lowest epiphyte biomass were defined by the combination of a low percentage of incident light and simple non-ramified macrophyte stems. In contrast, groups of highest biomass corresponded to samples collected in mid- to late-summer, under high relative irradiance and supported by ramified stems.

CART models identified eight homogeneous groups of samples that differed significantly in average epiphyte biomass with residual errors presenting a quasi-normal distribution on a log scale. Mean epiphyte biomass per group ranged from 0.1 to 1.8 mg Chl*a* g^{-1} DW (Fig. 6). In both CART-All and CART-Myr models, the hierarchy of environmental effects was similar. Under light intensities lower than 13–22%, non-ramified stems supported lowest epiphyton biomass (0.1 mg Chl*a* g^{-1} DW) whereas more complex stems supported 3–6 times more epiphyton. Under high light intensities, samples collected before July 14 averaged 0.73 mg Chl*a* g^{-1} DW, regardless of the supporting macrophyte species. Finally, epiphyton samples collected after July 14 from a subset of macrophyte species reached the highest biomass (0.89–1.79 Chl*a* g^{-1} DW). Epiphyton biomass was highest on *Elodea canadensis*, *Myriophyllum* spp., *Vallisneria americana*, and filamentous algae.

Table 2. Comparison of the performance of different environmental variables in explaining the variability of epiphytic biomass derived from two CART models

Environmental variable	Critical threshold		Data subset	
			CART-All	CART-Myr
Light (I_z/I_0)	0.025	↑	4.8	
	0.13–0.22	↑	20	40.2
	0.27–0.29	↑	2.4	10.2
Date	July 14	↑	6.3	7.4
Temperature (°C)	23.7	↓		4.9
Stem type	0 ♦ 1, 2, 3	↑	8.4	11.1
Plant relative abundance	1, 2, 3♦ 4	↓	4.9	
Host plant species	HDU, PPE ♦ Alg, ECA, MSP, VAM	↑	3.3	
Total variance explained by complete model (%)			50.1	73.8

Plant species legend: MSP: *Myriophyllum* spp.; HDU: *Heteranthera dubia*; PPE: *Stuckenia* (*Potamogeton*) *pectinata*; Alg: filamentous algae; ECA: *Elodea canadensis*; VAM: *Vallisneria americana*.
Models predicting biomass per unit of dry weight were derived either from samples dominated by a single dominant host species (CART-All) or dominated by *Myriophyllum* spp. (CART-Myr). The critical threshold at which nodes of the CART models separate significantly different groups of samples are indicated for each model. Arrows ↑ or ↓ indicate whether the critical threshold coincides with an increase or a decrease in epiphytic biomass. Shaded values indicate best predictor environmental variables.

Lesser epiphyton biomass values (by a factor of 2×) were found on *Heteranthera dubia* and *Stuckenia pectinata* (*Potamogeton pectinatus*) under otherwise similar physical conditions.

The model was tested using the 33 samples for which prediction was likely the most difficult, as they corresponded to epiphyte biomass removed from a mixture of macrophyte species, without clear dominance. Comparisons between predicted and observed values revealed no bias (sign test on the differences; $p > 0.1$; Fig. 7), with a residual mean square error of 39.2%

Discussion

Our study aimed to investigate some of the major physical variables expected to affect epiphyte biomass (i.e. light, depth, and macrophyte architecture) at the scale of a single multispecific macrophyte bed, which is usually considered as a homogeneous unit in comparative studies. The bed we selected was uniformly sheltered from dominant winds and waves and covered a wide range of the chosen axes of variability. Factors which co-varied significantly, as in most environmental studies, were prevented from appearing together in the final model-building process. The small size of our sampling device allowed collecting epiphyton samples in homogeneous physical (light) and biological (macrophytes) environments. In this study, several variables affecting epiphytic algal biomass in macrophyte beds were recognized, which we will examine in decreasing order of importance.

Light (I_z/I_0) played a key role and explained between 27 and 50% of the variance in epiphyte biomass depending on the CART models (Table 2). A critical threshold of 13–22% surface light was identified. Higher biomass was observed for epiphytes exposed to >13% of surface light, whereas lower and less variable biomass was found at irradiance <13%. This value corresponds to an irradiance of about 100 μE m^{-2} s^{-1} for midday at our study site in mid- and late-summer. Our study clearly shows that, in dense macrophyte beds, light can be drastically reduced even close to the surface. Depth is therefore not a proxy for light, except very close to the bottom.

CART models revealed some influence of macrophyte morphology, either through stem type or plant species. A significant relationship between macrophyte morphology and attached organisms

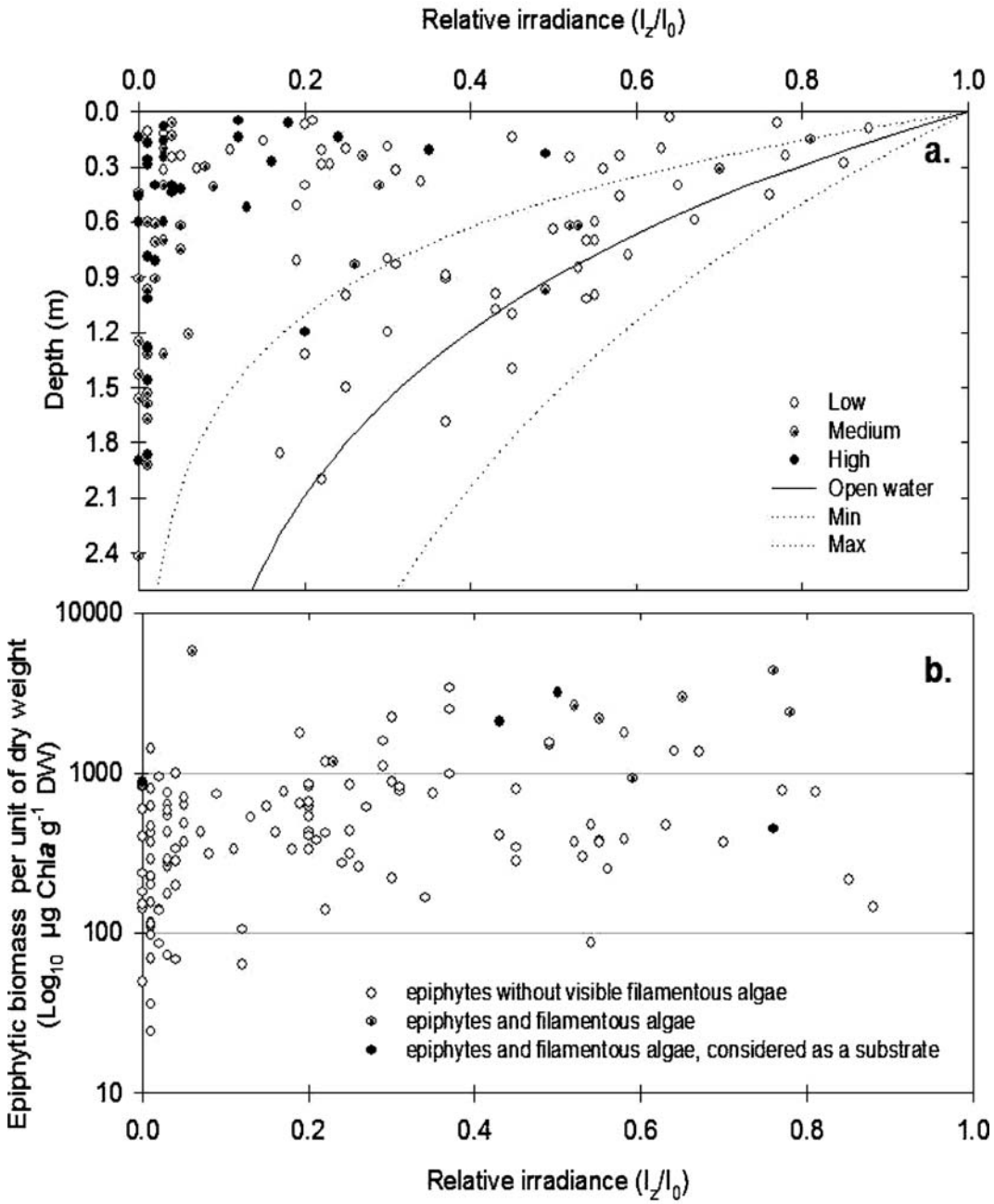

Figure 4. (a) Relationship between relative irradiance (I_z/I_0) and depth (m) of epiphyte collection in the Boucherville islands. Symbols identify epiphytic biomass samples collected under low (○), medium (⊙) and high (●) macrophyte abundance. The mean I_z/I_0 resulting from seasonal average (full line), minimum and maximum (dotted lines) open-water light extinction coefficients (average $K = 0.77$ m^{-1}, range = 0.45–1.46 m^{-1}) are indicated. (b) Relationship between epiphytic biomass (expressed as $\log_{10}$ µg Chl*a* g^{-1} DW) and % I_z/I_0 at the depth of epiphyte sampling in the studied macrophyte bed at Boucherville in 1999. Samples comprising epiphytes alone (○), a mixture of epiphytes and filaments (⊙) and for which epiphytes and filamentous metaphyton were distinguished (●) are identified.

has been documented both for epiphytic algae and invertebrates (Krecker, 1939; Brönmark, 1985; Lalonde & Downing, 1991, 1992; Jeffries, 1993; Zimba, 1995). Ramified stems within and among taxa tend to support higher epiphyte biomass than simple stems (Figs 1 and 6).

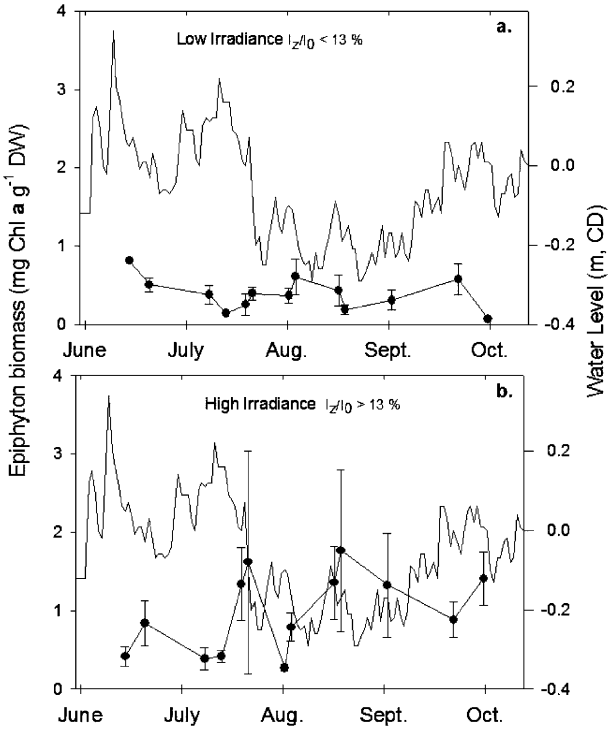

Figure 5. Seasonal variations in average (±1 se) biomass of epiphytic algae (mg Chl*a* g^{-1} DW) for samples exposed to (a) low (% I_z/I_0 < 13%) and (b) high (% I_z/I_0 > 13%) irradiance. On both graphs, daily water levels (right *Y* axis, – –) in Montreal Harbor are superimposed for reference.

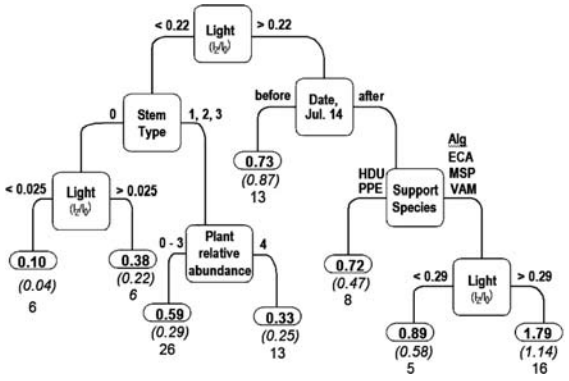

Figure 6. Predictions of epiphyte biomass per unit of dry weight (mg Chl*a* g^{-1} DW) from CART-All model carried out on samples dominated by a single macrophyte species. Predicted values (circles at the terminal nodes) represent the non-transformed mean (±sd, *n*) values of all samples within each group. Variables and threshold values defining each tree branch are identified. Species are: Alg = filamentous algae; ECA = *Elodea canadensis*; HDU = *Hetheranthera dubia*; MSP = *Myriophyllum* spp.; PPE = *Stuckenia* (*Potamogeton*) *pectinata*; VAM = *Vallisneria americana*.

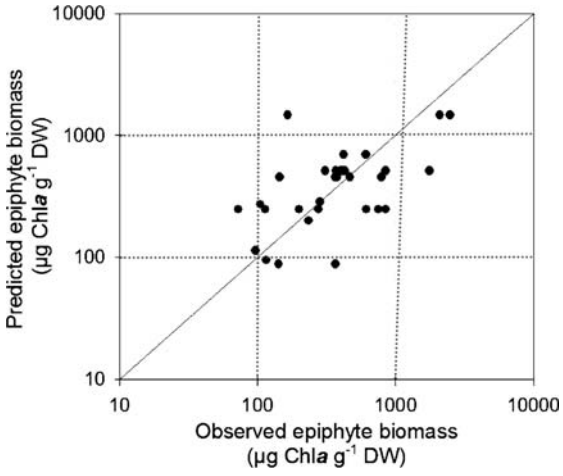

Figure 7. Comparisons of epiphyte biomass (μg Chl*a* g^{-1} DW) predicted from CART-All model with values measured in 33 additional samples of mixed macrophyte composition not included in the original model.

The highest epiphyte biomass was recorded after mid-July, coinciding with maximum macrophyte and metaphyton biomass and a sharp decrease in water level (Figs 2 and 3). If date was omitted from the CART model, water level explained equally well the seasonal changes in epiphytic biomass. The mechanism by which low water levels would foster high epiphyte biomass is not clear. One possible explanation could be an increasing accidental inclusion of metaphyton in our epiphyton samples. Metaphytic algae are generally associated with high light, low flow, and sheltered areas, and are thus more abundant in shallow and warm waters (Goldsborough & Robinson, 1996; Pillsbury & Lowe, 1999). Temperature *per se* did not account for a large part of total variability of epiphyte biomass (maximum 4.9% of total variation for CART-Myr) probably because its effect generally co-varies with other factors, as is the case in the majority of field studies (DeNicola, 1996).

Conclusion

This study shows that in a single multispecific macrophyte bed, epiphyte biomass can span over two orders of magnitude; our models, based mainly on physical variables, could explain more than 50% of this variability. Epiphyton sampling should be stratified according to the fraction of surface light intensity, macrophyte architecture, and seasonal water level variations, in decreasing order of influence. These factors are likely to induce major increases in epiphytic biomass in the future, given the important environmental changes predicted by climate scenarios in temperate areas.

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